Social interactions and activity patterns of old Barbary macaques: further insights into the foundations of social selectivity

Laura Almeling¹,², Holger Sennhenn-Reulen³, Kurt Hammerschmidt²,³, Alexandra M. Freund⁴, Julia Fischer¹,²,³

Short title: Activity patterns of old macaques

¹University of Göttingen, Germany
²Cognitive Ethology Laboratory, German Primate Center - Leibniz Institute for Primate Research, Germany
³Leibniz ScienceCampus Göttingen ‘Primate Cognition’, Göttingen, Germany
⁴Department of Psychology, University of Zurich, Switzerland

Correspondence to: Laura Almeling, Cognitive Ethology Laboratory, German Primate Center - Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany, E-Mail: lalmeling@dpz.eu, Phone: +49 551 3851-475
ABSTRACT

Human aging is accompanied by a decrease in social activity and a narrowing in social networks. Studies in nonhuman primates may provide valuable comparative insights in which way aging impacts social life, in the absence of cultural conventions and an awareness of a limited lifetime. For female Barbary macaques at ‘La Forêt des Singes’ in Rocamadour, France, we previously reported an age-associated decrease in active grooming time and network size. Here, we aimed to extend these findings by investigating in which way physical decline, spatial proximity, and aggression vary with age in female Barbary macaques. We analyzed > 1200 hours of focal observations for 46 females aged 5 - 29 years. As expected, older females engaged less frequently in challenging locomotor activity, such as climbing or running, than younger ones. The previously reported decrease in grooming time was not due to shorter grooming bout duration. Instead, active grooming bouts lasted even longer, which discounts the idea that manual fatigue explains the shift in grooming pattern. We found that older females tended to be spatially reclusive and that they were less frequently the targets of aggression. Although older females showed aggressive behaviors at similar rates as younger females, the proportion of low-level aggression (i.e. threats) increased with age. We suggest that these threats are not simply a signal of dominance, but also function to deter approaches by others. Overall, these findings are in line with the idea that older females aim to avoid potentially negative interactions, specifically if these are costly. In sum, these findings support the idea that shifts in female Barbary macaques’ grooming activity, do not simply result from physical deterioration, but are instead due to a higher selectivity in the choice of social partners.
KEYWORDS: aging, social behavior, avoidance, Barbary macaques, selectivity
INTRODUCTION

Human aging is associated with a decrease in social activity and network size [Ajrouch, Antonucci, & Janevic, 2001; Fung, Stoeber, Yeung, & Lang, 2008]. With increasing age, people tend to narrow their social networks and focus on emotionally meaningful relationships such as close friends or relatives [Charles & Carstensen, 2010; Lang, 2000]. According to socio-emotional selectivity theory [SST; Carstensen, Isaacowitz, & Charles, 1999; Charles & Carstensen, 2010], the increasing awareness of a limited remaining future time that older people experience, leads to an enhanced selectivity in their choice of social partners.

SST is in line with a more general theory of lifespan development stressing the importance of selectivity: the model of selection, optimization, and compensation [SOC-model; Baltes & Baltes, 1990; Freund & Baltes, 2002]. According to the SOC-model, successful aging encompasses the management of limited resources across the life span by focusing one’s resources on a subset of possible alternatives (i.e., selection), optimizing functioning in the selected domains by investing available resources, and by compensating for potential losses.

According to the strength and vulnerability integration model [SAVI; Charles, 2010], one of the losses that older adults experience is a decrease in the capacity to cope with stressors, presumably due to physiological changes. SAVI provides an integrative framework to explain the observation that emotional wellbeing is stable into old age. In stressing the importance to adapt to and manage losses for successful aging, SAVI is consistent with the SOC model. The strength in the SAVI model refers to better emotion regulation skills with age due to life experience; the vulnerability refers to a reduced physiological flexibility that impedes emotion regulation. Therefore, SAVI predicts that
older adults are more likely and better than younger adults in avoiding negative situations that lead to high arousal. Similar to SST, SAVI considers future time perspective as an important aspect shaping older adults’ social lives. However, extending SST, Charles [2010] pointed out that time lived (i.e., life experience) is also essential for understanding how older adults regulate their social relations.

