Sniffing behavior of semi free-ranging Barbary macaques (*Macaca sylvanus*)

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Abstract

Olfaction is one of the evolutionarily oldest senses and plays a fundamental role in foraging and social interactions across mammals. In primates, the role of olfaction is now well recognized, but better investigated in strepsirrhine and platyrrhine primates than in catarrhines. We observed the sniffing behavior of semi-free ranging Barbary macaques, *Macaca sylvanus*, at Affenberg Salem, Germany, to assess how frequently macaques sniff and in which contexts, and how sniffing is affected by sex and age. Focal observations of 24 males and 24 females aged 1 to 25 years showed that Barbary macaques sniffed, on average, 5.3 times per hour, with more than 80% of sniffs directed at food. Irrespective of the context, younger individuals sniffed more often than older ones. Females' sniffs were more often directed at food than male sniffs, while males sniffed more often than females in a social context. Sniffs at conspecifics occurred primarily in a sexual context, with 70% of social sniffs directed at female anogenital swellings performed by males. Of the observed 176 anogenital inspections, 51 involved sniffing of the swelling. Olfactory inspections were followed by copulation significantly less often than merely visual inspections, suggesting that anogenital odors provided additional information guiding male mating decisions. In sum, results show that Barbary macaques routinely use olfaction during feeding, but also in a social context. Our study further suggests that odors may guide mating decisions, but the role of olfaction in sexual interactions warrants further investigations.

Keywords

olfaction, macaques, sniffing, anogenital inspection, copulation

Introduction

Primates, like other mammals, use various sensory modalities to gain information about their social and physical environment. Olfaction is one of the evolutionarily oldest senses and represents an important pathway of information transfer that is used in fundamental behaviors such as foraging (e.g. capuchin monkeys (*Cebus imitator*), Melin et al. 2019), predator avoidance (e.g. mouse lemurs (*Microcebus murinus*), Suendermann et al. 2008) or mating (e.g. ring-tailed lemurs (*Lemur catta*), Boulet et al. 2010).

Among primates, optic convergence and stereoscopic vision represent significant parts of their evolution, accompanied by a relative shrinking of the olfactory apparatus (Kay 2018). Thus, it was long assumed that olfaction is of little relevance in taxa with advanced visual capabilities. Accordingly, the role of olfaction has been studied more intensely in strepsirrhine primates, which are often nocturnal, possess less specialized vision and more developed olfactory structures (Barton 2006) than other taxa. For example, it is well-established that odor plays an important role in their sociality by providing information about sex, age or group membership (Janda et al. 2019; Scordato & Drea 2007) as well as in their foraging behavior (Cunningham et al. 2021; Rushmore et al. 2012). However, it has become increasingly evident that diurnal primates, including haplorrhine primates, may rely strongly on olfaction in a range of contexts. In platyrrhines particularly, several species use active olfaction (i.e. sniffing)

in feeding situations, and olfaction may be modulated by visual information. For example, white-faced capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi)* sniff fruits that give cryptic visual cues about their ripeness more often than less cryptic ones (Nevo & Heymann 2015; Hiramatsu et al. 2009). Moreover, olfaction also plays a role in the sociality of platyrrhine species, including in the context of mating. For instance, anogenital odor secretions of female common marmosets (*Callithrix jacchus*) vary with fertile phases and males inspect peri-ovulatory odors more intensely than odor samples from follicular and luteal phases (Kücklich et al. 2019).

Catarrhine primates show trichromatic vision in both sexes along with only half the number of olfactory receptor genes and relatively smaller olfactory bulbs compared to strepsirrhine primates (Niimura et al. 2018). In this taxonomic group, the assumption of 'microsmatic' primates has persisted over decades (Smith & Bhatnagar 2004). However, a more recent viewpoint suggests that features like the number of olfactory genes are not always predictive of olfactory sensitivity (Smith & Bhatnagar 2004; Laska et al. 2007a; Matsui et al. 2010) and that olfactory behavior is prevalent in many species (Jänig et al. 2018; Vaglio et al. 2021). Furthermore, the importance of proportionally smaller olfactory bulbs has been questioned, because the mere proportional correlation of body size to organ size and, therefore, function may not apply in olfactory systems (Smith & Bhatnagar 2004). In addition, the traditionally assumed separation of the main and the accessory olfactory system appears to be vaguer than previously thought (Sipos et al. 1995; Petrulis et al. 1999).

