Oil palm cultivation critically affects sociality in an endangered Malaysian primate

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32   **<u>Abstract</u>**

33   Human-induced habitat alterations globally threaten animal populations, often evoking diverse and

34   complex behavioural responses in wildlife. This may be particularly dramatic when negatively

35   affecting social behaviour, which fundamentally determines individual fitness and offspring survival

36   in group-living animals. Here, we provide first evidence for critical behavioural modifications of

37   Southern pig-tailed macaques visiting Malaysian oil palm plantations in search of food. Specifically,

38   we found significant reductions of positive social interactions, an increase of non-physical aggression

39   and shifts in the macaques' social network structure, with the central positions of high-ranking adult

40   females and immatures being passed to low-ranking individuals likely resulting from socio-ecological

41   risks posed by plantations. Deviations from natural behaviour also affected the smallest but crucial

42   social units within groups, mother-infant pairs, with increased maternal protectiveness at

43   plantations. Our study provides strong evidence that although primates, and more generally group-

44   living wildlife, can persist in human-altered habitats, their ability to adapt may come with a trade-off

45   for their natural sociality potentially hampering infant development and individual survival.

2

Introduction

The ongoing expansion of anthropogenic landscapes threatens rainforest ecosystems and the survival of many species[1]. Land conversion for food production and the cultivation of cash crops is the main driver for the global forest loss of estimated 10 million hectares per year[2]. Disturbing natural habitats and presenting sources of anthropogenic food, such modifications create novel and rapidly changing environments for animal populations[3]. With 60% of species being threatened[4], non-human primates (hereafter 'primates') may be particularly susceptible to human disturbance. The Southern pig-tailed macaque (*Macaca nemestrina*, IUCN: Endangered[4]) has lost large parts of its natural forest habitat in Malaysia and Indonesia to oil palm monocultures[5]. Habitat fragmentation, hunting and conflicts with farmers are only some of the threats the macaques face in the forest-oil palm matrix[3,6]. Plantations also lack protection by dense forest vegetation and ease access for potential predators[3,7]. Largely understudied in the wild and described as elusive species that tend to avoid human contact[6], it is imperative to better understand *M. nemestrina*'s ability to adapt to these human-altered habitats.

Frequently, adaptive alterations in behaviour (also referred to as behavioural plasticity[8]) are one of the first visible responses of animals to anthropogenic disturbance. In primates, these responses are diverse and very complex, with most previous studies focusing on their ability to exploit new feeding grounds, shifts in activity budgets or ranging behaviour, and the negative consequences of the human-primate interface, such as increased stress levels among animals or high rates of aggression (reviewed in [9]).

Despite growing research interest in this topic, differences in primate sociality between natural and anthropogenic habitats have not been systematically assessed. Yet, social behaviour plays a fundamental role in group-living animals. Macaques typically live in complex multi-male, multi-female societies, often following a dispersal regime with males leaving their birth group to breed elsewhere, while females are philopatric[10]. Strong and enduring social bonds significantly increase fitness in both sexes, with social integration offering energetic benefits and buffering social and environmental stress[11,12]. Specifically, the quality of affiliative relationships was found to predict individual reproductive performance[13,14], longevity[15] and infant survival[16]. Grooming is one of the most common affiliative interactions among primates, and has a key role in establishing and maintaining social relationships that underlie complex social features such as an animal's role within the group's social network[17,18]. Further, juvenile play constitutes a springboard for social competence during the first years of an individual's life[19], allowing immatures to construct and expand their social networks and grow into their social roles as adults[19,20]. On the other hand, also agonistic interactions are crucial in social groups, e.g. for the acquisition and maintenance of dominance status and

80   certainty which directly impacts individual health[21]. Shifts in any of these behaviours and

81   (consequently) in individuals' social network roles may impair social bonds and thus have

82   downstream effects on group stability and survival[22].

83   Though widely overlooked in previous research, behavioural plasticity in the smallest but most

84   essential social unit of a group, i.e. mother-infant pairs, may indicate how well a species can cope in

85   human-altered landscapes. Primate mothers provide extensive care to their offspring, and their

86   behaviour strongly affects the development of a wide range of infant behaviours, including

87   environmental exploration, affiliation and aggression, and later sexual and parental behaviour[20,23].

88   Depending on the social system of a species, but also on individual characteristics such as

89   personality, dominance rank, parity, or infant age and sex[24–27], mothering styles can vary from highly

90   protective to highly tolerant, with the reduction of body contact and maternal permissive behaviours

91   being particularly critical components for infant independence[28]. In this context, disruptions of the

92   mother-infant relationship caused by habitat alterations may have severe consequences for offspring

93   health and survival.

94   *Macaca nemestrina* frequently enters oil palm plantations to complement its diet with palm fruits

95   and plantation rats[29,30], yet it remains unclear whether and how the macaques' sociality deviates

96   from their natural behaviour when ranging in these modified habitats. Here, we investigated to what

97   extent macaque social behaviour may undergo changes during the time they spend at oil palm

98   plantations compared to their natural forest habitat. Firstly, we examined quantitative differences in

99   individual frequencies of affiliative and agonistic interactions. Secondly, we assessed changes in the

100   macaques' social network roles. Finally, we investigated dynamics in the mother-infant relationship

101   during the first six months after infant birth. We predicted affiliation to be low at the risky plantation

102   environment that lacks shelter and increases the visibility to predators[3,7], but rates of aggression to

103   increase based on the assumption that plantations likely evoke stress in macaques and create

104   competition for energy-rich food sources[31,32]. In line with this, we expected reductions in the number

105   of individual interaction partners and the connectedness in social networks during plantation visits.

106   Finally, we predicted macaque mothers to be more protective of their dependent offspring when

107   ranging at the plantation compared to the forest.

108

109   **Results**

110   *Social interactions in forest and oil palm plantation*

111   Behavioural observations of two habituated groups of macaques inhabiting the Segari Melintang

112   Forest Reserve in Peninsular Malaysia and the surrounding oil palm plantation revealed strong

differences in the primates' activity between habitats. As plantation areas in close proximity to the forests provide additional shelter and protection for animals through close-by forest vegetation, we distinguished between forest habitat, the plantation edge, i.e. plantation areas within 50 meters from the forest border, and areas further inside the plantation (hereafter 'plantation'). As expected, approximately two thirds of the time the macaques spent at the plantation edge and inside the plantation, respectively, were dedicated to the search and consumption of food. Social contact to conspecifics, in contrast, could only rarely be observed inside the plantation (mean ± SD = 0.003 ± 0.006), and was clearly reduced at the plantation edge (mean ± SD = 0.07 ± 0.07) compared to the forest (mean ± SD = 0.14 ± 0.08, for details on activity budgets see Supplemental Fig. S1).