In older humans, both the awareness of their limited future time and cultural conventions could potentially contribute to changes in self-reported and behavioral selectivity. Due to the absence of elaborate future planning abilities and normativity in nonhuman primates (hereafter ‘primates’), studies on primates can provide important insights into the evolutionary foundations of human social aging [Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016; Crockford, 2016]. Humans and primates have a similar life history [Bronikowski et al., 2011] and both experience physiological senescence [Müller, Heistermann, Strube, Schülke, & Ostner, 2017; Roth et al., 2004], although, in contrast to humans, primates do not experience menopause [Alberts et al., 2013]. As humans do, primates also seem to experience conflicts as stressful, as indicated by increased levels of self-scratching and glucocorticoid-metabolite levels in both the actor and recipient of aggression [Aureli, 1997; Wittig, Crockford, Weltring, Deschner, & Zuberbühler, 2015; but see Koski, Koops, & Sterck, 2007]. In addition to the diminished fighting abilities observed in older primates [Berghänel, Ostner, & Schülke, 2011; Bissonnette, Lange, & van Schaik, 2009; Fischer, Kitchen, Seyfarth, & Cheney, 2004], age-associated physiological changes may result in a decreased ability to cope with stressors [Jensen, Blanton, & Gribble, 1980; Sapolsky & Altmann, 1991].
Given these biological changes, a number of studies have addressed the question in which way aging affects social behavior [Corr, Martin, & Boysen, 2002], also referred to as ‘social aging’ [Hosaka & Huffman, 2015]. Empirical studies focused mostly on females. This may be due to the fact, that males experience a higher mortality across the primate order [Colchero et al., 2016], and thus old primate males may be less frequently available as study subjects compared to old females. Studies on female social aging yielded partly conflicting results [Borries & Koenig, 2008]: For wild chimpanzees (Pan troglodytes) [Huffman 1990], wild toque macaques (Macaca sinica) [Ratnayeke 1994], semi-free ranging Japanese macaques (Macaca fuscata) [Hauser & Tyrrell, 1984; Nakamichi 1984] and captive stump-tailed macaques (Macaca arctoides) [Hauser & Tyrrell, 1984] a reduced spatial integration of older females was observed. Moreover, older females of various species and different rearing conditions showed reductions in active grooming: Wild chimpanzees [Huffman 1990], semi-free ranging rhesus macaques (Macaca mulatta) [Brent, Ruiz-Lambides, & Platt, 2017; Corr, 2003], semi-free ranging Japanese macaques [Nakamichi, 1984] and captive long-tailed macaques (Macaca fascicularis) [Veenema et al., 1997]. In contrast, Pavelka [1990] reported no evidence for an age-related decrease studying the same population of Japanese macaques as Nakamichi. Remarkably, older females received the same amount of grooming as younger females [Brent et al., 2017; Corr, 2003; Huffman 1990; Nakamichi, 1984, 2003]. While older female rhesus macaques [Corr, 2003] and long-tailed macaques [Veenema et al., 1997] affiliated with fewer social partners, such a pattern was not found in older female Japanese macaques [Pavelka, 1991].

In terms of agonistic behavior, aging was associated with lower levels of aggression given in wild female toque macaques [Ratnayeke, 1994] and captive female
chimpanzees [Baker, 2000]. In contrast, Piqc [1992] observed an age-related increase in the frequency of aggression given in captive mouse lemurs (*Microcebus murinus*).

Captive long-tailed macaques [Veenema et al., 1997] and semi-free ranging rhesus macaques at Cayo Santiago [Brent et al., 2017] experienced age-related reductions in aggression received. Studying the same population, however, Corr [2003] observed the opposite pattern, namely an age-associated increase in the frequency of aggression received. Yet, several other studies did not provide evidence for age-associated changes in aggression or dominance-related behavior in rhesus macaques [Brent et al., 2017], Japanese macaques [Pavelka, 1990], long-tailed macaques [Veenema et al., 1997], stump-tailed macaques [Hauser & Tyrrell, 1984] and vervet monkeys (*Chlorocebus pygerythrus*) [Fairbanks & McGuire, 1986]. Taken together, then, the empirical evidence regarding social aging in primates is not completely consistent.

For female Barbary macaques (*Macaca sylvanus*) at ‘La Forêt des Singes’, we showed an age-associated decrease in overall active grooming time and number of adult partners that females groomed [Almeling et al, 2016]. This age-related change seemed to be driven by the aging individual itself when considering that the time females received grooming and the number of adult partners who groomed them did not vary significantly with age. Moreover, the effect of a decreased active grooming time could not be explained by a general loss in social interest, as Barbary macaques continued to be interested in social information. More specifically, this became apparent in older females’ vocal ‘commenting’ [Brumm, 2005] on social interactions in their immediate surrounding at similar rates compared to younger ones.