88 Hence, it is not surprising that research has also started to focus on the
89 involvement of olfaction in catarrhine sociality and ecology (Matsumoto-Oda et al.
90 2007; Setchell et al. 2010; Vaglio et al. 2021; Rigaill et al. 2022). For instance, rhesus
91 macaques (*Macaca mulatta*) as well as chimpanzees (*Pan troglodytes*) were shown to
92 differentiate between group and non-group members when presented with samples of
93 body odor (Henkel et al. 2015; Henkel & Setchell 2018). In mandrills (*Mandrillus*
94 *sphinx*), group members infected with parasites were discovered to have a different
95 fecal odour than non-infected members, whereby healthy individuals avoided the fecal
96 matter of infected conspecifics and avoided grooming them (Poirotte et al. 2017). Both
97 in the wild and in captivity, chimpanzees were observed to sniff at food as well as at
98 conspecifics. While females used olfaction to inspect food more frequently than males
99 did, males were observed to sniff more often in a social and sexual context than
100 females, which was attributed to their fission-fusion society and the high level of male
101 competition (Matsumoto-Oda et al. 2007; Jänig et al. 2018). Hence, evidence is
102 accumulating that catarrhine primates also rely on olfaction in a range of contexts, but
103 the number of studies and species investigated remains low, thereby hampering a
104 more general understanding of the role of olfaction in catarrhine lives.
105 To contribute to closing the knowledge gap regarding olfaction in catarrhine
106 species, the present study investigated the natural sniffing behavior of Barbary
107 macaques (*Macaca sylvanus*), a catarrhine species native to northern Africa and
108 Southern Europe. Their diet consists of various plants as well as insects (Fooden 2007).
109 Like many other catarrhine species, Barbary macaques live in multi-male, multi-female
110 groups and show a promiscuous mating system (Modolo & Martin 2008). They are

111 sexually active year-round, but show increased sexual behavior during the mating
112 season from late autumn to late winter (Kuester & Paul 1992). Females show a
113 conspicuous visual fertility signal, the anogenital swelling, which is directly linked to
114 estrogen levels and reaches its maximum size during the most fertile phase (Brauch et
115 al. 2007). Nonetheless, observations of genital inspections by looking, sniffing and
116 touching, as well as mating behavior suggest that males may have more than visual
117 information available to determine female fertility (Young et al. 2013).

118 Hence, we aimed to investigate sniffing behavior in Barbary macaques in
119 different contexts (feeding, social and non-social), and to examine possible variation in
120 sniffing behavior related to sex and age. We hypothesized that individuals who benefit
121 more from olfactory information than others would sniff more frequently, with distinct
122 difference between sexes, age and context. Similar to a study in chimpanzees (Jänig et
123 al. 2018), we, hence, predicted that 1) male Barbary macaques sniff more in the social
124 context than females, with males sniffing particularly females, given that the
125 anogenital swelling was suggested to be a probabilistic cue of fertility (Brauch et al.
126 2007) and olfactory information would be beneficial in male mating competition. By
127 contrast, we predicted 2) females to sniff edible items more frequently than males, as
128 females are energetically more constrained, similar to findings in female chimpanzees
129 (Matsumoto-Oda et al. 2007). More stringent food inspection has been shown to
130 benefit the long-term reproductive success of females by lowering contamination risks
131 (Rolff 2002; Poirotte et al., 2019). With regard to age, we predicted 3) younger Barbary
132 macaques to sniff more frequently than older individuals irrespective of the context.
133 Infants and juveniles are in a process of learning about their environment and