Accounting for 96% of the total time spent socializing, grooming and play were the most common positive social interactions. During focal observations, we recorded a total of 1,607 grooming bouts and 574 bouts of juvenile social play. Grooming frequencies significantly differed between habitats, while controlling for potentially confounding factors, particularly an individual's dominance rank and age-sex class, the study group and daytime (LRT: χ^2 = 120.96, df = 2, P < 0.001, N = 1,535 focal observations of 50 individuals, Fig. 1a3, for details see Supplementary Tab. S1). Specifically, the highest grooming rate was observed in the forest, an intermediate rate at the plantation edge, and the lowest rate inside the plantation (Fig. 1a1-2). Similarly, juvenile social play was significantly higher in the forest than in both plantation habitats (LRT: χ^2 = 40.28, df = 2, P < 0.001, N = 510 focal observations of 16 individuals, Fig. 1b1-3, see Supplementary Tab. S1).

As predicted, differences in aggressive behaviour across habitats were generally in contrast to patterns of affiliation, although they were less clear, and varied according to the intensity of aggression. From a total of 496 observed aggressive interactions, 96 included physical aggression, while the others involved more ritualized forms, such as facial or vocal threats (hereafter 'non-physical aggression'). Whereas physical aggression was low in all three habitats and did not significantly differ between forest and plantation habitats (LRT: χ^2 = 2.11, df = 2, P = 0.35, N = 1535 focal observations of 50 individuals), non-physical aggression was significantly higher inside the plantation compared to the forest and plantation edge (LRT: χ^2 = 6.06, df = 2, P = 0.048, N = 1,535 focal observations of 50 individuals, Fig. 1c1-3, see Supplementary Tab. S1).
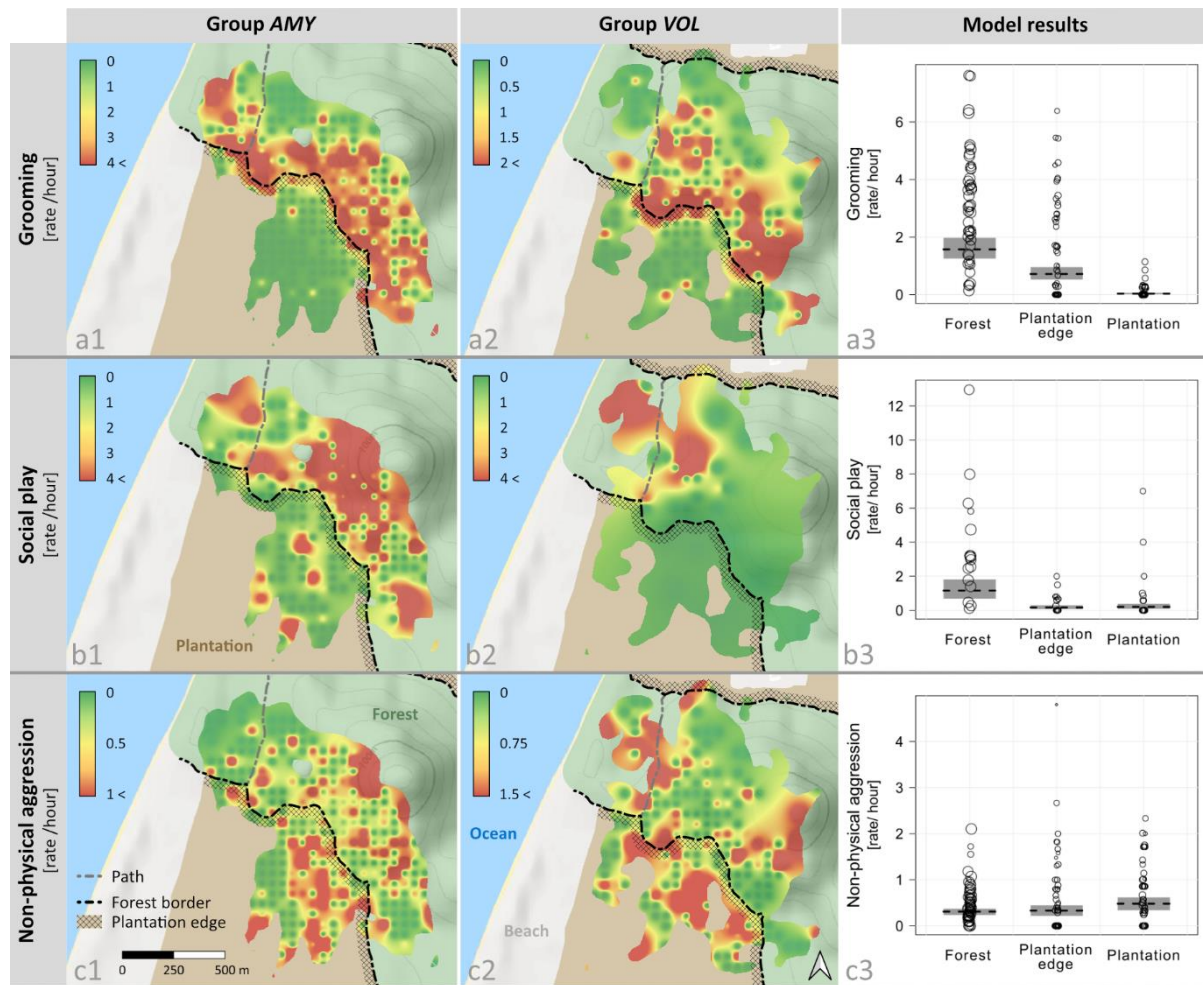
Figure 1. Rates of grooming (a), social play (b) and non-physical aggression (c) for Southern pig-tailed macaques at Segari, Peninsular Malaysia, shown for forest, plantation edge and plantation habitat. Interpolation maps indicate the mean rates per hour of grooming, social play and non-physical aggression, respectively, occurring during focal observations per 50 x 50 m grid cell within the home range areas of group *AMY* (1) and group *VOL* (2). Model results (3) indicate predictions of the behavioural rates in the different habitats. Circles represent observation values, averaged per individual and habitat, with circle areas corresponding to respective sample sizes. The dashed lines show the fitted model and the shaded areas its 95% confidence intervals, conditional on rank being on its average, and based on age-sex class, group and daytime manually dummy coded and then centred (N = 1535 focal observations of 50 individuals (36 of *AMY*, 14 of *VOL*) for grooming and non-physical aggression and 510 focal observations of 16 individuals (14 of *AMY*, 2 of *VOL*) for social play).
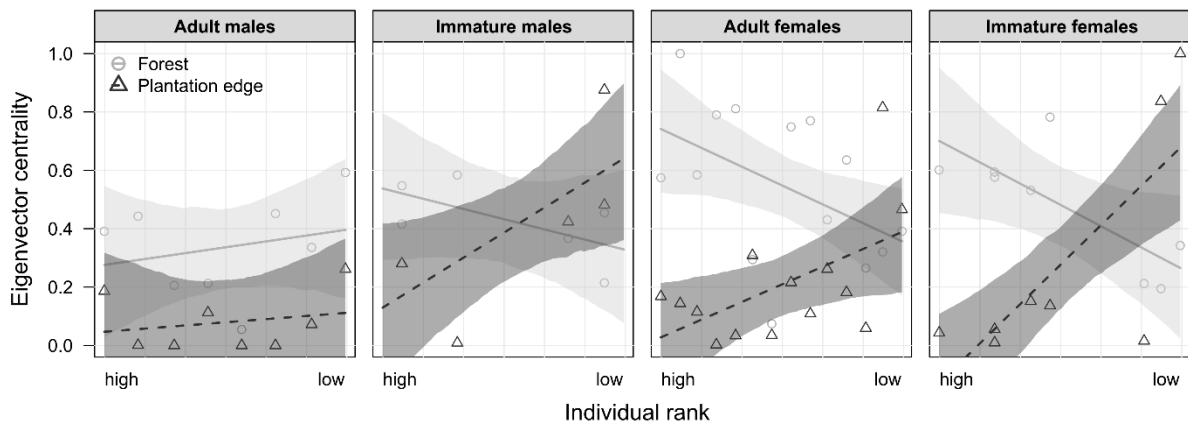
Social network in forest and oil palm plantation

