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9 # Social interactions and activity patterns of old Barbary macaques:

10 # further insights into the foundations of social selectivity

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14 **Short title**: Activity patterns of old macaques

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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.

51 **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

76 older adults are more likely and better than younger adults in avoiding negative

77 situations that lead to high arousal. Similar to SST, SAVI considers future time

78 perspective as an important aspect shaping older adults' social lives. However,

79 extending SST, Charles [2010] pointed out that time lived (i.e., life experience) is also

80 essential for understanding how older adults regulate their social relations.

81   In older humans, both the awareness of their limited future time and cultural

82 conventions could potentially contribute to changes in self-reported and behavioral

83 selectivity. Due to the absence of elaborate future planning abilities and normativity in

84 nonhuman primates (hereafter 'primates'), studies on primates can provide important

85 insights into the evolutionary foundations of human social aging [Almeling,

86 Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016; Crockford, 2016].

87 Humans and primates have a similar life history [Bronikowski et al., 2011] and both

88 experience physiological senescence [Müller, Heistermann, Strube, Schülke, & Ostner,

89 2017; Roth et al., 2004], although, in contrast to humans, primates do not experience

90 menopause [Alberts et al., 2013]. As humans do, primates also seem to experience

91 conflicts as stressful, as indicated by increased levels of self-scratching and

92 glucocorticoid-metabolite levels in both the actor and recipient of aggression [Aureli,

93 1997; Wittig, Crockford, Weltring, Deschner, & Zuberbühler, 2015; but see Koski,

94 Koops, & Sterck, 2007]. In addition to the diminished fighting abilities observed in

95 older primates [Berghänel, Ostner, & Schülke, 2011; Bissonnette, Lange, & van Schaik,

96 2009; Fischer, Kitchen, Seyfarth, & Cheney, 2004], age-associated physiological

97 changes may result in a decreased ability to cope with stressors [Jensen, Blanton, &

98 Gribble, 1980; Sapolsky & Altmann, 1991].

99   Given these biological changes, a number of studies have addressed the question

100   in which way aging affects social behavior [Corr, Martin, & Boysen, 2002], also

101   referred to as 'social aging' [Hosaka & Huffman, 2015]. Empirical studies focused

102   mostly on females. This may be due to the fact, that males experience a higher mortality

103   across the primate order [Colchero et al., 2016], and thus old primate males may be less

104   frequently available as study subjects compared to old females. Studies on female social

105   aging yielded partly conflicting results [Borries & Koenig, 2008]: For wild chimpanzees

106   (*Pan troglodytes*) [Huffman 1990], wild toque macaques (*Macaca sinica*) [Ratnayeke

107   1994], semi-free ranging Japanese macaques (*Macaca fuscata*) [Hauser & Tyrrell, 1984;

108   Nakamichi 1984] and captive stump-tailed macaques (*Macaca arctoides*) [Hauser &

109   Tyrell, 1984] a reduced spatial integration of older females was observed. Moreover,

110   older females of various species and different rearing conditions showed reductions in

111   active grooming: Wild chimpanzees [Huffman 1990], semi-free ranging rhesus

112   macaques (*Macaca mulatta*) [Brent, Ruiz-Lambides, & Platt, 2017; Corr, 2003], semi-

113   free ranging Japanese macaques [Nakamichi, 1984] and captive long-tailed macaques

114   (*Macaca fascicularis*) [Veenema et al., 1997]. In contrast, Pavelka [1990] reported no

115   evidence for an age-related decrease studying the same population of Japanese

116   macaques as Nakamichi. Remarkably, older females received the same amount of

117   grooming as younger females [Brent et al., 2017; Corr, 2003; Huffman 1990;

118   Nakamichi, 1984, 2003]. While older female rhesus macaques [Corr, 2003] and long-

119   tailed macaques [Veenema et al., 1997] affiliated with fewer social partners, such a

120   pattern was not found in older female Japanese macaques [Pavelka, 1991].

121   In terms of agonistic behavior, aging was associated with lower levels of

122   aggression given in wild female toque macaques [Ratnayeke, 1994] and captive female

123   chimpanzees [Baker, 2000]. In contrast, Piqc [1992] observed an age-related increase in

124   the frequency of aggression given in captive mouse lemurs (*Microcebus murinus*).

125   Captive long-tailed macaques [Veenema et al., 1997] and semi-free ranging rhesus

126   macaques at Cayo Santiago [Brent et al., 2017] experienced age-related reductions in

127   aggression received. Studying the same population, however, Corr [2003] observed the

128   opposite pattern, namely an age-associated increase in the frequency of aggression

129   received. Yet, several other studies did not provide evidence for age-associated changes

130   in aggression or dominance-related behavior in rhesus macaques [Brent et al., 2017],

131   Japanese macaques [Pavelka, 1990], long-tailed macaques [Veenema et al., 1997],

132   stump-tailed macaques [Hauser & Tyrrell, 1984] and vervet monkeys (*Chlorocebus*

133   *pygerythrus*) [Fairbanks & McGuire, 1986]. Taken together, then, the empirical

134   evidence regarding social aging in primates is not completely consistent.