134 conspecifics surrounding them. Hence, olfactory information could be beneficial for
135 exploring and gaining experience in all contexts, as observed in great apes (Jänig et al.
136 2018). We also assessed the role of olfaction in inspection behavior of the female
137 sexual swelling and hypothesized an involvement of olfactory information in male
138 mating decision, as male Barbary macaques are suggested to rely not only on swelling
139 size but other information to recognize the female fertile phase (Young et al. 2013). In
140 particular, we predicted that sniffing in the sexual context is influenced by 4) male age,
141 with olfactory inspections being more prevalent in younger males which may lack the
142 experience in visually assessing anogenital swellings and may therefore be more prone
143 to attend to additional cues. Furthermore, the fertility and reproductive success of
144 female Barbary macaques as well as other primates varies across age, with higher
145 variability in interbirth intervals in young females and a decline in reproductive
146 performance from mid age to old age (Paul et al. 1993, Campos et al. 2022).
147 Accordingly, we also predicted that sniffing in the sexual context is affected by 5)
148 female age, with olfactory inspections being aimed more often towards young and old
149 females whose fertility status may be uncertain to the respective male compared to
150 those of prime age. Finally, olfactory inspections were frequently followed by
151 copulations in olive baboons (*Papio anubis*) when females were in their fertile phase
152 but not when they were post-fertile (Rigaill et al. 2013). Hence, we expected that 6)
153 olfactory inspections would affect copulatory behavior in Barbary macaques, although
154 we were not able to address this aspect in as much detail as by Rigaill et al (2013) given
155 that we did not have systematic data on the fertile state of the females during our
156 study period.

157 **Methods**

158 Study site

159 The study was conducted at Affenberg Salem close to Lake Constance,
160 Germany, which is home to ~ 200 Barbary macaques living in 20 hectares of fenced
161 forest year-round under near-natural conditions, allowing continuous full contact
162 between animals. The park is open to visitors from March to November. Visitors are
163 restricted to a path in one third of the enclosure, while the monkeys can roam freely
164 across the entire area. For more details on the park, see de Turckheim & Merz (1984).
165 The monkeys feed on natural vegetation and insects and receive daily supplements of
166 fruits and vegetables. Furthermore, wheat is distributed widely on and around the
167 clearings and meadows where the food is distributed. Water is accessible at several
168 ponds and water troughs *ad libitum*. The park is home to three naturally formed social
169 groups, each consisting of 50-70 individuals of both sexes and all age classes. All
170 monkeys are individually identifiable by tattoos and natural markings. To control
171 population size, about two thirds of the adult females receive subcutaneous hormonal
172 implants (Implanon NXT), which contain etonogestrel to inhibit the release of egg cells
173 from the ovaries by reducing the luteinising hormone level and impede entry of sperm
174 into the uterus. Implanted females show cyclical changes in anogenital swelling size
175 similar to non-contracepted females (B.M.W., personal observation). This study was
176 purely observational and in accordance with the legal requirements of Germany, all
177 national and institutional guidelines for the care and use of animals, and adhered to
178 the American Society of Primatologists (ASP) Principles for the Ethical Treatment of
179 Non-Human Primates.

Behavioral observations

Observations of sniffing behavior were conducted between October 17, 2020, and December 6, 2020, and thus, from the onset of the mating season to its peak (Fooden 2007). We observed 48 focal animals from two of the three groups. Focal animals comprised 24 females and 24 males from ages 1 to 25 (supplementary table S1), and thus covered all age classes, from juveniles (up to 2.5 years of age, N = 6) and subadults (up to 4.5 years of age, N = 9) to adults (5 years and older, N = 33, Kuester et al. 1995; Paul & Kuester 1990). 13 of 18 adult focal females had hormone implants. Each focal animal was observed six times for 20 minutes over the study period (total observation time = 48*2 hours = 96 hours). For each focal animal, three of six observations occurred in a feeding context (defined as at least ten minutes of feeding per protocol) and three in a non-feeding context. We spread the timing and context of observations per focal animal as equally as possible over the study period by observing the majority of individuals once before moving on to the next set of observations, and by conducting the subsequent observation of a given individual in a different context than the previous one whenever possible. During the focal protocols all instances of sniffing as well as details about the targets of sniffing were recorded. Observations were randomly distributed across the available daylight hours from 08:00 am to 05:00 pm. Because our study involved focal animals in the field, it was not possible to record data blind.