In order to capture complex patterns of an individual's social role that go beyond frequencies of interactions, we further examined changes in the macaques' connectedness in social networks when ranging at the oil palm plantation compared to the forest. Therefore, we constructed social networks separately for each habitat based on dyadic affiliation which was measured as the proportion of proximity scans two individuals were in social contact (i.e. grooming, social play or affiliative body contact) during behavioural observations. With only 0.2% of scans including positive social contact, dyadic affiliation was nearly absent inside the plantation. In contrast, 14.9% and 7.5% of scans in the forest and at the plantation edge, respectively, included affiliative contact. Therefore, further

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161   analysis was limited to describing differences in social network parameters between forest and

162   plantation edge.

163   We used binary degree as a measure of partner diversity, reflecting the overall number of social

164   partners for each individual. This did not significantly differ between habitats, when controlling for

165   individual dominance rank, age-sex class and the sampling effort (χ^2 = 9.54, df =8, P = 0.30, N = 36

166   individuals). Mean partner diversities, i.e. the overall number of partners divided by the total number

167   of proximity scans per individual, were 0.048 and 0.050 for forest and plantation edge, respectively.

168   We further investigated relative changes in individual scores of eigenvector centrality (EC) between

169   habitats, uncovering in how far an individual's position in its social group may differ between forest

170   and plantation. Additionally, we explored whether such differences in network positions might be

171   dependent on an individual's socio-demographic attributes, particularly its dominance rank and age-

172   sex class. In contrast to partner diversity, EC significantly differed between habitats as indicated by

173   the likelihood ratio test (LRT: χ^2 = 11.50, df = 3, P = 0.009, N = 36 individuals). To account for inter-

174   dependency of network measures such as the EC, we additionally ran node-swapping permutation

175   tests which confirmed the significant effect of different habitats on EC (Tab. 1, Supplementary Fig.

176   S2). We found a significant three-way interaction between habitat, dominance rank and age-sex

177   class, with a clear, yet opposite, effect of rank on EC in different habitats. Specifically, EC decreased

178   with decreasing dominance rank in the forest, while it increased with decreasing rank at the

179   plantation edge. In other words, high ranking individuals were better connected compared to lower

180   ranking individuals when the group was ranging in the forest, while low-ranking individuals occupied

181   the most central positions in the group at the plantation edge. This combined effect of dominance

182   rank and habitat was found to be strongest for immature and adult females, moderate for immature

183   males and absent in adult males (Fig. 2).

184
185   **Figure 2. Eigenvector centrality as a function of individual rank.** Shown are individual scaled scores of eigenvector centrality,
186   separately for the forest and the plantation edge, and for adult and immature males and females, respectively. The lines show
187   the fitted model and the shaded areas its 95% confidence interval (N = 36 individuals).

188 Table 1. Results of the GLMM exploring the effect of habitat and its interaction with dominance rank and age-sex class on the
189 macaques' individual scores of eigenvector centrality (model 6). Shown are model estimates, standard errors (SE), lower and
190 upper confidence intervals (CI) as well as original and permuted p-values of the three-way interaction. Permuted p-values
191 were obtained by comparing the observed regression coefficients with a distribution of 1000 coefficients generated by
192 randomly swapping the nodes of the social network prior to extracting centrality scores. Significance is indicated in bold.