135   For female Barbary macaques (*Macaca sylvanus*) at 'La Forêt des Singes', we

136   showed an age-associated decrease in overall active grooming time and number of adult

137   partners that females groomed [Almeling et al, 2016]. This age-related change seemed

138   to be driven by the aging individual itself when considering that the time females

139   received grooming and the number of adult partners who groomed them did not vary

140   significantly with age. Moreover, the effect of a decreased active grooming time could

141   not be explained by a general loss in social interest, as Barbary macaques continued to

142   be interested in social information. More specifically, this became apparent in older

143   females' vocal 'commenting' [Brumm, 2005] on social interactions in their immediate

144   surrounding at similar rates compared to younger ones.

145   Here, we combined focal observations obtained from Barbary macaque females

146   over several years, to determine how physical activity, spatial proximity, and agonistic

147 behavior vary with age. We used the frequency of females' engagement in demanding

148 locomotor activities such as running, climbing, jumping and branch-shaking as a proxy

149 for physical strength. To test whether the observed decrease in active grooming duration

150 was due to manual fatigue [Roth et al., 2004], we assessed active grooming bout

151 duration for cases that were initiated and terminated by the female, as a proxy for their

152 endurance. We recorded spatial integration in the group and conflict behavior to assess

153 in more detail how interactions changed with age. Since dominance rank was found to

154 be an important factor determining sociality in Barbary macaques [Sosa, 2016] and

155 other species [Kato, 1999; Veenema et al., 1997], we considered dominance rank as a

156 potential confounding factor. With these analyses, we aim to contribute to a more

157 nuanced understanding of aging processes in nonhuman primates and macaques.

158 **METHODS**

159 **Ethics statement**

160 This study was non-invasive and based on observational data collection in a private

161 facility. This type of data collection is in accordance with the European Directive

162 2010/63/EU and was approved by the scientific director of the enclosure. Moreover, it

163 adheres to the American Society of Primatologists' principles for the ethical treatment of

164 primates.

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166 **Study species, study site and subjects**

167 Barbary macaques live in female bonded multi-male groups [Wrangham, 1980] with

168 female philopatry and male migration [Menard & Vallet, 1993; Paul & Kuester, 1985],

169 and have a rather tolerant social style [Thierry, 2000]. Females establish strong

170 relationships to related and non-related individuals of both sexes characterized by

171 frequent grooming [Patzelt, Pirow, & Fischer, 2009; Roubová, Konečná, Šmilauer, &

172 Wallner, 2015]. They also exhibit a relative stable linear dominance hierarchy based on

173 matrilines. Senescent females are outranked by their daughters [Paul & Kuester, 1987].

174   We conducted the study in the visitor park 'La Forêt des Singes' in Rocamadour,

175 France, where monkeys are outdoors throughout the year [Turckheim & Merz, 1984].

176 During the time of April until November the summer enclosure is open to visitors who

177 are restricted to a circular path system, while monkeys can range freely within the entire

178 area. Thus, monkeys are habituated to human observers but also have the possibility to

179 avoid them. Monkeys forage on vegetation of the park as oak leaves, bark, grass and

180 insects. Additionally, food such as pellets, wheat, fruits and vegetables is offered several

181 times a day. Water is available *ad libitum* from large ponds or one of the three water

182 basins in the park. The majority of adult females received hormonal transplants in order

183 to control reproduction. All monkeys are tattooed at the inner thigh.

184   Within the park there are three stable social groups. Females of two of the

185 groups served as focal subjects (see Table 1 for details). Individuals were classified as

186 adult at the age they commonly reach sexual maturity (males 5 years, females 4 years

187 [Menard & Vallet, 1993]; see Table 1 for group composition). Under these housing

188 conditions, female Barbary macaques may reach an age of 30 years. Altogether 46

189 individual focal females (age range: 5-29 yrs.) were included in the study.

190   Data were collected in four periods over the course of several years (see Table 1

191 for details). The subset of focal females observed in period 2 and 3 comprised all

192 females observed in period 1, except for one that had died.

193

194 ###insert Table 1 here###

195

Behavioral observations

197 We recorded half-hour protocols of predefined behaviors using the focal sampling

198 method for a total of ≈ 1204 hours during 4 periods of observation (see Table 1 for

199 details). During all periods of observation, we recorded the occurrence of agonistic

200 behaviors threats (open-mouth face with raised eyebrows), chase away (threats

201 accompanied by following the victim for at least a few meters) and fights with physical

202 contact (beating and biting). For periods 2 - 4, we also recorded the duration of

203 grooming given and received. For a detailed description of the ethogram of Barbary

204 macaques see Hesler and Fischer [2007]. In period 4, we additionally recorded the

205 occurrence of locomotor activities (running > 5 m with high velocity, jumping, climbing

206 > 1.5 m, and branch-shaking). Moreover, in period 4, we noted the number of

207 individuals in a 5-m radius before the onset of the focal observation ($N = 561$ scans).

208 Throughout all observation periods, we noted *ad libitum* dyadic conflicts and

209 displacements for the purpose of establishing a dominance hierarchy. A handheld

210 computer (Palm, Model Zire) or tablet (Samsung Galaxy S4) running a custom program

211 created with Pendragon Forms (Pendragon Software Corporation, Libertyville, IL,

212 U.S.A.) was used to record the data.

213 When a focal female was out of sight during observation, proceedings were as

214 follows: if the female could be located again within 5 - 10 minutes, the time lacking was

215 added to the half hour session; if the female could not be located again, the time lacking

216 was noted and added to the next session of the focal female in the same period of day.