All focal observations were recorded with a digital video camera (Panasonic HC-V180) by one observer (M.S.). If the recorded subject moved out of sight during filming, the video was usually discarded. In 11 instances, two shorter videos were

203 combined as one observation if the first video was of substantial length (around ten
204 minutes). Seven individuals were juveniles who proved to be harder to film as they
205 were more playful and tended to climb the trees out of sight, while three individuals
206 were adult males that were rather shy and more difficult to observe. For these
207 individuals we combined videos if the second video was recorded in a similar
208 behavioral context, on the same day and was of sufficient length to complete the 20
209 min observation. For eight out of the 11 instances filming was resumed within 30
210 minutes, and for the remaining three instances up to 4.5h after the end of the first
211 video. Sniffs were scored from the videos using the recorded video image as well as
212 commentaries verbally recorded onto the video during the focal observations (see Tab.
213 1 for ethogram). We followed Jänig et al. (2018) in assigning each sniff recorded in the
214 videos to one of three target categories: food, social (sniffs directed at a conspecific or
215 its excretions) or other (sniffs directed at the environment, human-made objects and
216 self-sniffs). We also noted the target object of each observed sniff and the behavior of
217 the monkey after the sniff. All videos were analyzed by one observer (M.S.), however,
218 five percent of the data were also analyzed by an additional observer trained by M.S.
219 to check for inter-observer reliability. The audio-track of the video was unavailable to
220 the second coder to avoid bias. By comparing the respective observed sniffs, the intra-
221 class correlation coefficient (ICC) was calculated and revealed good reliability
222 (ICC=0.86; Koo & Li 2016).
223 Besides the focal video protocols, *ad libitum* data were collected for every sniff
224 that was observed outside the focal observations for focal and non-focal animals.
225 Furthermore, whenever inspections of female swellings by males were observed, the

following data were noted *ad libitum*: male and female ID, group, date, time, whether visual and/or olfactory inspection occurred and which inspection happened first, and if inspection was followed by a copulation (Tab. 1).

Table 1 Ethogram of observed behavior in this study

Behavior	Description
Sniff	individual bringing their nose ≤ 3cm towards an object/conspecific/themselves or touching an object with the hand and then bringing the hand towards the nose
visual inspection	males focusing on the female anogenital swelling from a close range ≤= 1m
olfactory inspection	a sniff (as defined above) directed at the female anogenital swelling
copulation	male mounting female and thrusting

Statistical Analysis

Statistical analysis was conducted in R version 4.0.3 (R core team 2020) using Generalized Linear Mixed Models (GLMM) to allow accounting for repeated observations of the same individuals (Bates et al. 2015). We conducted three sets of models that were fitted by using the function ‘glmer‘ from the package ‘lme4‘ version 1.1-31 (Bates et al. 2015).

Model A: Sniffing frequencies

The aim of model A was to investigate the influence of sex, age and context on sniffing frequencies and, hence, to test our predictions 1), 2) and 3). Accordingly, we used 'number of sniffs' as the response variable, fitted with a Poisson error distribution. To be able to compare sniffing frequencies between our predictors, we extracted three sniffing frequencies, i.e., the number of sniffs at food, the number of

245 sniffs at social targets and the number of sniffs at other targets separately from each
246 20min focal observation (N = 288 focal protocols x 3 target categories = 864 sniffing
247 frequencies). Data collected *ad libitum* was not used in this model. Sex, age (years),
248 observational context and target category ('food', 'social' or 'other') were fitted as
249 fixed effects test predictors. Observational context referred to the context 'feeding' or
250 'non-feeding' in which each protocol was recorded, while target category referred to
251 the object that was actually sniffed at, irrespective of whether the general
252 observational context was feeding or not. Group, daytime and Julian day were fitted as
253 fixed effects control predictors. Daytime was coded as morning (until 12:30 pm) or
254 afternoon (after 12:30pm). Julian day was included to control for the progress of the
255 mating season. Several two-way interactions were included in the model: I) sex and
256 target category to address the prediction that males sniff more in a social setting and
257 females more on food; II) sex and Julian day, since the observational period started at
258 the early beginning of the mating season and ended at its height. Therefore, male and
259 female sniffing behavior could show different patterns from the beginning to the end
260 of the observation period; III) observational context and target category, because the
261 observational contexts 'feeding' or 'non-feeding' presumably influence the probable
262 targets of sniffing; IV) age and target category, to account for the possibility that age
263 affects which objects the monkeys sniff at, and V) daytime and target category, as
264 fresh food got distributed every morning at 08:00 and we accordingly expected more
265 sniffs at edible items in the morning than in the afternoon. Individual ID and the ID of
266 the observational protocol were included as a random effects control terms. To
267 achieve more reliable p-values (Barr et al. 2013), we fitted random slopes of all

predictors showing sufficient variation within the respective random intercept, i.e., the random slopes of Julian day, context*target category, and daytime*target category within individual ID, and target category within protocol ID.