Predictor variable	Estimate	SE	lower CI	upper CI	P	$P_{permuted}$
Intercept	0.34	0.07	0.20	0.48		
Predictors included in interaction						
Habitat (forest = 0, plantation edge = 1)	-0.26	0.10	-0.45	-0.05	[d]	[d]
Rank[a]	0.04	0.07	-0.11	0.19	[d]	[d]
Age-sex class (adult ♂ vs. adult ♀)[b]	0.21	0.09	0.03	0.38	[d]	[d]
Age-sex class (adult ♂ vs. immature ♀)[b]	0.14	0.10	-0.06	0.35	[d]	[d]
Age-sex class (adult ♂ vs. immature ♂)[b]	0.10	0.11	-0.12	0.30	[d]	[d]
Two-way interaction						
Habitat[c] * rank	-0.02	0.10	-0.22	0.17	[d]	[d]
Habitat[c] * age-sex class (adult ♂ vs. adult ♀)[b]	-0.08	0.12	-0.33	0.15	[d]	[d]
Habitat[c] * age-sex class (adult ♂ vs. immature ♀)[b]	0.05	0.14	-0.22	0.34	[d]	[d]
Habitat[c] * age-sex class (adult ♂ vs. immature ♂)[b]	0.21	0.14	-0.11	0.50	[d]	[d]
Rank * age-sex class (adult ♂ vs. adult ♀)[b]	-0.17	0.09	-0.35	0.02	[d]	[d]
Rank * age-sex class (adult ♂ vs. immature ♀)[b]	-0.19	0.10	-0.39	0.003	[d]	[d]
Rank * age-sex class (adult ♂ vs. immature ♂)[b]	-0.11	0.10	-0.31	0.07	[d]	[d]
Three-way interaction						
Habitat[c] * rank * age-sex class (adult ♂ vs. adult ♀)[b]	0.27	0.13	0.008	0.52	0.038	**0.050**
Habitat[c] * rank * age-sex class (adult ♂ vs. immature ♀)[b]	0.43	0.14	0.15	0.74	0.002	**0.007**
Habitat[c] * rank * age-sex class (adult ♂ vs. immature ♂)[b]	0.26	0.14	-0.02	0.52	0.073	0.108

193 [a] z-transformed to mean = 0 and SD = 1 prior to model fitting; original mean (SD) was 0.50 (0.33).
194 [b] Reference level is adult male
195 [c] Reference level is forest.
196 [d] Values are not shown because of having a very limited interpretation as they are part of the interaction.

197

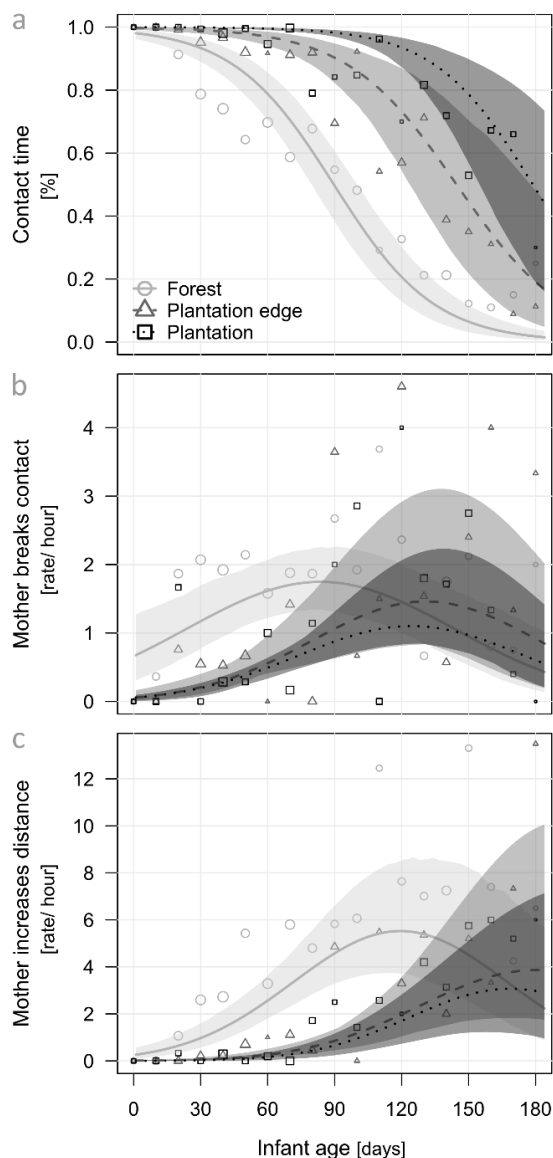198 *Mother-infant relationship in forest and oil palm plantation*

199 Looking at the smallest social units of the group, we studied affiliation between macaque mothers

200 and their dependent offspring as well as maternal behaviour encouraging infant independence. Both

201 were strongly influenced not only by infant age but also by the habitat the macaques were ranging

202 in.

203 The proportion of body contact between macaque mothers and their offspring significantly differed

204 between habitats, while controlling for infant age and sex, mothers' rank, parity and daytime (LRT: χ^2

205 = 45.02, df = 4, P < 0.001, N = 491 observations of 11 mother-infant pairs, for details see

206 Supplementary Tab. S2). As expected, contact time decreased with infant age, yet the start of this

207 decrease was highly dependent on the habitat (Fig. 3a). Specifically, body contact between mothers

208 and infants already decreased within the first month after infant birth in the forest, after one to two

209 months at the plantation edge, and only after approximately three months inside the plantation (Fig.

210 3a).

211 Examining to what extent mothers facilitate their infants' independence, we looked at three different

212 maternal behaviours, i.e. mother breaks contact, mother increases spatial proximity, and maternal

213 rejection. With a total of only 15 occurrences during focal observations, rejection was very rare in

8

macaque mothers and thus not considered for multivariate analysis. We further recorded 346

contacts broken by mothers and 838 events of mothers increasing spatial proximity to their

offspring. Infant age had a non-linear effect on both maternal behaviours, with the highest rates of

breaking contact and increasing spatial proximity being observed at an age between 3 to 5 and 4 to 6

months, respectively (Fig. 3b,c). As indicated by the full-null model comparisons, the rates of both

breaking contact and increasing spatial proximity, were significantly influenced by the habitat (LRT: χ^2

= 39.51/ 64.22 for breaking contact/ increasing spatial proximity, df = 6, P < 0.001, N = 491

observations of 11 mother-infant pairs, see Supplementary Tab. S2). Specifically, the significant

interaction between habitat and infant age indicates an earlier increase of mothers' facilitation of

infant independence in the forest than at the plantation (Fig. 3b,c). Accordingly, the maximum rates

of both behaviours were reached earlier in the forest compared to the planation habitats (Fig. 3b,c).

Overall, besides temporally shifted patterns, habitat type and infant age likewise affect both

maternal behaviours indicating the mothers' incentive to facilitate infant independence.