Here, we combined focal observations obtained from Barbary macaque females over several years, to determine how physical activity, spatial proximity, and agonistic
behavior vary with age. We used the frequency of females’ engagement in demanding
locomotor activities such as running, climbing, jumping and branch-shaking as a proxy
for physical strength. To test whether the observed decrease in active grooming duration
was due to manual fatigue [Roth et al., 2004], we assessed active grooming bout
duration for cases that were initiated and terminated by the female, as a proxy for their
endurance. We recorded spatial integration in the group and conflict behavior to assess
in more detail how interactions changed with age. Since dominance rank was found to
be an important factor determining sociality in Barbary macaques [Sosa, 2016] and
other species [Kato, 1999; Veenema et al., 1997], we considered dominance rank as a
potential confounding factor. With these analyses, we aim to contribute to a more
nuanced understanding of aging processes in nonhuman primates and macaques.

METHODS

Ethics statement

This study was non-invasive and based on observational data collection in a private
facility. This type of data collection is in accordance with the European Directive
2010/63/EU and was approved by the scientific director of the enclosure. Moreover, it
adheres to the American Society of Primatologists' principles for the ethical treatment of
primates.

Study species, study site and subjects

Barbary macaques live in female bonded multi-male groups [Wrangham, 1980] with
female philopatry and male migration [Menard & Vallet, 1993; Paul & Kuester, 1985],
and have a rather tolerant social style [Thierry, 2000]. Females establish strong
relationships to related and non-related individuals of both sexes characterized by
frequent grooming [Patzelt, Pirow, & Fischer, 2009; Roubová, Konečná, Šmilauer, &
Wallner, 2015]. They also exhibit a relative stable linear dominance hierarchy based on
matrilines. Senescent females are outranked by their daughters [Paul & Kuester, 1987].

We conducted the study in the visitor park ‘La Forêt des Singes’ in Rocamadour,
France, where monkeys are outdoors throughout the year [Turckheim & Merz, 1984].
During the time of April until November the summer enclosure is open to visitors who
are restricted to a circular path system, while monkeys can range freely within the entire
area. Thus, monkeys are habituated to human observers but also have the possibility to
avoid them. Monkeys forage on vegetation of the park as oak leaves, bark, grass and
insects. Additionally, food such as pellets, wheat, fruits and vegetables is offered several
times a day. Water is available *ad libitum* from large ponds or one of the three water
basins in the park. The majority of adult females received hormonal transplants in order
to control reproduction. All monkeys are tattooed at the inner thigh.

Within the park there are three stable social groups. Females of two of the
groups served as focal subjects (see Table 1 for details). Individuals were classified as
adult at the age they commonly reach sexual maturity (males 5 years, females 4 years
[Menard & Vallet, 1993]; see Table 1 for group composition). Under these housing
conditions, female Barbary macaques may reach an age of 30 years. Altogether 46
individual focal females (age range: 5-29 yrs.) were included in the study.

Data were collected in four periods over the course of several years (see Table 1
for details). The subset of focal females observed in period 2 and 3 comprised all
females observed in period 1, except for one that had died.
Behavioral observations

We recorded half-hour protocols of predefined behaviors using the focal sampling method for a total of \( \approx \) 1204 hours during 4 periods of observation (see Table 1 for details). During all periods of observation, we recorded the occurrence of agonistic behaviors threats (open-mouth face with raised eyebrows), chase away (threats accompanied by following the victim for at least a few meters) and fights with physical contact (beating and biting). For periods 2 - 4, we also recorded the duration of grooming given and received. For a detailed description of the ethogram of Barbary macaques see Hesler and Fischer [2007]. In period 4, we additionally recorded the occurrence of locomotor activities (running > 5 m with high velocity, jumping, climbing > 1.5 m, and branch-shaking). Moreover, in period 4, we noted the number of individuals in a 5-m radius before the onset of the focal observation (\( N = 561 \) scans).

Throughout all observation periods, we noted ad libitum dyadic conflicts and displacements for the purpose of establishing a dominance hierarchy. A handheld computer (Palm, Model Zire) or tablet (Samsung Galaxy S4) running a custom program created with Pendragon Forms (Pendragon Software Corporation, Libertyville, IL, U.S.A.) was used to record the data.

When a focal female was out of sight during observation, proceedings were as follows: if the female could be located again within 5 - 10 minutes, the time lacking was added to the half hour session; if the female could not be located again, the time lacking was noted and added to the next session of the focal female in the same period of day.
The focal females were observed semi-randomly by following an order which was arranged daily for the observation day so that observation times for single individuals were similarly distributed for each female in period 1 (3/5 of protocols during 9:00 - 14:00 and 2/5 during 14:00 - 18:00 and approximately evenly distributed throughout the day (morning: 9:00 - 11:30, midday: 11:30 - 14:00, afternoon 14:00 - 16:30 and evening (16:30 - 19:00) for period 2 - 4.