Model B: Olfactory inspection of females

The aim of model B was to investigate the influence of female and male characteristics and the progression of the mating season on whether male inspections of female sexual swellings included olfaction or not (N = 176 genital inspections) and therefore our predictions 4) and 5). For this purpose, we fitted a GLMM with binominal error distribution using all genital inspections observed during focal observations as well as those recorded during *ad libitum* sampling, comprising data from 35 sexually mature and 3 immature males and from 37 sexually mature females. Female age (linear and squared) and male age, whether or not the female was contracepted and Julian day were fitted as fixed effects test predictors, while daytime and group were included as fixed effects control predictors. The two-way interactions of male age and female age (linear and squared), respectively, were included to account for the possibility that an effect of male age on olfactory inspection could be modulated by the age of the female partner in a linear or non-linear fashion. We also included an interaction between male age and contraception to address the possibility that inexperienced males might be more prone to gather additional cues about female fertility. Female and male ID were included as random effects control terms. For the random effect of male ID, the random slopes of Julian day, female age and contraception were incorporated. For female ID, the random slopes of Julian day and male age were included.

Model C: Genital inspections and copulation

Using focal and *ad libitum* data as described for model B, model C was fitted with binominal error distribution to investigate the influence of female and male characteristics and the occurrence of olfactory inspection on whether or not a genital inspection was followed by a copulation (N = 176 genital inspections) and, hence, test prediction 6. Female and male age, contraception (yes/no) and olfactory inspection (yes/no) were fitted as fixed effects test predictors while daytime, group and Julian day were included as fixed effects control predictors. We initially incorporated four two-way interactions: I) female and male age; II) female age and olfactory inspection; III) Julian day and olfactory inspection and IV) contraception and olfactory inspection. However, the interaction terms were too imbalanced, which caused stability issues (see general model procedures for stability checks), and were therefore removed again from the model. After removing all interactions, the model showed no stability issues. Female and male subject were included as random effects control terms. For the random effect of male ID, we included Julian day, olfactory inspection, contraception and female age as random slopes. For female ID, we included Julian day, olfactory inspection and male age as random slopes.

General Model Procedures

For all models, covariates were z-transformed to a mean of zero and a standard deviation of one before running the models to facilitate interpretation of model coefficients and model convergence (Schielzeth 2010). Variance Inflation Factors (VIF)

were computed using the function ‘vif’ of the package ‘car’ (Fox & Weisberg 2019) to check for collinearity between the predictors (Quinn & Keough 2002). With largest VIFs of 1.08 (model A), 1.3 (model B) and 1.1 (model C), no collinearity issue could be detected in either model. All three models were tested for over- and underdispersion, with resulting dispersion parameters of 0.12 (model A), 0.87 (model B), and 0.65 (model C). As model A and C were underdispersed, the computed p-values should be considered as conservative (i.e. potentially biased towards higher p-values). Model stabilities were assessed by excluding levels of random effects one at a time. As mentioned above, with the exception of model C when fitted with interactions, none of the models showed stability issues.

A Likelihood Ratio Test (LRT) was used to determine the effects of the test predictors on the response variables by comparing the null model without fixed effects test predictors to the respective full model containing all predictors (Dobson, 2002; Forstmeier & Schielzeth 2011). If the full-null model comparison was significant ($p < 0.05$) or a trend ($p < 0.1$), the p-values of the individual predictors were afterwards determined by using the function ‘drop1‘ from the package ‘lme4‘ version 1.1-31. This function determines p-values by dropping single terms from the model and compares results with and without the respective predictor using LRTs (Bates et al. 2015). We computed pseudo-R^2 values for Generalized Mixed-Effect models for the fixed effects (marginal R^2) and for all model terms (conditional R^2) to assess how much variance is explained by the models. R^2 values were computed using the function 'r.squaredGLMM' from the package 'MuMIn' version 1.47.1, using the recommended trigamma method for Poisson, and delta method for binomial models. To facilitate

interpretation of the main terms, interactions with a $p > 0.1$ were removed from the models, but only after conducting the respective full-null model comparison to ensure that predictions were tested with all predictors included. We report results for the dropped interactions in Tables 3 and 4. We computed 95% confidence intervals for all terms that remained in the model with parametric bootstrapping (n = 1000 simulations) using the 'bootMer' function from the package 'lme4' version 1.1-31.