Figure 3. Contact time between macaque mothers and their dependent offspring (a) and maternal facilitation of infant independence, measured as rates of breaking contact (b) and increasing distance (c), as a function of infant age, shown separately for forest, plantation edge and plantation. The lines show the fitted model, separately for each habitat, the shaded areas their 95% confidence intervals, conditional on continuous control predictors being on their average, and based on infant sex and parity manually dummy coded and then centred. For visual clarity, infant age was binned into 10-day sections. The area of the points corresponds to the respective sample size (Total N = 491 focal observations of 11 mother-infant pairs).

Discussion

The present study provides important insights into the effects of anthropogenic environments on primate social behaviour, which is crucial to understand a species' ability to coexist with humans. Our results demonstrate the presence of behavioural alterations in the macaques' sociality while ranging at oil palm plantations, with social interactions being strongly affected at both the individual level and within mother-infant pairs. Specifically, macaques significantly reduced positive social interactions during plantation visits while increasing non-physical aggression, and experienced shifts in their social network structure with the central positions of high-ranking females and immatures of both sexes being passed to low-ranking individuals. Further, we found dynamics in the mother-infant relationship, with mothers being more protective at the plantation compared to the forest as indicated by higher proportions of body contact and less maternal behaviours facilitating infant independence.

Our results confirm previous studies, according to which oil palm plantations function as foraging and feeding ground for macaques[29,30,33]. Their motivation to enter plantations likely lies in the broad abundance of food, as previous studies suggested higher rates of plantation visits and extended plantation ranges during periods of lower fruit availability in the forest[33,34]. It may be further triggered by the high nutritional value of available food sources, as the macaques do not only feed on palm fruits, but also consume a high number of plantation rats[30], an excellent source of protein. Yet, highly clumped and energy-rich food sources may increase competition and aggression among animals[35,36], as also shown for urban and semi-provisioned primate groups[31,32]. This was partly confirmed by our findings, with non-physical aggression being significantly increased inside the plantation. However, no such effect was found for physical aggression, which is particularly rare in our study species, agreeing with *M. nemestrina*'s intermediate position between despotic (i.e. less tolerant) and egalitarian (i.e. more tolerant) macaque species[27].

Remarkably, socializing was rare at the oil palm plantation. Considering the socio-ecological risks posed by plantations (e.g. predation from feral dogs and raptors, human contact, or intense feeding competition) the macaques may restrict plantation visits to feeding activities and avoid time-consuming social affiliations, which can be carried out more safely in the protected environment of the forest. As previously reported for other primate species, close proximity to humans and/or direct interactions with humans in touristic or urban areas may evoke stress in animals[37,38] and significantly alter affiliative interactions[37,39]. Our results add to these findings by showing that also indirect human impact through the conversion of rainforest into agricultural land can profoundly affect primate sociality. We found rates of both grooming and social play to be close to zero inside the plantation and significantly reduced at the plantation edge compared to the natural forest habitat. However,

291   contrary to our expectations, the number of affiliative social partners did not differ between forest

292   and plantation edge. This finding is nonetheless consistent with those by Marty et al.[37], who revealed

293   that long-tailed macaques (*M. fascicularis*) living in human-impacted areas in Malaysia spend less

294   time grooming but preserved the same number of grooming partners under time constraints[37] (for

295   contradictory findings see [40]). This retention of partner diversity is critical since both strong

296   connections, i.e. frequent affiliative interactions, to an individual's favoured partners, but also a large

297   number of weak connections to many different partners play an important role for individual fitness

298   in Cercopithecine primates[41].

299   Typically, animal social networks are influenced not only by individuals' demographic characteristics

300   (e.g. age-sex class, dominance rank[42,43]), but also by extrinsic factors like their ecology (reviewed in [44])

301   or exposure to human impact[45], with particulatly the latter having been shown to decrease

302   cohesiveness and connectivity of wildlife social networks[46,47]. Here we extend previous findings, by

303   revealing how environmental modifications may *differentially* affect the network roles of individual

304   animals depending on their socio-demographic characteristics, using EC as a measure of social

305   integration. As the dispersing sex, male macaques generally have less central positions in the group[42],

306   while philopatric females strongly rely on being well integrated into an intact social network in order

307   to survive and successfully raise offspring[16]. As reported in previous studies, top-ranking females

308   occupy more central, i.e. socially connected, network positions, as they are attractive social partners

309   (e.g. by offering agonistic support in exchange for grooming)[48,49]. Consistent with this, we observed a

310   gradient in female centrality in the forest, with both high-ranking adult females as well as their

311   immature female offspring being the most central, best-connected individuals. Interestingly, this

312   relationship was reversed at the plantation edge, possibly due to high- and low-ranking females using

313   different strategies to handle high pressure posed by intense feeding competition at the plantation.

314   Reacting to time constraints, dominants may compromise on their affiliative social connections in

315   order to be more vigilant of competing conspecifics. At the same time, subordinates may increase

316   their affiliative network aiming at higher tolerance of dominant group members which may allow

317   them improved access to energy-rich food sources. In immature males, we observed a similar,

318   though less strong effect to that observed in females. This is unsurprising as immature males are still

319   integrated in the maternal network, holding their mothers' rank during childhood, yet they already

320   start to grow into their later role as the dispersing sex[20]. In contrast, centrality in adult males was not

321   affected by rank and habitat, potentially relating to their more peripheral positions in the group.

322   Behavioural modifications in the groups' smallest social units can negatively affect both macaque

323   mothers and their offspring. With mothers behaving more protective during plantation visits,

324   increasingly keeping body contact, infant independence may be delayed compared to the macaques'

325   natural behaviour. Yet, weaning ages in our study groups did not obviously deviate from the broader

326   literature (N. Ruppert, unpublished data) which suggests that weaning in macaques occurs at an age

327   of approximately twelve months[50]. Further studies could shed light on how potential delays in infant

328   independence may imply prolonged inter-birth intervals for macaques living in the forest-oil palm

329   matrix. On the other hand, alterations in mother-infant bonds may affect the development of infants.

330   Already during early development, offspring are prepared for their later sexual role in the group[20].

331   Particularly the young males' preparation for their later dispersal may be hampered by the increased

332   physical proximity between mothers and infants. Ultimately, the disruption of an intact mother-

333   infant relationship through plantation visits may imply negative consequences for offspring health

334   and survival. Long-term data from our field site revealed infant mortality within the first year of life

335   to be approximately 55% between 2014 and 2018, with the highest rate (71%) observed in 2016 (N.

