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Moor Macaques (*Macaca maura*) Remember Earlier Habituation Despite Changes in Group Composition

Fiqhi Rahman[1] · Risma Illa Maulany[1] · Putu Oka Ngakan[1] · Cesar Rodriguez del Castillo[2] · Bonaventura Majolo[3] · Federica Amici[4,5]

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Habituation, in which repeated neutral contacts with human observers lead to reduced, and eventually no, response by primates, is commonly used to study animals in the wild (Williamson & Feistner, 2011). Understanding how habituation affects animal behaviour is important to better evaluate its ethical implications and to improve habituation methods. The time needed to successfully habituate study animals depends on several factors, including their socioecological characteristics, personality, and previous experience with humans (Allan et al., 2020; Williamson & Feistner, 2011). For example, animals that have previously experienced neutral exposure to humans may habituate more quickly than animals that have rarely encountered or have been threatened by humans (Sak et al., 2013; Hernandez-Tienda et al., 2022).

Very few empirical data exist concerning whether, or for how long, animals remain habituated when they are not continuously exposed to researchers. If the memory of habituation is long-term, animals should remain habituated after a period with no exposure to researchers. Moreover, when recontacted, animals should show a high proportion of neutral responses and a low distance to researchers if negative exposure to other humans did not attenuate habituation in the meantime (Prediction

Bonaventura Majolo and Federica Amici contributed equally to this work.

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✉ Federica Amici
amici@eva.mpg.de

[1] Forestry Department, Hasanuddin University, Makassar, Sulawesi, Indonesia

[2] Fundació UdG: Innovació i Formació, Universitat de Girona, Girona, Spain

[3] School of Psychology, University of Lincoln, Lincoln, UK

[4] Institute of Biology, Human Biology and Primate Cognition, Leipzig University, Leipzig, Germany

[5] Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

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1). In group-living species, changes in group composition, as a result of immigration during periods with no exposure to researchers, may reduce the overall habituation of the group, because not all individuals were initially habituated. However, if animals that were not previously habituated are more relaxed when other group members do not respond negatively to researchers, we might expect the study group to habituate more readily. Animals would initially show a low proportion of neutral responses and high distance to researchers after a period with no exposure to researchers, but their response would improve faster than during the first habituation (Prediction 2).

The outbreak of COVID-19 in 2020 provided us with the rare opportunity to test these predictions on a wild group of moor macaques (*Macaca maura*), which are endemic to Sulawesi, Indonesia. Our study group was located at Bara Beach (5°36'S, 120°26'E), South Sulawesi, in a seaside limestone secondary forest area of around 415,000 ha with access to cultivated fields and beaches (Hernandez-Tienda et al., 2022). The group was first habituated (phase 1) from October 2019 to March 2020 (Hernandez-Tienda et al., 2022), when it consisted of 41 individuals (6 adult males, 13 adult females and 22 immatures). We followed the macaques during 6-hr shifts starting at 6 AM or 12 PM. An encounter began when researchers located the group and established visual contact with the macaques and ended when we could not see any macaques. During each encounter, we recorded: 1) GPS location of the group; 2) date and encounter number; 3) number of researchers following the group; 4) number of visible macaques; 5) position of macaques when the encounter started (i.e., ground, trees or ≥2-m rocks); 6) whether the group showed a neutral response; and 7) the minimum distance between observers and macaques.

In March 2020, we interrupted the project to ensure the safety of the macaques and researchers during the pandemic. For 3 years, local researchers monitored the group occasionally, visiting the area about 20 times. It is likely that the group had regular contact with other humans (e.g., local farmers). Although we could not monitor the frequency and type of these interactions, we estimate (based on our non-published data from phase 1) that the majority of these interactions where neutral, but some competitive interactions also likely occurred (e.g., if macaques attempted to forage in a field). Moreover, construction workers spent several months clearing some trees along an existing road that passes through the study group's home range. In February 2023, when we resumed fieldwork, the study group consisted of 36 individuals (i.e., 8 adult males, 12 adult females, and 16 immatures). Of these, just over half of the adults (4 males and 7 adult females) were the same individuals as in 2020. The proportion of immatures was similar (0.5 in 2020, 0.4 in 2023), and the home range remained mostly unchanged (unpublished data). We habituated the animals again from February to May 2023 (phase 2) following the same procedure as in 2020.