Analyses

To determine the effect of age on the frequency that females engaged in ‘locomotor activities’ we ran a Generalized Linear Model in R version 3.3.1 [R Core Team, 2015], using data obtained in observation period 4, for 26 females of one group (see Table 1). The estimation was performed using BayesX [Belitz et al., 2015]. We assumed a negative binomial distributed response [Zeileis, Kleiber, & Jackman, 2008]. We chose this distribution as, in contrast to the Poisson distribution, we directly control for potential overdispersion. We entered ‘age’ as linear regression coefficient and used the offset log(observation time) in order to take slightly varying observation length into consideration.

In the further analyses addressing the effect of age on various types of social behavior, we included the potential confounder ‘dominance rank’. To determine the dominance relations among adult females for each group and observation period we used MatMan 1.1 (Noldus, Wageningen, Netherlands) [de Vries, Netto, & Hanegraaf, 1993], in which we entered a winner-looser matrix using ad libitum and focal data of dyadic encounters and approach retreat interactions. We observed linear dominance
hierarchies in females for both groups and all data collection periods (Group A: period 1: $\chi^2 = 115.29$, $df = 31.29$, $h' = 0.48$, $P < 0.001$, $N = 25$; period 2: $\chi^2 = 88.56$, $df = 30.36$, $h' = 0.42$, $P < 0.001$, $N = 24$; period 3: $\chi^2 = 87.1$, $df = 30.36$, $h' = 0.41$, $P < 0.001$, $N = 24$; group B: period 4: $\chi^2 = 132.60$, $df = 32.23$, $h' = 0.52$, $P < 0.001$, $N = 26$). In the analyses, we used a females’ relative dominance rank position (hereafter: ‘dominance rank’) within the female hierarchy instead of absolute values, in order to correct for differences in numbers of females in the groups and across periods of observation. In our subset of focal females ($N = 46$), ‘dominance rank’ was weakly positively correlated with ‘age’ (Spearman-Rho = 0.36, $P = 0.002$, $N$ observations = 72), i.e. older females tended to be lower in rank.

We checked for potential collinearity between ‘age’ and ‘dominance rank’ in the different models using the function ‘vif’ from R add-on package ‘car’ [Fox et al., 2016]. Variance inflation factors were never larger than 1.43, indicating that there is no collinearity. This also accounts for ‘observation period’, which was incorporated as a potential confounder in the analyses, if appropriate.

The following analyses were conducted using a Bayesian inference algorithm (Markov chain Monte Carlo, MCMC) as implemented in BayesX Version 3.0.2 [Belitz et al., 2015]. Markov chain Monte Carlo (MCMC) estimation is a general tool for the estimation of Bayesian regression models that allows quantifying the joint posterior distribution of the model’s coefficients with high accuracy [Gelman, 2006]. In the absence of substantial prior knowledge, we used non-informative priors for the regression coefficients included in the different models. Typically, the data provides enough information to estimate $\beta_0$, $\beta_1$, ... by the use of any reasonable non-informative prior distribution [Gelman, 2006]. This is, however, generally not the case for scale
parameters such as $\sigma^2_v$, and the use of (weakly) informative priors is needed. For the variance $\sigma^2_v$ of the prior for varying intercept model coefficient $y_i \sim N(0, \sigma^2_v)$, for individuals $i = 1, \ldots, n$, we therefore used a weakly informative inverse Gamma prior with hyper-parameters $a = b = 0.001$, i.e. $\sigma^2_v \sim IG(a = 0.001, b = 0.001)$ [Belitz et al., 2015]. For the MCMC set-up, we used a burn-in of 12,000 iterations, a thinning rate of 40, and 52,000 iterations in total.

Concerning the dependent variable ‘active grooming bout duration’, we used the data recorded in observation periods 2 - 4 (see Table 1) and restricted the analysis to those events that were initiated and terminated by the focal female, and which were not truncated by the beginning or the end of the focal observation ($N = 394$). This selection reduced the number of focal females in our sample to 39 females, as 6 individuals were not observed to engage in active grooming given the selection criteria. The dependent variable was log$_e$-transformed in order to meet the normality assumption on residuals.

We conducted a Linear Multilevel Model with ‘age’, ‘dominance rank’ and ‘observation period’ as factor covariate. We controlled for variation across ‘focal females’ by the use of varying intercepts. Inspection of QQ- and residuals vs. fitted values plots indicated no relevant deviation from normally and homogeneously distributed residuals.