Results

In total, 511 sniffs were observed across all focal observations (96 hours total observation time), with 1.78 ± 1.70 (mean ± SD) sniffs per individual per 20 min observation period (corresponding to 5.34 sniffs per hour). Females were observed to sniff a total of 314 times (mean ± SD: 6.54 ± 8.7 per hour) and males 197 times (mean ± SD: 4.11 ± 5.43 per individual per hour, see Tab. 2). The vast majority of sniffs (83%) observed during focal observations was directed at food items (423/511), while 8% (40/511) and 9% (47/511) were directed at social or other targets, respectively (Tab. 2).

Table 2 Number of sniffs observed at different targets for 48 focal animals in 96 hours of focal observations

Sniffer sex	Food	Social	Other	Sum
Male	150	29	18	**197**
Female	274	11	29	**314**
Sum	**423**	**40**	**47**	***511***

In the target context ‘food’, 49 different identifiable edible items (see supplementary table S2) were observed to be inspected via olfaction by the monkeys.

In 288 (68%) of the 423 cases, the edible item was eaten after sniffing it, while it was discarded in the remainder. When food items had already been bitten into or torn apart (observable in 128 cases), they were eaten 89 times and thrown away 39 times after sniffing them. Items that appeared to be fresh (observable in 27 cases) were eaten 20 times and thrown away 7 times after sniffing. No corresponding data were collected on edible items that were not sniffed at, hence these results are only of a descriptive nature and were not further analyzed statistically.

Social sniffs were directed at a female swelling in 70% (28/40) of cases (26 by adult males, 2 by adult females). Eleven of the social sniffs were directed at an infant (1 by an adult male, 7 by adult females and 3 by another infant). One sniff was directed at a juvenile male by a five-year old male. Of the 47 sniffs at 'other' targets, 27 were self-sniffs, almost exclusively directed at their own hand after scratching themselves, 14 were directed at the environment (e.g. tree branch or ground) and 6 at human-made objects (e.g. bottle cap, camera trap).

In addition, 136 sniffs were observed *ad libitum*, of which 70 were directed at food, 44 at conspecifics and 22 at other targets. Of the 136 sniffs, 41 were observed for infants too young to identify. 87 sniffs were observed for identifiable individuals, with distributions across sex and age classes similar to data recorded during focal observations. Moreover, 52 sniffs were recorded for females, with 36 being directed at food, 8 at conspecifics, mostly infants, and 13 at themselves or the environment. Finally, 30 sniffs were recorded for males, with 16 being directed at food, 10 at conspecifics and four at themselves or the environment. Sniffs observed *ad libitum*

included 18 cases of infants sniffing at their mother's, or in one case their grandmother's, mouth while they were eating.

Model A: Sniffing frequencies

The test predictors in model A had a significant effect on the number of sniffs at a given target per individual per observation (LRT, N = 864, $\chi2$ = 203.45, df = 14, P < 0.001, marginal R^2 = 0.309, conditional R^2 = 0.864). Specifically, sniffing frequencies differed between the sexes, whereby the effect of sex tended to depend on the target of the sniff. In particular, more sniffs were directed at food and 'other' targets by females compared to males. Males, on the other hand, sniffed more often at social targets than females (see Tab. 2 & 3, Fig. 1). We observed more sniffs during feeding than during non-feeding focal follows. Furthermore, younger individuals sniffed significantly more often than older individuals (Tab. 3, Fig. 2).

Table 3 Results of the GLMM (model A) investigating sniffing frequency (number of sniffs) per focal animal, observation period and target category as response variable with Poisson error distribution (N = 288 observations x 3 target categories = 864). Terms in parentheses indicate trait levels relative to the respective reference level. Values for dropped interactions represent values before removal of the respective terms from the model. SE = standard error, CI = confidence interval. χ^2 and P values are derived from Likelihood Ratio Tests to determine the significance of the individual test predictors

term	**Estimate**	**SE**	**CI 2.5**	**CI 97.5**	**χ2**	**P**
Intercept	-0.088	0.223	-0.523	0.353	†	†
test predictors						
sex (male)	-0.588	0.207	-1.035	-0.182	†	†
target category (other)	-6.941	1.469	-8.477	-6.43	†	†
target category (social)	-6.177	1.188	-8.43	-6.13	†	†
age	-0.374	0.108	-0.549	-0.173	10.991	0.001
observ. context (non-feeding)	-1.160	0.210	-1.491	-0.689	31.154	<0.001
control predictors						