217 The focal females were observed semi-randomly by following an order which was

218 arranged daily for the observation day so that observation times for single individuals

219 were similarly distributed for each female in period 1 (3/5 of protocols during

220 9:00 - 14:00 and 2/5 during 14:00 - 18:00 and approximately evenly distributed

221 throughout the day (morning: 9:00 - 11:30, midday: 11:30 - 14:00, afternoon

222 14:00 - 16:30 and evening (16:30 - 19:00) for period 2 - 4.

223

Analyses

225 To determine the effect of age on the frequency that females engaged in 'locomotor

226 activities' we ran a Generalized Linear Model in R version 3.3.1 [R Core Team, 2015],

227 using data obtained in observation period 4, for 26 females of one group (see Table 1).

228 The estimation was performed using BayesX [Belitz et al., 2015]. We assumed a

229 negative binomial distributed response [Zeileis, Kleiber, & Jackman, 2008]. We chose

230 this distribution as, in contrast to the Poisson distribution, we directly control for

231 potential overdispersion. We entered 'age' as linear regression coefficient and used the

232 offset *log*(observation time) in order to take slightly varying observation length into

233 consideration.

234 In the further analyses addressing the effect of age on various types of social

235 behavior, we included the potential confounder 'dominance rank'. To determine the

236 dominance relations among adult females for each group and observation period we

237 used MatMan 1.1 (Noldus, Wageningen, Netherlands) [de Vries, Netto, & Hanegraaf,

238 1993], in which we entered a winner-looser matrix using *ad libitum* and focal data of

239 dyadic encounters and approach retreat interactions. We observed linear dominance

240 hierarchies in females for both groups and all data collection periods (Group A: period

241 1: $\chi^2 = 115.29$, $df = 31.29$, $h' = 0.48$, $P < 0.001$, $N = 25$; period 2: $\chi^2 = 88.56$, $df = 30.36$,

242 $h' = 0.42$, $P < 0.001$, $N = 24$; period 3:$\chi^2 = 87.1$, $df = 30.36$, $h' = 0.41$, $P < 0.001$,

243 $N = 24$; group B: period 4: $\chi^2 = 132.60$, $df = 32.23$, $h' = 0.52$, $P < 0.001$, $N = 26$). In the

244 analyses, we used a females' relative dominance rank position (hereafter: 'dominance

245 rank') within the female hierarchy instead of absolute values, in order to correct for

246 differences in numbers of females in the groups and across periods of observation. In

247 our subset of focal females ($N = 46$), 'dominance rank' was weakly positively correlated

248 with 'age' (Spearman-Rho = 0.36, $P = 0.002$, N observations = 72), i.e. older females

249 tended to be lower in rank.

250   We checked for potential collinearity between 'age' and 'dominance rank' in the

251 different models using the function 'vif' from R add-on package 'car' [Fox et al., 2016].

252 Variance inflation factors were never larger than 1.43, indicating that there is no

253 collinearity. This also accounts for 'observation period', which was incorporated as a

254 potential confounder in the analyses, if appropriate.

255   The following analyses were conducted using a Bayesian inference algorithm

256 (Markov chain Monte Carlo, MCMC) as implemented in BayesX Version 3.0.2 [Belitz

257 et al., 2015]. Markov chain Monte Carlo (MCMC) estimation is a general tool for the

258 estimation of Bayesian regression models that allows quantifying the joint posterior

259 distribution of the model's coefficients with high accuracy [Gelman, 2006]. In the

260 absence of substantial prior knowledge, we used non-informative priors for the

261 regression coefficients included in the different models. Typically, the data provides

262 enough information to estimate $\beta_0, \beta_1, ...$ by the use of any reasonable non-informative

263 prior distribution [Gelman, 2006]. This is, however, generally not the case for scale

264 parameters such as σ_γ^2, and the use of (weakly) informative priors is needed. For the

265 variance σ_γ^2 of the prior for varying intercept model coefficient $\gamma_i \sim N(0, \sigma_\gamma^2)$, for

266 individuals $i = 1, \ldots, n$, we therefore used a weakly informative inverse Gamma prior

267 with hyper-parameters $a = b = 0.001$, i.e. $\sigma_\gamma^2 \sim IG(a = 0.001, b = 0.001)$ [Belitz et

268 al., 2015]. For the MCMC set-up, we used a burn-in of 12,000 iterations, a thinning rate

269 of 40, and 52,000 iterations in total.

270   Concerning the dependent variable 'active grooming bout duration', we used the

271 data recorded in observation periods 2 - 4 (see Table 1) and restricted the analysis to

272 those events that were initiated and terminated by the focal female, and which were not

273 truncated by the beginning or the end of the focal observation ($N = 394$). This selection

274 reduced the number of focal females in our sample to 39 females, as 6 individuals were

275 not observed to engage in active grooming given the selection criteria. The dependent

276 variable was $\log_e$-transformed in order to meet the normality assumption on residuals.