To assess the influence of age on the ‘number of individuals in 5-m radius’ we used data recorded of 26 females of one group in observation period 4 (see Table 1). We conducted a Generalized Linear Multilevel Model with a negative binomial response, in this way controlling for potential overdispersion [Zeileis et al., 2008]. We incorporated ‘age’ and ‘dominance rank’ in the model and used the offset log(observation time) to account for slightly varying observation times. Moreover, we controlled for variation across ‘focal females’ by the use of varying intercepts. To estimate a potential non-
linear relationship between ‘age’ and the dependent variable, we used a non-parametric Bayesian P-spline approach [Brezger & Lang, 2005], a standard non-parametric method to assess non-linear effects [Eilers, Marx, & Durbán, 2015].

For the dependent variable ‘aggression given’, we used data from 46 females across observation periods 1 – 4 (see Table 1). To estimate a regression coefficient for age on the frequency females show aggressive behavior, we conducted a Generalized Linear Multilevel Model with a negative binomial response, controlling for potential overdispersion [Zeileis et al., 2008], and included ‘age’, ‘dominance rank’ and ‘observation period’ as factor covariate. We added ‘focal females’ as varying intercepts and used the offset log(observation time) to correct for varying observation times.

For the dependent variable ‘aggression received’, we used data from 46 females across observation periods 1 – 4 (see Table 1). To estimate the role of age on how frequently females were the target of aggression, we conducted a Generalized Linear Multilevel Model with a negative binomial response [Zeileis et al., 2008], and included ‘age’, ‘dominance rank’, and ‘observation period’ as factor covariate. We added ‘focal females’ as varying intercepts and used the offset log(observation time) to correct for varying observation times. To estimate a potential non-linear relationship between ‘age’ and the dependent variable, we used a non-parametric Bayesian P-spline approach [Brezger & Lang, 2005].

For the proportion of ‘threats relative to all aggression (threats, chase away and physical fights)’ the focal females engaged in, we used data obtained in observation periods 1 – 4 (see Table 1). One female (age = 29 yrs) was removed from this analysis, as she was never observed to engage in aggression throughout the observation period, yielding observations for 45 females instead of the 46 observed in total. To estimate a
regression coefficient for age on the proportion females engage in ‘threats relative to all aggression’, we conducted a Generalized Linear Multilevel Model with a binomial response and included ‘age’, ‘dominance rank’, and ‘observation period’ as factor covariate. We added ‘focal females’ as varying intercepts.

The results of the described models are presented in a graphical way (Figures 2-6). Pairs of expected values with exclusive credible intervals reveal strong evidence for age-related differences in the distribution of the response. Note, that expected values vary non-linearly in all figures, although ‘age’ was incorporated as a non-linear term only in the models for ‘number of individuals in 5-meter radius’ and ‘aggression received’. The non-linear shapes of expected values in the other models result from non-linear response functions and, in the case of ‘active grooming bout duration’, from the log-transformation. For an improved readability of these graphs, the values of the estimated expected values are given in numerical form for age at values of 5, 15, and 25 years in the respective figure legends. Moreover, we provide coefficient estimates for the models, except for those that were P-spline based (‘number of individuals in 5-meter radius’ and ‘aggression received’). For this type of analysis, coefficient estimates cannot be obtained. Finally, we also provide such graphical displays for the potential confounder ‘dominance rank’ as well as coefficient estimates, whenever applicable.

RESULTS

Age had a negative effect on the frequency females ($N = 26$) engaged in demanding locomotor activities (Generalized Linear Model: Est. = -0.073, SE = 0.015, $P < 0.001$, $N$ events = 449, Figure 1). Note that any further statistical inference result are given as the
estimated expected values and credible intervals, generally set at 99 %, with the aid of plots (Figures 2 - 6). The estimated expected value of active grooming bout duration increased with age (Figure 2a). For the influence of age on grooming bout duration, we obtained a coefficient estimate of 0.034, with a 99% credible interval from 0.009 to 0.065. The estimated expected value of active grooming bout duration did not vary with dominance rank (Figure 2b). For the influence of dominance rank on grooming bout duration, we obtained a coefficient estimate of 0.024 with a 99% credible interval from -0.500 to 0.510.