336   Ruppert, unpublished data). This is unexpectedly high, considering that infant mortality in other

337   macaque species ranges between 2.7 and 32%[51–56]. However, our data are not sufficient to prove

338   whether infant mortality is directly connected to the macaques' ability to cope with human-induced

339   habitat changes.

340   This is the first study that provides thorough insight into the impact of oil palm cultivation on sociality

341   in wild primates. We observed behavioural plasticity in the macaques' overall network structure

342   through to the smallest social units of the group, demonstrating that anthropogenic impacts even

343   without frequent direct contact with humans may strongly restrict affiliative interactions among

344   macaques and potentially lead to delays in infant development. High rates of infant mortality and

345   prolonged inter-birth intervals may ultimately cause difficulties for endangered species to maintain

346   their viable population size. This is dramatic as most primate species globally suffer from population

347   decline due to habitat loss and fragmentation[3]. Only recently, *M. nemestrina* was classified as

348   Endangered by the IUCN[4]. In this context, it is essential to protect the remaining populations and

349   facilitate their coexistence with humans in anthropogenic landscapes. As umbrella species, primates

350   represent a wide range of other species characterizing primary rainforest. Hence, their protection

351   will ultimately contribute to maintain biodiversity and important ecosystem functions of tropical

352   habitats. Studying the effects of both direct and indirect anthropogenic disturbances on primate

353   social behaviour can serve as a basis for understanding the degree to which a species can adapt to

354   human-altered habitats and may aid in developing effective conservation strategies and species

355   management plans. Looking at the most important affiliative behaviours in primates, our results

356   suggest that the proximity to the forest is a key factor for macaques to be able to perform their

357   natural behavioural repertoire. Maintaining forest corridors, an important conservation tool to

358   create viable interfaces between forests and agricultural landscapes, may therefore not only

359   facilitate natural dispersal and link fragmented wildlife populations, but also enable animals to

display essential social behaviours, improving the well-being and ensuring the long-term survival of primates and other species.

Methods

Study site and subjects

From January 2017 to September 2018, we collected data on two habituated groups of wild Southern pig-tailed macaques (*M. nemestrina*) at the Segari Melintang Forest Reserve and the oil palm plantations bordering its south-western edge (4°19-20'N, 100°34-36'E). Its area comprises a total of 2742 hectares of which 408 hectares are strictly protected Virgin Jungle Reserve[29].

According to the macaques' dispersal regime, the size and composition of the study groups changed slightly during the study period, either due to male immigration or dispersal, animals dying or being born, or juveniles reaching sexual maturity. The average group sizes of group 1 (named *AMY*) and group 2 (named *VOL*) were 41 and 50 individuals, respectively (for details on group composition see Supplementary Methods). Both groups visited the plantation area bordering their forest habitat almost daily (mean ± SD (*AMY/ VOL*) = 3.1 ± 1.8/ 2.7 ± 1.8 hours per day)[30]. The annual home ranges of group *AMY* and *VOL* were 92.7 and 96.6 hectares, respectively, with used plantation areas accounting for approximately one third of the total home range areas[30]. As group *VOL* has not been fully habituated before the start of 2018, assessments of the macaques' social network and the mother-infant relationship were performed only on group *AMY*.

Behavioural data collection

In order to assess the impact of anthropogenic environments on the macaques' social activities, we divided the home range areas of our study groups into three habitats, i.e. forest, plantation edge and plantation (Supplementary Fig. S3). As plantation edge we defined the plantation area which is located within 50 metres from the forest border, whereas plantation refers to all plantation areas which have a distance of more than 50 metres from the forest border. This distinction was made to account for the fact that plantation areas in close proximity to the forest provide additional shelter and protection for the macaques through close-by forest vegetation. So-called ecotones that form transitional areas between two distinct ecological habitats were reported to be of great environmental importance, potentially serving as speciation and biodiversity centres[57]. We chose the distance of 50 metres according to the average diameter of the macaque groups' dispersion (edge-centre-edge).

392   <u>Individual focal sampling</u>: We collected data using 30-minute focal animal sampling[58] in the forest, at

393   the plantation edge and inside the plantation. We observed a total of 50 individually recognizable

394   macaques (36 of group *AMY*, 14 of group *VOL*). Focal individuals were chosen to represent all age-sex

395   classes. The order of focal observations was randomized, aiming at sampling each individual only

396   once per day. If a focal animal entered another habitat during a 30-minute sampling protocol or went

397   out of sight for more than ten minutes, this observation was stopped. Incomplete protocols were

398   considered for analysis if they lasted at least 15 minutes. Total observation time was 724 hours

399   (mean ± SD = 14.5 ± 3.6 hours per subject).

400   During focal observations, we continuously recorded the macaques' activity and social interactions

401   based on a species-specific ethogram established for the study species (adapted from Thierry et

402   al.[59]). Recorded activities included moving (i.e. locomotion without other activity), feeding (i.e.

403   ingesting food), foraging (i.e. searching for or manipulating food), resting (i.e. lying, sitting or

404   standing without other activity), socializing (i.e. all positive social interactions, e.g., grooming and

405   groom presenting, social play and huddling) and others (e.g. sexual and agonistic interactions or self-

406   grooming). We recorded the frequency, measured as rate per hour, and duration of all bouts of

407   grooming and social play between the focal subject and other group members. As measures of

408   frequency and duration were highly correlated (Pearson's r = 0.78/ 0.81, p < 0.001 for grooming/

409   social play), we considered only frequencies for analyses. Further, we recorded aggressive behaviour

410   exchanged between the focal subject and other group members, considering both physical (i.e.

411   attack, bite, grab, hit, push) and non-physical aggression (i.e. charge, chase, lunge, stare and vocal or

412   open mouth threat). Social data were complemented by *ad libitum* data[58] on aggression,

413   displacement and submission among adult males and adult females to construct dominance

414   hierarchies (see below). Data on social interactions included information on both the initiator and

415   the recipient. Following previous studies[60], a repetition of a behaviour was scored as a new bout if (i)

416   more than 10 seconds had elapsed between occurrences, or (ii) at least one partner had switched to

417   a mutually exclusive activity (e.g., from grooming to aggression). During an aggressive event in which

418   a number of different agonistic patterns occur in quick succession, only the most intense kind of

419   aggression was considered for analyses[60].