277 We conducted a Linear Multilevel Model with 'age', 'dominance rank' and 'observation

278 period' as factor covariate. We controlled for variation across 'focal females' by the use

279 of varying intercepts. Inspection of QQ- and residuals vs. fitted values plots indicated

280 no relevant deviation from normally and homogeneously distributed residuals.

281   To assess the influence of age on the 'number of individuals in 5-m radius' we

282 used data recorded of 26 females of one group in observation period 4 (see Table 1). We

283 conducted a Generalized Linear Multilevel Model with a negative binomial response, in

284 this way controlling for potential overdispersion [Zeileis et al., 2008]. We incorporated

285 'age' and 'dominance rank' in the model and used the offset log(observation time) to

286 account for slightly varying observation times. Moreover, we controlled for variation

287 across 'focal females' by the use of varying intercepts. To estimate a potential non-

288 linear relationship between 'age' and the dependent variable, we used a non-parametric

289 Bayesian P-spline approach [Brezger & Lang, 2005], a standard non-parametric method

290 to assess non-linear effects [Eilers, Marx, & Durbán, 2015].

291   For the dependent variable 'aggression given', we used data from 46 females

292 across observation periods 1 – 4 (see Table 1). To estimate a regression coefficient for

293 age on the frequency females show aggressive behavior, we conducted a Generalized

294 Linear Multilevel Model with a negative binomial response, controlling for potential

295 overdispersion [Zeileis et al., 2008], and included 'age', 'dominance rank' and

296 'observation period' as factor covariate. We added 'focal females' as varying intercepts

297 and used the offset log(observation time) to correct for varying observation times.

298   For the dependent variable 'aggression received', we used data from 46 females

299 across observation periods 1 – 4 (see Table 1). To estimate the role of age on how

300 frequently females were the target of aggression, we conducted a Generalized Linear

301 Multilevel Model with a negative binomial response [Zeileis et al., 2008], and included

302 'age', 'dominance rank', and 'observation period' as factor covariate. We added 'focal

303 females' as varying intercepts and used the offset log(observation time) to correct for

304 varying observation times. To estimate a potential non-linear relationship between 'age'

305 and the dependent variable, we used a non-parametric Bayesian P-spline approach

306 [Brezger & Lang, 2005].

307   For the proportion of 'threats relative to all aggression (threats, chase away and

308 physical fights)' the focal females engaged in, we used data obtained in observation

309 periods 1 – 4 (see Table 1). One female (age = 29 yrs) was removed from this analysis,

310 as she was never observed to engage in aggression throughout the observation period,

311 yielding observations for 45 females instead of the 46 observed in total. To estimate a

312 regression coefficient for age on the proportion females engage in 'threats relative to all

313 aggression', we conducted a Generalized Linear Multilevel Model with a binomial

314 response and included 'age', 'dominance rank', and 'observation period' as factor

315 covariate. We added 'focal females' as varying intercepts.

316   The results of the described models are presented in a graphical way (Figures

317 2 - 6). Pairs of expected values with exclusive credible intervals reveal strong evidence

318 for age-related differences in the distribution of the response. Note, that expected values

319 vary non-linearly in all figures, although 'age' was incorporated as a non-linear term

320 only in the models for 'number of individuals in 5-meter radius' and 'aggression

321 received'. The non-linear shapes of expected values in the other models result from non-

322 linear response functions and, in the case of 'active grooming bout duration', from the

323 log-transformation. For an improved readability of these graphs, the values of the

324 estimated expected values are given in numerical form for age at values of 5, 15, and 25

325 years in the respective figure legends. Moreover, we provide coefficient estimates for

326 the models, except for those that were P-spline based ('number of individuals in 5-meter

327 radius' and 'aggression received'). For this type of analysis, coefficient estimates cannot

328 be obtained. Finally, we also provide such graphical displays for the potential

329 confounder 'dominance rank' as well as coefficient estimates, whenever applicable.

330

331 **RESULTS**

332 Age had a negative effect on the frequency females ($N = 26$) engaged in demanding

333 locomotor activities (Generalized Linear Model: Est. = -0.073, $SE = 0.015$, $P < 0.001$, N

334 events = 449, Figure 1). Note that any further statistical inference result are given as the

335 estimated expected values and credible intervals, generally set at 99 %, with the aid of

336 plots (Figures 2 - 6). The estimated expected value of active grooming bout duration

337 increased with age (Figure 2a). For the influence of age on grooming bout duration, we

338 obtained a coefficient estimate of 0.034, with a 99% credible interval from 0.009 to

339 0.065. The estimated expected value of active grooming bout duration did not vary with

340 dominance rank (Figure 2b). For the influence of dominance rank on grooming bout

341 duration, we obtained a coefficient estimate of 0.024 with a 99% credible interval from -

342 0.500 to 0.510.