The expected value of number of individuals that were recorded within a 5-m radius around the focal females tended to decrease with age (Figure 3a) and did not vary with dominance rank (Figure 3b). We did not find evidence for a change in the frequency of aggression given with age (Figure 4a): the coefficient estimate was -0.025, with a 99% credible interval from -0.061 to 0.011. Because dominance rank was inferred from dyadic agonistic encounters among females, it is not surprising that rank varied with aggression given (Figure 4b): the coefficient estimate was -1.471, with a 99% credible interval from -2.239 to -0.784. The expected value of the frequency that females were the targets of aggression decreases at younger ages, and, starting at around 15 years, flats out (Figure 5a). Aggression received varied with dominance rank: The higher the rank, the less frequently a female received aggression (Figure 5b). Note, that dominance rank was inferred from dyadic agonistic encounters among females. The
proportion of threats relative to all aggression females engaged in (threats, chase away and physical fights) increased with age (Figure 6a). In other words, older females were more likely to engage in low-level aggression. For the influence of age on proportion of threats relative to all aggression females engaged in, the coefficient estimate was 0.043, with a 99% credible interval from 0.011 to 0.073. The proportion of threats relative to all aggression females engaged in, did not vary with dominance rank (Figure 6b): the coefficient estimate was 0.039, with a 99% credible interval from -0.581 to 0.647.

###insert Figure 3 here###

###insert Figure 4 here###

###insert Figure 5 here###

###insert Figure 6 here###

**DISCUSSION**

This study investigated the changing patterns of physical and social activity of aging female Barbary macaques. We observed a pronounced decrease in demanding locomotor activities with age, likely reflecting waning strength and physical fitness. Active grooming bouts were longer in older compared to younger females. Older females had fewer animals within a five meter proximity radius and were less likely to be the target of aggression than younger ones. Aggression directed against others did not decline, but there was a marked decrease in challenging and physical aggression, accompanied by a relative increase in the use of threats.

The decrease in physical activities could be due to the deterioration in physical status, but might also be caused by changes in motivation to engage in these behaviors.
Independent assessments of physical condition would be needed to disentangle these two factors. Yet, the presumed decrease in physical strength – specifically manual fatigue as a result of arthrosis [Roth et al., 2014] – does not explain the decrease in overall active grooming time we previously observed [Almeling et al., 2016], because single grooming bouts were on average longer in older females than in younger ones. Thus, older females in this population engaged in active grooming less frequently. One might speculate, that fewer but longer grooming bouts require less movement and, hence, are energetically less costly than frequent changes between social partners. Moreover, staying longer with one social partner instead of moving around might help to avoid potentially negative social encounters and the resulting stress. Indeed, there exists evidence that focused grooming networks were observed to be associated with lowered glucocorticoid metabolite levels [Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008].

The finding that the average grooming bout was longer for older females indicates that older primates do not only continue to be interested in their social environment [Almeling et al., 2016; Schino & Sciarretta, 2016; but see Corr, 2003], but also in affiliation. Pavelka [1990] observed in female Japanese macaques a positive correlation between age and contact calling, a behavior that indicates the desire for social contact. Similar to our observation, older female toque macaques showed a decrease in frequency of grooming, but had a significantly higher proportion of long-duration contact events (> 5 min) compared to younger ones [Ratnayeke, 1994]. Pavelka [1990] further suggested that once in a social interaction older females are less likely to switch partners or activities [see also Fitts, 1982; Veenema, van Hooff, Gispen, & Spruijt, 2001].
In an egalitarian society, such as the one of Barbary macaques, the outcome of interactions may be particularly difficult to predict [Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017]; it may thus be safer to keep a spatial distance or avoid interactions with potentially negative outcomes through the use of mild signals of aggression. Indeed, older females in our study tended to be more spatially reclusive from the group, which may reflect the motivation to avoid potentially negative situations [see also Ratnayeke, 1994]. Yet, changes in spatial group integration may also be explained by group members being less attracted to older females. However, as other group members continued to groom older females [Almeling et al., 2016], this explanation does not seem likely. Regardless of the specific causes, spatial reclusiveness appears to correlate with a lower likelihood of being aggressed. Brent and colleagues [2017] reported an age-associated decrease in the frequency with which rhesus macaque females were the target of aggression. The authors interpreted their finding as indicating that enhanced experience to navigate through their social lives may help older females to avoid aggression. The tendency for an age-associated avoidance of potentially stressful situations in our study could also be interpreted as a mechanism to counteract age-related losses in the physiological flexibility as assumed by SAVI [Charles, 2010]. Further studies are necessary to investigate to which extent the amount of aggression received is related to the behavior of the (potential) victim as well as the spatial positions of the (potential) victim and the aggressor, to establish whether spatial reclusion is a strategy by the older animals to avoid unpredictable or potentially negative interactions.