420   To assess affiliative social networks across different habitats, we recorded data on spatial proximity

421   between macaques. We took point time scans[58] every three minutes within the 30-minute sampling

422   protocol, recording all group members in body contact with the focal individual. We further recorded

423   whether or not this contact resulted from an affiliative interaction (e.g., during grooming, play or

424   huddling). This was the case for 98.3% of our observations. The total number of scans recorded was

425   14,205 (mean ± SD = 284 ± 71 scans per subject).

426 <u>Focal sampling of mother-infant pairs</u>: Additionally, we were able to observe eleven mother-infant

427 pairs from group *AMY* in the three different habitats for the first six months after infant birth. Total

428 observation time was 240 hours (mean ± SD = 21.8 ± 9.4 hours per mother-infant pair). We

429 continuously recorded maternal behaviour promoting infant independence[61]. Specifically, we

430 recorded the number of contacts broken (i.e. any movements disrupting body contact between

431 mother and infant), increases of spatial proximity (i.e. movements increasing the distance between

432 mother and infant from within arm's reach (about 60 cm) to outside of arm's reach) and maternal

433 rejection (i.e. attempts by the infant to make contact that were rejected by the mother, e.g., by

434 turning, running away, or holding the infant at a distance with an arm)[61]. To ensure independence

435 between these measures, increases of spatial proximity were only recorded if at least five seconds

436 elapsed since contacts were broken. To assess spatial proximity in mother-infant pairs we took point

437 time scans[58] every minute during focal observations, recording whether or not mothers and their

438 infants stayed in body contact, including ventro-ventral contact, nipple holding, side-by-side contact

439 and grooming.

440

441 *Occurrence of social interactions across habitats*

442 We collected individual location data with a Garmin GPSMAP62s daily during behavioural

443 observations, with the coordinates of each focal observation being taken at half-time of the

444 respective focal protocol. Annual home range areas of group *AMY* and *VOL* were adopted from

445 Holzner et al.[30], showing point Kernel Density Estimations (KDE) with 95% probability of use[62]. To

446 provide an overview on the occurrence of affiliative and aggressive social interactions across

447 different habitats within the macaques' home ranges, we created interpolation maps (see Fig. 2)

448 based on mean behavioural rates occurring during focal observations per 50 x 50 m grid cell using the

449 Inverse Distance Weighting (IDW) tool of the software QGIS (QGIS Development Team, 2020).

450

451 *Dominance hierarchy*

452 From 948 dyadic agonistic interactions with a clear winner and loser outcome collected during focal

453 and *ad libitum* observations, we estimated rank orders using David's scores[63] (for statistical details

454 see Supplementary Methods). As in macaques rank acquisition and function typically differ between

455 sexes, with non-natal males fighting for dominance, while females socially inherit the rank of their

456 mother[64], we estimated rank orders separately for males and females. Referring to literature[65],

457 immature males and females got assigned the same rank as their biological mother, or, if their

458 mother already died, the rank of their closest adult female relative.

459 *Social network analysis*

460 Based on affiliative interactions observed during individual focal sampling, we constructed the social

461 network of group *AMY* separately for forest and plantation habitats. Following Lehmann et al.[22], we

462 assessed dyadic affiliation as the proportion of scans two individuals were in social contact (i.e.

463 grooming, social play or affiliative body contact). We created social networks in R version 3.4.4 (R

464 Core Team 2020) using an undirected data structure with the function *graph_from_data_frame* from

465 the package 'igraph' (version 1.2.5)[66]. For each individual, we extracted the binary degree and

466 eigenvector centrality (EC), two commonly used network parameters to quantify individual social

467 connectedness[67,22]. The binary degree reflects an individual's overall number of interaction partners,

468 while EC is a measure of both direct and indirect network ties, reflecting a node's importance while

469 considering the importance of its neighbours. Thus, a high value of EC suggests that an individual has

470 many social partners who themselves also have many partners. While considering raw counts for

471 binary degree, with regard to EC we were particularly interested in an individual's connectedness in

472 relation to other group members. We therefore rescaled the obtained values of EC in each habitat to

473 get percentile scores lying between zero (minimum) and one (maximum).

474

475 *Statistical Analysis*

476 Multivariate statistical analyses assessing the impact of different habitats on the frequencies of

477 affiliation and aggression (models 1 to 4), social network parameters (models 5 and 6) and the

478 mother-infant relationship (models 7 to 9) were conducted in R version 3.4.4 (R Core Team 2020),

479 using Generalized Linear Mixed Models (GLMM)[68]. Models were fitted using the functions *lmer* and

480 *glmer* of the package 'lme4' (version 1.1.19)[69] with the optimizer *bobyqa*. To facilitate model

481 interpretation and convergence, we standardized all continuous predictors before model fitting to a

482 mean of zero and a standard deviation of one[70]. Full-null model comparisons were derived using

483 likelihood ratio tests (LRT)[71] using the R function *anova* with argument 'test' set to 'Chisq'[71]. Tests of

484 individual fixed effects were derived using the R function *drop1* with argument 'test' set to 'Chisq',

485 yet control predictors were not interpreted. Confidence intervals were derived using the function

486 *bootMer* of the package lme4 (version 1.1.19)[69], using 1,000 parametric bootstraps.

487 <u>Frequencies of affiliation and aggression (models 1 to 4)</u>: To investigate the impact of the habitat on

488 the display of grooming, social play, and physical and non-physical aggression, we constructed four

489 GLMMs[68] with Poisson error structure and log link function. As response variables we used the

490 number of grooming bouts (model 1), bouts of social play (model 2), bouts of physical aggression

491 (model 3) and bouts of non-physical aggression (model 4) per focal observation (N = 1,535 focal

492 observations of 50 individuals for models 1, 3 and 4, and N = 510 focal observations of 16 immature

493   individuals for model 2). The final model included the habitat (forest, plantation edge or plantation)

494   as fixed effect test predictor, while controlling for individual dominance rank and age-sex class (adult

495   male, adult female, immature male or immature female), as both rank and age-sex class have

496   previously been shown to affect the occurrence of affiliative and agonistic interactions in

497   macaques[20,48,72]. To account for changes in the overall group activity over the day, inter-group

498   variation and repeated observations of the same individuals, we further included the daytime,

499   divided into four time blocks (early morning: 7:00 - 09:59 am, late morning: 10:00 am - 12:59 pm,

500   early afternoon: 13:00 - 15:59 pm or late afternoon: 16:00 - 18:59 pm) and macaque group (*AMY* or

501   *VOL*) as fixed effect control predictors and the focal individual ID and sampling date as random

502   effects. Additionally, we included the random slopes of habitat and daytime within focal individual in

503   models 1 to 4 and the random slope of rank within sampling date in models 1, 3 and 4[71,73].