343

344 ###insert Figure 1 here###

345 ###insert Figure 2 here###

346

347   The expected value of number of individuals that were recorded within a 5-m

348 radius around the focal females tended to decrease with age (Figure 3a) and did not vary

349 with dominance rank (Figure 3b). We did not find evidence for a change in the

350 frequency of aggression given with age (Figure 4a): the coefficient estimate was -0.025,

351 with a 99% credible interval from -0.061 to 0.011. Because dominance rank was

352 inferred from dyadic agonistic encounters among females, it is not surprising that rank

353 varied with aggression given (Figure 4b): the coefficient estimate was -1.471, with a

354 99% credible interval from -2.239 to -0.784. The expected value of the frequency that

355 females were the targets of aggression decreases at younger ages, and, starting at around

356 15 years, flats out (Figure 5a). Aggression received varied with dominance rank: The

357 higher the rank, the less frequently a female received aggression (Figure 5b). Note, that

358 dominance rank was inferred from dyadic agonistic encounters among females. The

359 proportion of threats relative to all aggression females engaged in (threats, chase away

360 and physical fights) increased with age (Figure 6a). In other words, older females were

361 more likely to engage in low-level aggression. For the influence of age on proportion of

362 threats relative to all aggression females engaged in, the coefficient estimate was 0.043,

363 with a 99% credible interval from 0.011 to 0.073. The proportion of threats relative to

364 all aggression females engaged in, did not vary with dominance rank (Figure 6b): the

365 coefficient estimate was 0.039, with a 99% credible interval from -0.581 to 0.647.

366

367 ###insert Figure 3 here###

368 ###insert Figure 4 here###

369 ###insert Figure 5 here###

370 ###insert Figure 6 here###

371 **DISCUSSION**

372 This study investigated the changing patterns of physical and social activity of aging

373 female Barbary macaques. We observed a pronounced decrease in demanding

374 locomotor activities with age, likely reflecting waning strength and physical fitness.

375 Active grooming bouts were longer in older compared to younger females. Older

376 females had fewer animals within a five meter proximity radius and were less likely to

377 be the target of aggression than younger ones. Aggression directed against others did

378 not decline, but there was a marked decrease in challenging and physical aggression,

379 accompanied by a relative increase in the use of threats.

380   The decrease in physical activities could be due to the deterioration in physical

381 status, but might also be caused by changes in motivation to engage in these behaviors.

382 Independent assessments of physical condition would be needed to disentangle these

383 two factors. Yet, the presumed decrease in physical strength – specifically manual

384 fatigue as a result of arthrosis [Roth et al., 2014] – does not explain the decrease in

385 overall active grooming time we previously observed [Almeling et al., 2016], because

386 single grooming bouts were on average longer in older females than in younger ones.

387 Thus, older females in this population engaged in active grooming less frequently. One

388 might speculate, that fewer but longer grooming bouts require less movement and,

389 hence, are energetically less costly than frequent changes between social partners.

390 Moreover, staying longer with one social partner instead of moving around might help

391 to avoid potentially negative social encounters and the resulting stress. Indeed, there

392 exists evidence that focused grooming networks were observed to be associated with

393 lowered glucocorticoid metabolite levels [Crockford, Wittig, Whitten, Seyfarth, &

394 Cheney, 2008].

395   The finding that the average grooming bout was longer for older females

396 indicates that older primates do not only continue to be interested in their social

397 environment [Almeling et al., 2016; Schino & Sciarretta, 2016; but see Corr, 2003], but

398 also in affiliation. Pavelka [1990] observed in female Japanese macaques a positive

399 correlation between age and contact calling, a behavior that indicates the desire for

400 social contact. Similar to our observation, older female toque macaques showed a

401 decrease in frequency of grooming, but had a significantly higher proportion of long-

402 duration contact events (> 5 min) compared to younger ones [Ratnayeke, 1994].

403 Pavelka [1990] further suggested that once in a social interaction older females are less

404 likely to switch partners or activities [see also Fitts, 1982; Veenema, van Hooff, Gispen,

405 & Spruijt, 2001].

406   In an egalitarian society, such as the one of Barbary macaques, the outcome of

407 interactions may be particularly difficult to predict [Fischer, Farnworth, Sennhenn-

408 Reulen, & Hammerschmidt, 2017]; it may thus be safer to keep a spatial distance or

409 avoid interactions with potentially negative outcomes through the use of mild signals of

410 aggression. Indeed, older females in our study tended to be more spatially reclusive

411 from the group, which may reflect the motivation to avoid potentially negative

412 situations [see also Ratnayeke, 1994]. Yet, changes in spatial group integration may also

413 be explained by group members being less attracted to older females. However, as other

414 group members continued to groom older females [Almeling et al., 2016], this

415 explanation does not seem likely. Regardless of the specific causes, spatial

416 reclusiveness appears to correlate with a lower likelihood of being aggressed. Brent and

417 colleagues [2017] reported an age-associated decrease in the frequency with which

418 rhesus macaque females were the target of aggression. The authors interpreted their

419 finding as indicating that enhanced experience to navigate through their social lives may

420 help older females to avoid aggression. The tendency for an age-associated avoidance of

421 potentially stressful situations in our study could also be interpreted as a mechanism to

422 counteract age-related losses in the physiological flexibility as assumed by SAVI

423 [Charles, 2010]. Further studies are necessary to investigate to which extent the amount

424 of aggression received is related to the behavior of the (potential) victim as well as the

425 spatial positions of the (potential) victim and the aggressor, to establish whether spatial

426 reclusion is a strategy by the older animals to avoid unpredictable or potentially

427 negative interactions.