To test our predictions, we ran two generalized linear mixed models in R (R Core Team, 2020; version 4.2.2) by using the glmmTMB package (Brooks et al., 2017). For model #1, we used a binomial distribution to analyse the occurrence of neutral responses to encounters. We entered the interaction between habituation phase (first or second) and encounter number (z-transformed) and their main effects as predictors. We entered the number of researchers (1–3) and macaques observed

(z-transformed), and their position (ground or tree/rock; Hernandez-Tienda et al., 2022) as controls, and the date as random factor (as there were more than one encounters per day). For model #2, the response variable was the minimum distance between macaques and researchers during encounters. This variable was strongly right-skewed, even after squared-root-, cube-root-, log-, inverse-, reciprocal-, and Box-Cox transformations. Using ordinal logistic regression after categorizing distance in 10-m intervals led to convergence issues in the models. We therefore treated the response as binomial, assigning 0 to encounters in which the minimum distance was higher than the median (15.0 m) and 1 to encounters where the minimum distance was lower or equal to the median. We used the same predictors, controls, and random factor as model #1. We used likelihood ratio tests to compare the two full models to null models that only contained controls and the random factor. If the full model was significantly better than the null, we used the drop 1 function to assess which predictors had a significant effect on the response, and the emmeans package (Lenth, 2020) to explore the significant interaction. We found no convergence or collinearity issues in the models presented (all VIFs $\leq$1.89).

Phase 1 lasted 119 days and included 5339 encounters. During this phase, the mean probability of neutral responses increased from 50% in the first 30 encounters to 80% in the last 30 encounters, whereas the minimum distance (mean $\pm$ SD) between researchers and macaques decreased by 6.7 m from 20.2 $\pm$ 8.3 m to 13.5 $\pm$ 3.5 m. Phase 2 was shorter, including 60 days and 1,122 encounters, as animals appeared to habituate more quickly. During this phase, the mean probability of neutral responses increased from 17% in the first 30 encounters to 57% in the last 30 encounters, whereas the minimum distance decreased by 7 m, from 27.8 $\pm$ 6.9 m to 20.8 $\pm$ 3.6 m. Thus, a similar decrease in the minimum distance between researchers and macaques was obtained much faster in phase 2 than in phase 1, that is, it required one fourth of encounters in phase 2 compared with phase 1. Both full models were significantly better than the null models ($p < 0.001$; Tables S1, S2). The probability of neutral responses and the probability of coming closer than the median distance to macaques increased with the number of encounters in both phases but more quickly in the second than in the first habituation phase ($p \leq 0.004$; Fig. 1).

Contrary to Prediction 1, macaques were less likely to be tolerant to researcher proximity and to show neutral responses at the start of habituation phase 2 than at the start of phase 1. Although this result may suggest that the macaques did not remember the earlier habituation, it also may be linked to the roadwork that occurred during the pandemic. This prolonged disruptive and noisy human activity in their home range may have made the macaques more fearful of humans. This possibility is supported by the finding that macaque responses improved faster during phase 2 than they did in phase 1, in line with Prediction 2. This suggests that previous experience of neutral exposure to researchers facilitated the second habituation phase; previously habituated animals might have selectively responded to researchers, quickly improving their response to them in the second phase and thereby also positively affecting the reaction of the macaques that had not been previously habituated. The steeper changes in the second phase are unlikely to be due to the specific group composition or home range in the second phase (e.g., groups with a higher proportion of immatures or smaller home ranges might habituate more quickly), as