We found no significant variation in overall aggression directed against others across age. Yet, the proportion of low-level aggression increased with age. More
specifically, older females mostly used an open mouth threat face, while they less frequently chased after or physically attacked other group members. Picq [1992] reported an age-associated increase in aggression given in captive grey mouse lemurs, but the aggression was predominantly observed as a response to being approached by their cage-mate. The open-mouth threat face that we observed in our sample might function to deter others to approach and therewith might allow females to avoid situations with potentially negative outcomes. Alternatively, older females may prefer threats over more severe aggressions such as fights as they are the least physically demanding form of aggression. Future studies are needed to investigate the precise contingencies between signal usage and partner responses as a function of age to illuminate how old subjects maneuver in their societies.

How do our results relate to the human psychological literature? Similar to observations in humans [Carstensen et al., 1999], the slight increase in active grooming bout duration with age suggests that older females are still motivated to engage in social interactions. Yet, as the number of partners decreases [Almeling et al. 2016], this indicates that older females become more selective in their partner choice.

In line with the strength and vulnerability integration model [SAVI, Charles, 2010] older females in our study appeared to avoid negative situations to a greater extent than younger ones. In a similar vein, older people reported fewer interpersonal tensions and less frequent arguing than younger people [Birditt, Fingerman, & Almeida, 2005]. Older people also reported using passive strategies to avoid conflicts more often than did younger ones [Charles, Piazza, Luong, & Almeida, 2009].

At first glance, the observation that overall aggression did not decline with age speaks against the idea that older individuals avoid negative interactions [SAVI,
Charles, 2010]. Yet, we found that the relative proportion of mild aggression increased. This preferential use of mild aggression could serve to avoid ambivalent situations. Studies on humans suggest that unpredictability associated with ambivalent ties is related to stress [Uchino, Holt-Lunstad, Uno, & Flinders, 2001]. It has been proposed that feeling ambivalent about social ties but not aversion per se relates to accelerated physiological decline [Uchino et al., 2012]. Therefore, our study supports the view that age-related avoidance of negative situations [SAVI, Charles, 2010] may be a shared trait within the primate lineage. How aging subjects manage their social interactions deserves further research attention; the strategic avoidance of negative interactions appears to be an important explanatory variable contributing to similarities in old humans’ and monkeys’ behavioral patterns.

ACKNOWLEDGEMENTS

We are grateful to Ellen Merz, Gilbert de Turckheim and Guillaume de Turckheim for permission to conduct this study at ‘La Forêt des Singes’ in Rocamadour and the team in the park for support. Moreover, we thank Andreas Ploss, Annika Patzelt and Elena Jeß who helped with the data collection. We thank Rebecca Jürgens for comments and corrections on the manuscript. We thank the Leibniz ScienceCampus for Primate Cognition for funding. A.M.F. and J.F. would like to thank the Helmut C. Nanz foundation for their hospitality. The authors declare no conflict of interest.
AUTHOR CONTRIBUTIONS

REFERENCES


similar mortality patterns across primates. *Science*, 331(6022), 1325-1328. DOI: 10.1126/science.1201571


Müller, N., Heistermann, M., Strube, C., Schülke, O., & Ostner, J. (2017). Age, but not anthelmintic treatment, is associated with urinary neopterin levels in semi-free ranging Barbary macaques. Scientific Reports, 7, 2045-2322, DOI: 10.1038/srep41973.


Uchino, B. N., Cawthon, R. M., Smith, T. W., Light, K. C., McKenzie, J., Carlisle, M., ... Bowen, K. (2012). Social relationships and health: Is feeling positive, negative, or both (ambivalent) about your social ties related to telomeres? *Health Psychology*, 31(6), 789-796. DOI: 10.1037/a0026836


692 Table and Figure captions

693 Table 1: Observation period, subjects, group composition (numbers in parentheses refer to adjusted values in case of the death of animals in the progress of the observation period) and types of behavior recorded (Y=Yes, N=No).

696

<table>
<thead>
<tr>
<th>Observation period</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>2005</td>
<td>2009</td>
<td>2009</td>
<td>2014</td>
</tr>
<tr>
<td>Dates</td>
<td>Sep 18 - Dec 4</td>
<td>Apr 28 - Jun 26</td>
<td>Sep 3 - Oct 31</td>
<td>May 19 - Aug 5</td>
</tr>
<tr>
<td>Group</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>Focal females [N]</td>
<td>8</td>
<td>19</td>
<td>19</td>
<td>26</td>
</tr>
<tr>
<td>Observation time [h]</td>
<td>~ 320</td>
<td>~ 304</td>
<td>~ 294.5</td>
<td>~ 285</td>
</tr>
<tr>
<td>Females [N]</td>
<td>25</td>
<td>24</td>
<td>24</td>
<td>26</td>
</tr>
<tr>
<td>Males [N]</td>
<td>16 (15)</td>
<td>22</td>
<td>22</td>
<td>13</td>
</tr>
<tr>
<td>Juveniles [N]</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>12</td>
</tr>
<tr>
<td>Infants [N]</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>4 (3)</td>
</tr>
<tr>
<td>Locomotor activity</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Grooming duration</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Spatial proximity</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Agonistic behavior</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
</tbody>
</table>