428   We found no significant variation in overall aggression directed against others

429 across age. Yet, the proportion of low-level aggression increased with age. More

430 specifically, older females mostly used an open mouth threat face, while they less

431 frequently chased after or physically attacked other group members. Picq [1992]

432 reported an age-associated increase in aggression given in captive grey mouse lemurs,

433 but the aggression was predominantly observed as a response to being approached by

434 their cage-mate. The open-mouth threat face that we observed in our sample might

435 function to deter others to approach and therewith might allow females to avoid

436 situations with potentially negative outcomes. Alternatively, older females may prefer

437 threats over more severe aggressions such as fights as they are the least physically

438 demanding form of aggression. Future studies are needed to investigate the precise

439 contingencies between signal usage and partner responses as a function of age to

440 illuminate how old subjects maneuver in their societies.

441   How do our results relate to the human psychological literature? Similar to

442 observations in humans [Carstensen et al., 1999], the slight increase in active grooming

443 bout duration with age suggests that older females are still motivated to engage in social

444 interactions. Yet, as the number of partners decreases [Almeling et al. 2016], this

445 indicates that older females become more selective in their partner choice.

446   In line with the strength and vulnerability integration model [SAVI, Charles,

447 2010] older females in our study appeared to avoid negative situations to a greater

448 extent than younger ones. In a similar vein, older people reported fewer interpersonal

449 tensions and less frequent arguing than younger people [Birditt, Fingerman, & Almeida,

450 2005]. Older people also reported using passive strategies to avoid conflicts more often

451 than did younger ones [Charles, Piazza, Luong, & Almeida, 2009].

452   At first glance, the observation that overall aggression did not decline with age

453 speaks against the idea that older individuals avoid negative interactions [SAVI,

454 Charles, 2010]. Yet, we found that the relative proportion of mild aggression increased.

455 This preferential use of mild aggression could serve to avoid ambivalent situations.

456 Studies on humans suggest that unpredictability associated with ambivalent ties is

457 related to stress [Uchino, Holt-Lunstad, Uno, & Flinders, 2001]. It has been proposed

458 that feeling ambivalent about social ties but not aversion *per se* relates to accelerated

459 physiological decline [Uchino et al., 2012]. Therefore, our study supports the view that

460 age-related avoidance of negative situations [SAVI, Charles, 2010] may be a shared trait

461 within the primate lineage. How aging subjects manage their social interactions

462 deserves further research attention; the strategic avoidance of negative interactions

463 appears to be an important explanatory variable contributing to similarities in old

464 humans' and monkeys' behavioral patterns.

465 **ACKNOWLEDGEMENTS**

473

474 **AUTHOR CONTRIBUTIONS**

475   L.A., K.H., A.M.F. and J.F. designed the study, L.A. collected the data, H.S.-R. and

476   L.A. executed the analyses and L.A., A.M.F., K.H. and J.F. wrote the manuscript.

477

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691

692 **Table and Figure captions**

693 **Table 1:** Observation period, subjects, group composition (numbers in parentheses refer

694 to adjusted values in case of the death of animals in the progress of the observation

695 period) and types of behavior recorded (Y=Yes, N=No).

696

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

697

698

699 **Figure 1** Aging and locomotor activities. Depicted are the expected values (Generalized

700 Linear Model, solid line) for the frequency of locomotor activities behaviors and the

701 credible interval (99 %, dashed lines) for focal females across ages (N females = 26).

702

703 **Figure 2** Aging and grooming bout duration. (a) Depicted are the expected values

704 (Linear Multilevel Model, solid line) and the credible interval (99 %, dashed line) for

705 active grooming bouts ($N = 394$) that were initiated and terminated by the focal female

706 ($N = 39$) across age. The predicted value for active grooming bout durations of female

707 Barbary macaques was 1.08 min at the age of 5, 1.51 min at the age of 15 and 2.13 min

708 at the age of 25. (b) Depicted are the expected values (Linear Multilevel Model, solid

709 line) and the credible interval (99 %, dashed line) for active grooming bout durations

710   (*N* = 394) that were initiated and terminated by the focal female (*N* = 39) across

711   dominance rank (corrected for number of females in the group; 1 denotes the lowest

712   dominance rank).

713

714   **Figure 3** Aging and spatial proximity. (a) Depicted are the expected values for the mean

715   number of individuals in 5-m radius (Generalized Linear Multilevel Model, solid line)

716   and the credible interval (99 %, dashed line) across focal females' age (*N* females = 26).

