on continuous rotation, for a five minute duration each time. During foraging, we recorded the type of food item processed, noting whether the subject was cracking a sessile oyster or unattached gastropod, and recording the species whenever possible. We counted the number of prey items consumed per focal observation time of 5 min and conservatively estimated an average foraging time of 4 h (during low tide) per individual to extrapolate the number of shellfish items eaten per day (and per year) on Koram Island. We used the amount of daily prey consumption on Koram Island to estimate the total foraging pressure that one tool-using macaque can place on the prey population. We used this same value to estimate foraging pressure for the neighboring NomSao population, for which long-term focal observations were not available (Tan and Luncz, personal communication). We then used our data on snail abundance per island to extrapolate the potential time needed to deplete the existing prey population. For that calculation we multiplied the length of suitable coastal foraging areas per island with an average width of foraging grounds of 3 m. We used the resulting area and the number of snails found per surveyed square meter to estimate the total number of snails available on each island.

4.3 Statistical analyses

4.3.1 Tool choice
To analyze whether the weights of tools selected to crack open oysters differed between the two observed populations we used a linear mixed model (LMM) (Baayen, 2008). In this model, we included the population as fixed effect and individual ID as random effect. As response we used the weight of the stone tools. Prior to running the model, we square root transformed the response variable to achieve a more symmetrical distribution.

We also tested whether the weight of tools used to crack open snails differed between the two populations. As we had no information on the individuals that used the stones, we ran a linear model (LM). Into this model, we included the population as fixed effect and individual ID as random effect. As response we used the weight of the stone tools. To achieve a more symmetrical distribution, we log transformed the response variable prior to running the model.

To test whether the size of a given maturity stage (immature or mature) differed between the two populations we ran a linear model (LM) with the size category as fixed effect. As response we included the prey species into the model as well as the two-way-interaction between island and snail maturation stage. To increase the confidence of the linear mixed model and the linear model analyses, we ran a permutation test in which we randomized the assignment to the island for each individual. We did this 10000 times and compared the distribution of the revealed permutation results with the original test statistic to determine p-values.

For all models, we checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. In both models, we found no obvious deviations from these assumptions.

For the LMM, we additionally checked for model stability by excluding each individual at a time from the data. A comparison of the model estimates derived for the reduced data with those derived by the full data set indicated no influential cases to exist. For the LM, we tested model diagnostics using the R functions ‘dfmiss,’ ‘dfbeta,’ and ‘cooks.distance’, and we additionally checked for leverage and did not find any assumptions violated.

The p-values for the fixed effects were based on a likelihood ratio test (LRT), comparing the full with the model reduced by the fixed effect (Dobson and Barnett, 2002; Barr, 2013) using the R function anova with argument test set to ‘Chisq’ and in case of the LM’s to ‘F’. To allow for a LRT, we fitted the LMM using Maximum Likelihood (rather than Restricted Maximum Likelihood) (Bolker et al., 2009). For the third model (investigating snail maturation), we tested for the significance of our full model using a LRT by comparing the full with the null model (model reduced by all fixed effects).

The models were implemented in R (version 3.2.3) (R Development Core Team, 2010). The LMM was fitted using the function lmer of the R package lme4 (Bates and Maechler, 2010) and the LM using the function lm.

4.4 Impact on prey
To compare oyster size between the two islands, we bootstrapped the measured oyster sizes for each island 1000 times and compared the confidence intervals at the level of 95% to each other. To test for differences in snail size between the islands, we conducted the same procedure for two snail species (C. bifasciatus (N_{NamSao} = 101, N_{Koram} = 119); P. sulcatus (N_{NamSao} = 100, N_{Koram} = 123)). To compare the availability of the different snail species between islands for each species individually, we bootstrapped the number of snails we found on each transect 1000 times and compared the confidence intervals at the level of 95% between the islands.

To compare stone availability and stone size separated for island and location we bootstrapped i) the number, and ii) the weight of the stones we found per transect 1000 times and compared the confidence intervals at the level of 95% between the islands. For each test, we additionally applied two sample t-tests. All bootstraps and t-tests were implemented in R (version 3.2.3).
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REFERENCES


Branch GM, Odendaal F. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, Cymbula oculus, relative to protected areas on the population dynamics of a


Carpenter A. 1887. Monkeys opening Oysters. Nature 36:53. DOI: https://doi.org/10.1038/036053d0


Fernandes MEB. 1991. Tool use and predation of oysters (Crassostrea rhizophorae) by the tufted capuchin, Cebus apella appella, in brackish water mangrove swamp. Primates 32:529–531. DOI: https://doi.org/10.1007/BF02381944


Gumert MD, Malaviijitnond S. 2013. Long-tailed macaques select mass of stone tools according to food type. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120413. DOI: https://doi.org/10.1098/rstb.2012.0413


DOI: https://doi.org/10.1002/ajp.20342


DOI: https://doi.org/10.1016/j.jasrep.2016.05.040


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