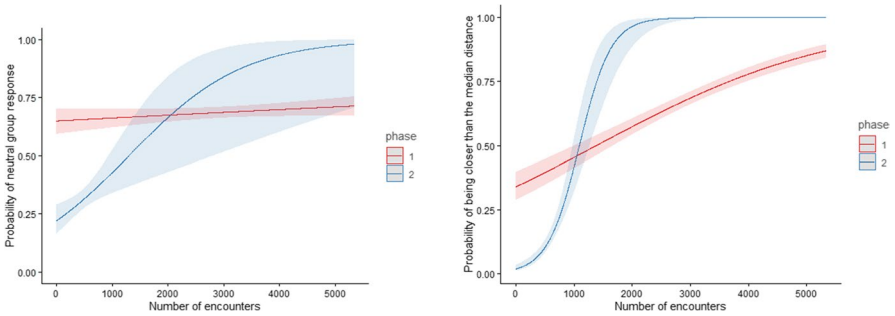

Fig. 1 For each of the two habituation phases, the probability of neutral group responses (**a**) and the probability of researchers coming closer to macaques than the median distance (15.0 m) (**b**), as a function of the encounter number in a wild group of moor macaques (*Macaca maura*) observed at Bara Beach, in South Sulawesi, Indonesia, from October 2019 to March 2020 (phase 1) and from February to May 2023 (phase 2). The lines represent the fitted models for the two phases, that is, model #1 (left) and model #2 (right), but unconditional on all the controls (which were standardized to visualize the effect of the predictor independently on the controls), and the corresponding shadings the 95% confidence intervals of the estimates. Phase 2 lasted 1,122 encounters, so that the model line for the further encounters represent a prediction for this phase.

the proportion of immatures was similar in the two habituation phases, and the home range of the study group remained mostly unchanged.

In the future, we should seek to better understand whether social learning facilitates the habituation in macaques, like in chimpanzees, *Pan troglodytes* (Samuni et al., 2014). Moreover, it will be important to disentangle how single individuals react to the habituation process, as there might be important differences depending on age, personality, or sex (Bertolani & Boesch, 2007). Finally, we need to determine whether primates respond selectively to researchers, as our results would suggest, or whether habituation generally increases the likelihood of their interactions with humans, which would imply higher risks for habituated groups.

Ethical note

This study was purely observational. Researchers never fed, interacted or were in contact with the monkeys, and always maintained a distance of ≥10 m from them (i.e., remaining still if monkeys approached closer than 10 m, and stepping back if they came closer than 5 m). The habituation procedure was approved by the Indonesian Foreign Research Permit Division, Ministry of Research and Technology/National Research and Innovation Agency, and by the Faculty of Forestry, Hasanuddin University. This study adhered to the American Society of Primatology Principles for the Ethical Treatment of Nonhuman Primates.

Data availability Data and script can be obtained from the corresponding author on reasonable request by email.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-023-00413-3.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

References

Allan, A. T. L., Balley, A. L., & Hil, R. A. (2020). Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Science*. *Advances, 6*, eaaz0870.

Bertolani, P., & Boesch, C. (2007). Habituation of wild chimpanzees (Pan troglodytes) of the South Group at Taï Forest, Côte d'Ivoire: Empirical measure of progress. *Folia Primatologica, 79*(3), 162–171.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., & Bolker, B. M. (2017). glmmTMB Balances speed and flexibility among packages for zero-inflated generalized linear mixed _odelling. *The R Journal, 9*, 378–400.

Hernandez-Tienda, C., Majolo, B., Romero, T., Illa Maulany, R., Ngakan, P. O., Beltrán Francés, V., Gregorio Hernandez, E., Gomez-Melara, J. L., Llorente, M., & Amici, F. (2022). The habituation process in two groups of wild moor macaques (*Macaca maura*). *International Journal of Primatology, 43*, 291–316.

Lenth R (2020) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.0. See https://CRAN.R-project.org/package=emmeans

R Core Team (2020). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing.

Sak, B., Petrzelkova, K. J., Kvetonova, D., Mynarova, A., Shutt, K. A., Pomajbikova, K., Kalousova, B., Modry, D., Benavides, J., Todd, A., & Kvac, M. (2013). Long-term monitoring of microsporidia, cryptosporidium and giardia infections in western lowland gorillas (*Gorilla gorilla gorilla*) at different stages of habituation in Dzanga Sangha protected areas. *Central African Republic. PLoS ONE, 8*, e71840.

Samuni, L., Mundry, R., Terkel, J., Zuberbühler, Z., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition, 17*, 997–1005.

Williamson, E., & Feistner, A. (2011). Habituating primates: Processes, techniques, variables and ethics. In J. Setchell & D. Curtis (Eds.), *Field and laboratory methods in primatology: a practical guide* (pp. 33–50). Cambridge University Press.