717   The predicted value for number of individuals recorded in 5-m radius around a female

718   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

719   the expected values for the mean number of individuals in 5-m radius (Generalized

720   Linear Multilevel Model, solid line) and the credible interval (99 %, dashed line) across

721   focal females' (*N* females = 26) dominance rank (corrected for number of females in the

722   group; 1 denotes the lowest dominance rank)

723

724   **Figure 4** Aging and aggression given. (a) Depicted are the expected values

725   (Generalized Linear Multilevel Model, solid line) for (a) the frequency of agonistic

726   behaviors given and (b) agonistic behaviors received for Barbary macaque females (*N*

727   females = 46) observed for one up to three periods of observation (*N* observations = 72)

728   and the credible interval (99 %, dashed line). The predicted value for the frequency per

729   hour a female directed aggression was 1.52 at the age of 5, 1.18 at the age of 15 and
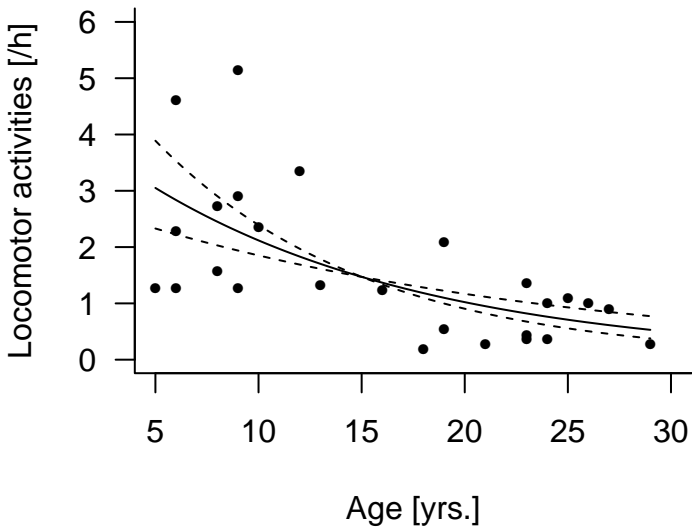
730   0.92 at the age of 25.

731

732   **Figure 5** Aging and agonistic behavior received. (a) Depicted are the expected values

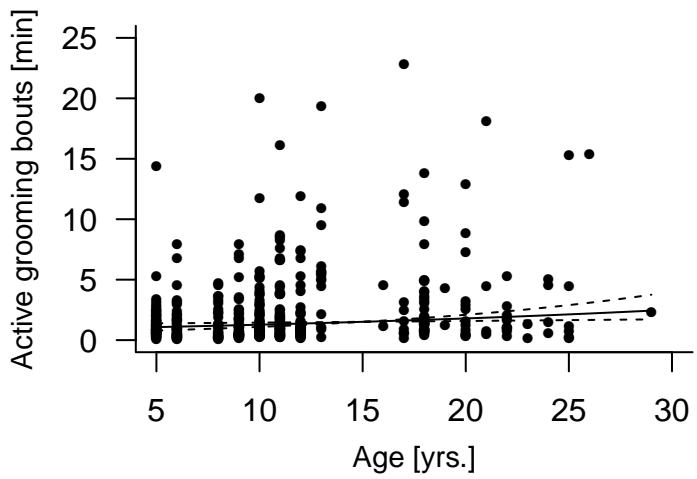733   (Generalized Linear Multilevel Model, solid line) for the frequency Barbary macaque

734   females (*N* females = 46) received aggression at different ages in one up to three periods

735   of observation (*N* observations = 72) and the credible interval (99 %, dashed line). The

736   predicted value for the frequency per hour a female received aggression was 2.47 at the

737   age of 5, 0.99 at the age of 15 and 0.91 at the age of 25. (b) Depicted are the expected

738   values (Generalized Linear Multilevel Model, solid line) for the frequency Barbary

739   macaque females (*N* females = 46) of different dominance rank positions (corrected for

740   number of females in the group; 1 denotes the lowest dominance rank) received

741   aggression in one up to three periods of observation (*N* observations = 72) and the

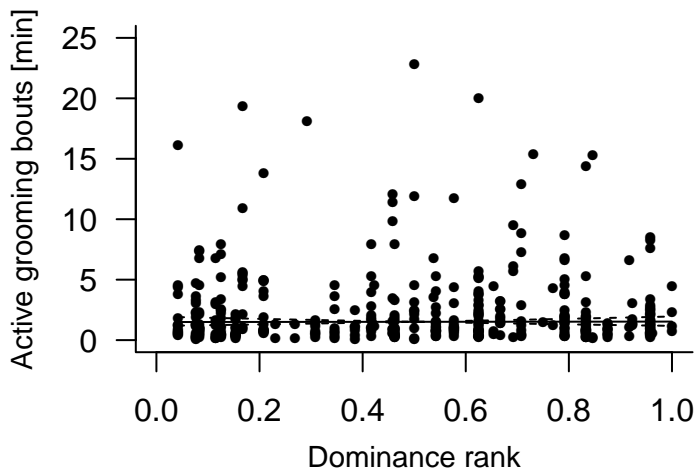742   credible interval (99 %, dashed line).