group (2)	0.105	0.205	-0.258	0.462	0.265	0.606
Julian day	-0.302	0.110	-0.477	-0.098	7.528	0.006
daytime (morning)	0.768	0.192	0.355	1.071	13.087	<0.001
interactions						
target category*sex					4.697	0.096
target category (other)*sex (male)	0.493	2.185	-0.237	1.562		
target category (social)*sex (male)	1.739	1.424	0.302	2.172		
dropped interactions						
sex (male)*Julian day	-0.274	0.197			2.019	0.155
observ. context*target category					4.482	0.106
context (non-feeding)*target (other)	2.015	0.931				
context (non-feeding)*target (social)	0.071	1.000				
age*target category					0.707	0.702
age*target (other)	-0.335	0.513				
age*target (social)	-0.228	0.430				
daytime*target category					2.591	0.274
daytime(morning)*target (other)	-1.141	0.892				
daytime(morning)*target (social)	-0.787	0.732				

† not presented because of having a very limited interpretation

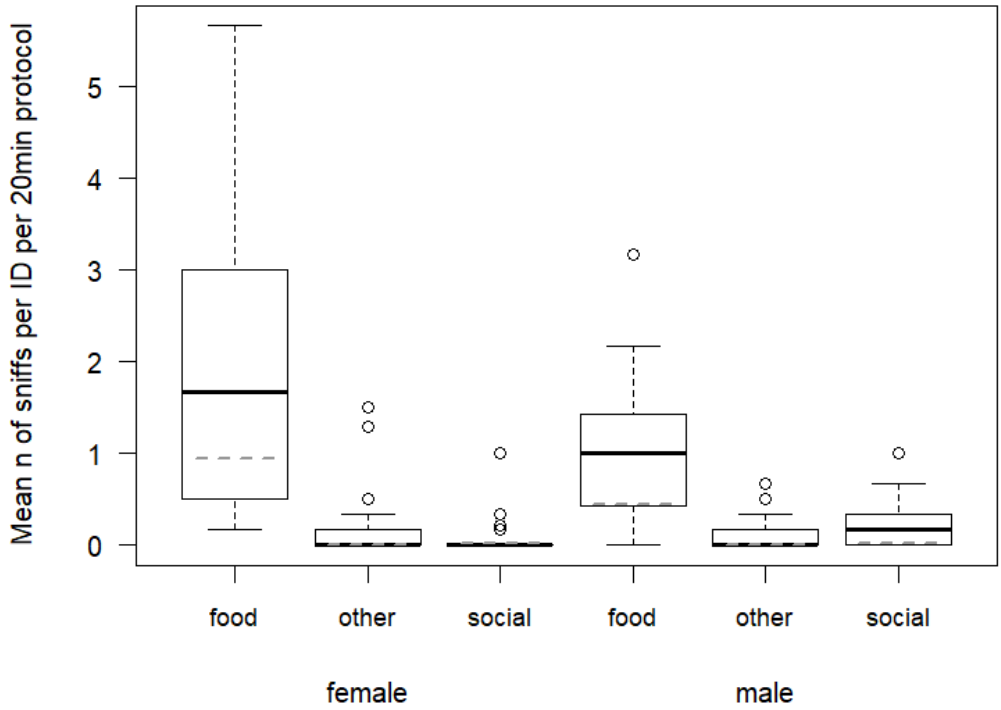

Fig. 1 Mean number of sniffs per individual per 20 min focal observation for both sexes divided into the target categories food, other and social. Boxes represent medians and first and third quartiles, while the whiskers represent 1.5 times the interquartile range. Outliers are represented by data points. The horizontal dashed lines represent the model estimates when all other predictors are at their average.