504   Controlling for differences in the sampling effort, we further included the duration of each focal

505   observation as an offset term into the models[74]. To test the effect of different habitats, we compared

506   the full models with respective reduced models lacking only our test predictor (habitat) using a LRT[71].

507   Binary degree and EC (models 5 and 6): To investigate the impact of the habitat on two common

508   network parameters, i.e. the binary degree and EC defined above, we constructed two GLMMs[68] with

509   Poisson and Gaussian error structure, respectively. As response variables we used the individuals'

510   binary degree (model 5) and scaled EC (model 6) in each habitat (N = 68 observations of 34

511   individuals). We included the habitat (forest or plantation edge) and its interactions with individual

512   dominance rank and age-sex class (as defined above) as fixed effects and the focal individual ID as

513   random effect. Controlling for differences in the sampling effort, we further included the total

514   number of point time scans per individual as an offset term into model 5[74]. To test the effect of

515   different habitats on the binary degree, we performed a LRT[71], comparing the full model with a

516   reduced model lacking our test predictor (habitat) and its interactions with dominance rank and age-

517   sex class. Using the scaled EC as response variable, we were specifically interested in the effect of the

518   three-way interaction between the habitat, dominance rank and age-sex class. Thus, we compared

519   the full model with a reduced model lacking only the three-way interaction using a LRT[71].

520   To account for inter-dependency of network measures used as outcome variables in our GLMMs, we

521   used a node-swapping permutation approach, based on 1000 permutations of the outcome

522   variable[18]. This included re-calculating the network parameters after randomly swapping the nodes

523   of the original networks. We used node-swapping (as opposed to generating random graphs or using

524   pre-network 'edge-swapping' randomizations) since this approach seemed better-suited for our

525   purposes of testing regression-based null-hypotheses in a taxon with a largely stable group

526   composition and relatively low observation biases[75,76]. Specifically, node-swapping preserves the

527 overall size, number of connections, and structure of the network, thereby also preserving the

528 overall distribution of node-level measures such as degree and EC. It is therefore a more conservative

529 approach that may be less susceptible to Type I errors, compared to random graph generation or

530 edge-swapping[75,76]. After each permuted swapping event, we re-fit the same GLMM using these

531 newly created parameters as response variable. Comparing the observed model coefficients with the

532 distribution of the 1000 permuted coefficients, we calculated p-values as the number of times the

533 coefficient value of the observed network is smaller than a randomized network, divided by the

534 number of randomizations[18].

535 <u>Mother-infant relationship (models 7 to 9)</u>: To investigate the impact of the habitat on the mother-

536 infant relationship, we constructed three GLMMs[68], with the proportion of body contact between

537 mothers and offspring (model 7), the number of maternal breaks of contact (model 8) and the

538 number of maternal increases of spatial proximity (model 9) per focal observation being the

539 response variables (N = 491 focal observations of 11 mother-infant pairs for models 7-9).

540 Investigating effects on the proportion of time spent in contact (model 7), we used a GLMM[68] with

541 binomial error structure and logit link function[68]. In R, this analysis of proportions is possible by using

542 a two-columns matrix with the number of contacts and non-contacts per individual as the

543 response[68]. Models 8 and 9 were created using a count response with Poisson error structure and log

544 link function. Here, we controlled for differences in the sampling effort by including the duration of

545 each focal observation as an offset term[74]. In all three models, we included the habitat (forest,

546 plantation edge or plantation) as a fixed effect test predictor, while controlling for infant and

547 maternal characteristics which were previously shown to affect the mother-infant bond, i.e. infant

548 age[61] and sex (male or female)[26], as well as maternal rank and parity (primiparous or

549 multiparous)[24,25]. As in models 1-4, we accounted for changes in the overall group activity over the

550 day by included the daytime as fixed effect control predictor. Further, we included the mother-infant

551 pair and sampling date as well as the combination of these two as random effects, as mother-infant

552 pairs were frequently observed more than once on a given day. Additionally, we included the

553 random slopes of habitat, infant age and daytime within the mother-infant pair[71,73]. As we expected

554 infant age to have a non-linear effect on the rates of maternal breaking contact and increasing spatial

555 proximity, we additionally incorporated squared infant age into models 8 and 9. Further, we included

556 the two-way interaction between habitat and infant age in model 7 and its interactions with infant

557 age and squared infant age in models 8 and 9. To test the effect of different habitats, we compared

558 the full models with the respective reduced models lacking our test predictor (habitat) and its

559 interactions with infant age and squared infant age, respectively, using LRTs[71]. In case of a non-

560 significant interaction, we re-ran the model without the interaction term to facilitate the

561 interpretation of the main effects in the model.

18

562 For models 1 to 9, we tested model stability and performed model diagnostics related to collinearity,

563 overdispersion in Poisson and binomial models and normally distributed and homogeneous residuals

564 in the Gaussian model. The assumptions were met in all models (for details on model diagnostics see

565 Supplementary Methods).

566

567 *Ethical note*

568 We obtained permits to study *Macaca nemestrina* from the Department of Wildlife and National

569 Parks Peninsular Malaysia (permit holder: Dean of School of Biological Sciences, Universiti Sains

570 Malaysia). We obtained permits to enter the forest reserve bordering the oil palm plantation from

571 the Forestry Department Peninsular Malaysia (permit holder: Asyraf Mansor, School of Biological

572 Sciences, Universiti Sains Malaysia). No written permit was needed to enter the plantations, but we

573 informed the local management about the study. This non-invasive study was conducted in line with

574 Universiti Sains Malaysia's animal ethics requirements.

575

586

587 **Declaration of interests**

588 The authors declare no competing interests.

589

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