699 Figure 1 Aging and locomotor activities. Depicted are the expected values (Generalized Linear Model, solid line) for the frequency of locomotor activities behaviors and the credible interval (99 %, dashed lines) for focal females across ages (N females = 26).

702 Figure 2 Aging and grooming bout duration. (a) Depicted are the expected values (Linear Multilevel Model, solid line) and the credible interval (99 %, dashed line) for active grooming bouts (N = 394) that were initiated and terminated by the focal female (N = 39) across age. The predicted value for active grooming bout durations of female Barbary macaques was 1.08 min at the age of 5, 1.51 min at the age of 15 and 2.13 min at the age of 25. (b) Depicted are the expected values (Linear Multilevel Model, solid line) and the credible interval (99 %, dashed line) for active grooming bout durations
that were initiated and terminated by the focal female (N = 39) across dominance rank (corrected for number of females in the group; 1 denotes the lowest dominance rank).

**Figure 3** Aging and spatial proximity. (a) Depicted are the expected values for the mean number of individuals in 5-m radius (Generalized Linear Multilevel Model, solid line) and the credible interval (99%, dashed line) across focal females’ age (N females = 26). The predicted value for number of individuals recorded in 5-m radius around a female was 2.02 at the age of 5, 1.07 at the age of 15 and 0.76 at the age of 25. (b) Depicted are the expected values for the mean number of individuals in 5-m radius (Generalized Linear Multilevel Model, solid line) and the credible interval (99%, dashed line) across focal females’ (N females = 26) dominance rank (corrected for number of females in the group; 1 denotes the lowest dominance rank).

**Figure 4** Aging and aggression given. (a) Depicted are the expected values (Generalized Linear Multilevel Model, solid line) for (a) the frequency of agonistic behaviors given and (b) agonistic behaviors received for Barbary macaque females (N females = 46) observed for one up to three periods of observation (N observations = 72) and the credible interval (99%, dashed line). The predicted value for the frequency per hour a female directed aggression was 1.52 at the age of 5, 1.18 at the age of 15 and 0.92 at the age of 25.

**Figure 5** Aging and agonistic behavior received. (a) Depicted are the expected values (Generalized Linear Multilevel Model, solid line) for the frequency Barbary macaque
females (\(N_{\text{females}} = 46\)) received aggression at different ages in one up to three periods of observation (\(N_{\text{observations}} = 72\)) and the credible interval (99 %, dashed line). The predicted value for the frequency per hour a female received aggression was 2.47 at the age of 5, 0.99 at the age of 15 and 0.91 at the age of 25. (b) Depicted are the expected values (Generalized Linear Multilevel Model, solid line) for the frequency Barbary macaque females (\(N_{\text{females}} = 46\)) of different dominance rank positions (corrected for number of females in the group; 1 denotes the lowest dominance rank) received aggression in one up to three periods of observation (\(N_{\text{observations}} = 72\)) and the credible interval (99 %, dashed line).

Figure 6 Aging and the proportion of threats relative to all aggression females engaged in. (a) Depicted are the expected values (Generalized Linear Multilevel Model, solid line) for the proportion of threats relative to all aggression Barbary macaque females (\(N_{\text{females}} = 45\)), observed in one up to three periods of observation (\(N_{\text{observations}} = 71\)), engaged in across ages and the respective credible interval (99 %, dashed line). The predicted value for the percentage of threats relative to all aggression given was 51.0 % at the age of 5, 61.2 % at the age of 15 and 70.4 % at the age of 25. (b) Depicted are the expected values (Generalized Linear Multilevel Model, solid line) for the proportion of threats relative to all aggression Barbary macaque females (\(N_{\text{females}} = 45\)), observed in one up to three periods of observation (\(N_{\text{observations}} = 71\)), engaged in across dominance rank (corrected for number of females in the group; 1 denotes the lowest dominance rank) and the respective credible interval (99 %, dashed line).
(a) Active grooming bouts [min] vs. Age [yrs.]

(b) Active grooming bouts [min] vs. Dominance rank