743

744   **Figure 6** Aging and the proportion of threats relative to all aggression females engaged

745   in. (a) Depicted are the expected values (Generalized Linear Multilevel Model, solid

746   line) for the proportion of threats relative to all aggression Barbary macaque females (*N*

747   females = 45), observed in one up to three periods of observation (*N* observations = 71),

748   engaged in across ages and the respective credible interval (99 %, dashed line). The

749   predicted value for the percentage of threats relative to all aggression given was 51.0 %

750   at the age of 5, 61.2 % at the age of 15 and 70.4 % at the age of 25. (b) Depicted are the

751   expected values (Generalized Linear Multilevel Model, solid line) for the proportion of

752   threats relative to all aggression Barbary macaque females (*N* females = 45), observed

753   in one up to three periods of observation (*N* observations = 71), engaged in across

754   dominance rank (corrected for number of females in the group; 1 denotes the lowest

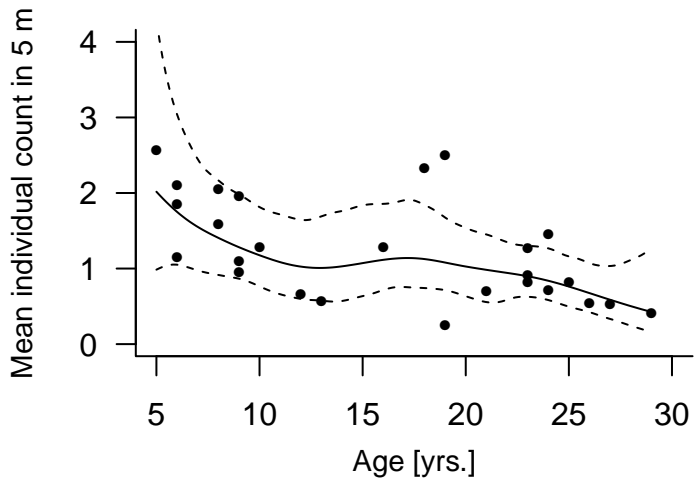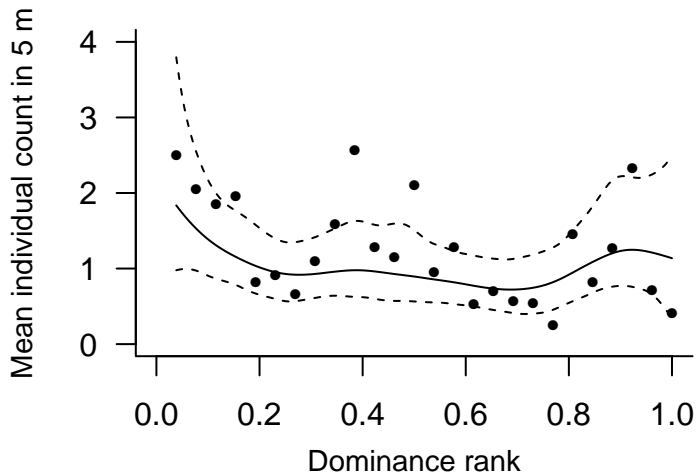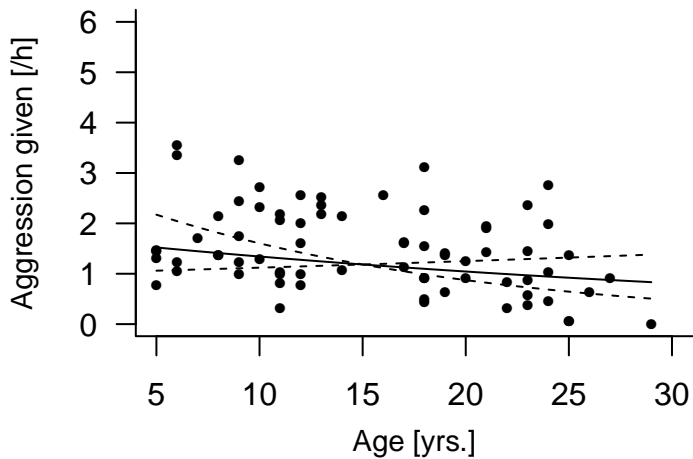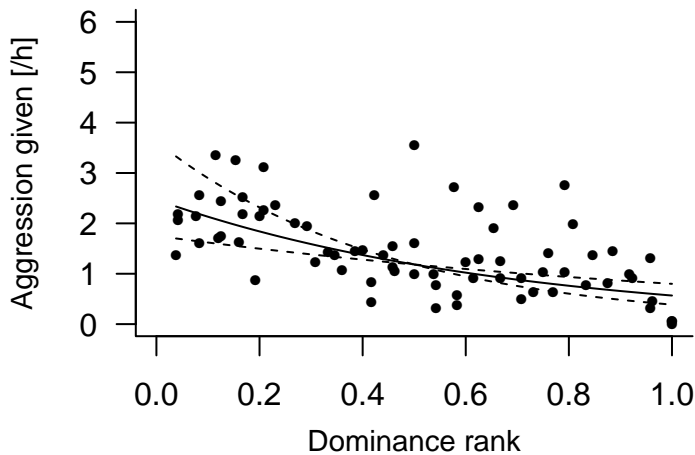755   dominance rank) and the respective credible interval (99 %, dashed line).

(a)

Active grooming bouts [min] vs Age [yrs.]

(b)

Active grooming bouts [min] vs Dominance rank

(a)

Mean individual count in 5 m

Age [yrs.]

(b)

Mean individual count in 5 m

Dominance rank

(a)

Aggression given [/h]

Age [yrs.]

(b)

Aggression given [/h]

Dominance rank

(a)

Aggression received [/h] vs Age [yrs.]

(b)

Aggression received [/h] vs Dominance rank

(a)

Threats to all aggression [%] vs Age [yrs.]

(b)

Threats to all aggression [%] vs Dominance rank