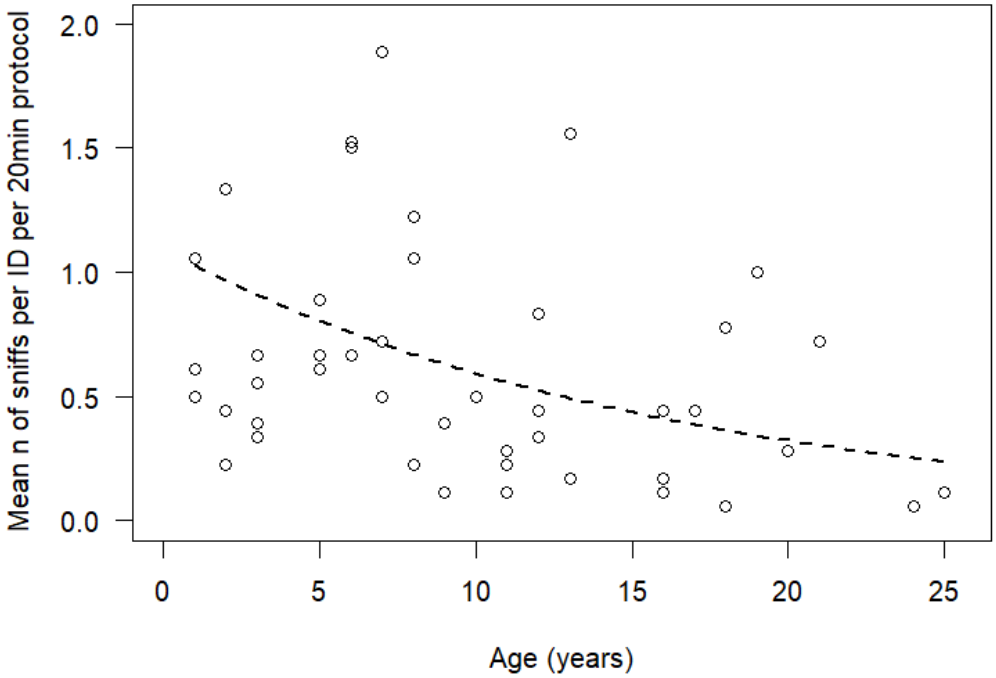

Fig. 2 Mean number of sniffs per individual per 20 min focal observation across age. The dashed line represents the model estimate when all other predictors are at their average

Of the control predictors, Julian day and daytime significantly affected sniffing frequencies (see Tab. 3). In particular, we observed more sniffs earlier in the season and in the morning than in the afternoon. None of the other predictors had a significant influence on sniffing frequencies (Tab. 3).

Model B: Olfactory inspection of females

Data on male inspections of sexual swellings, collected *ad libitum* as well as from focal observations, showed that out of 176 observed visual inspections, 51 were accompanied by an olfactory inspection of the swelling. The full-null comparison of model B investigating which parameters affected the occurrence of olfactory inspections revealed a trend (LRT, N = 176, $\chi 2$ =15.262, df = 8, P = 0.054, marginal R^2 =

423 0.212, conditional R^2 = 0.411). Specifically, the interaction between male age and
424 contraception tended to influence the probability of an olfactory inspection (Tab. 4),
425 whereby younger males generally tended to sniff slightly more during an inspection
426 than older ones, but this effect was more pronounced when inspecting non-
427 contracepted females (Fig. 3).

428 **Table 4** Results of the binomial GLMM (model B) investigating the probability of an olfactory
429 inspection during genital inspections (N = 176 inspections). Values in parentheses indicate trait
430 levels relative to the respective reference level. Values for dropped interactions represent
431 values before removal of the respective terms from the model. SE = standard error, CI =
432 confidence interval. χ^2 and P values are derived from Likelihood Ratio Tests to determine the
433 significance of the individual test predictors

Term	Estimate	SE	CI 2.5	CI 97.5	χ2	P
Intercept	-1.7391	0.726	-5.981	-0.505	†	†
test predictors						
male age	-1.2686	0.5249	-4.826	-0.563	†	†
female age	0.425	0.2628	-0.071	1.271	2.461	0.117
female age^2	0.2542	0.1708	-0.163	0.861	2.041	0.153
contraception (yes)	0.7468	0.7714	-0.762	4.872	†	†
control predictors						
Julian day	-0.1512	0.2441	-0.854	0.445	0.355	0.552
daytime (morning)	0.222	0.4129	-0.757	1.181	0.271	0.603
group (2)	-0.715	0.5745	-2.208	0.677	1.269	0.260
interactions						
male age*contraception (yes)	1.0138	0.599	0.01	4.366	2.998	0.083
dropped interactions						
male age*female age	0.363	0.262			1.954	0.162
male age*female age^2	0.018	0.197			0.009	0.925

† not presented because of having a very limited interpretation

434

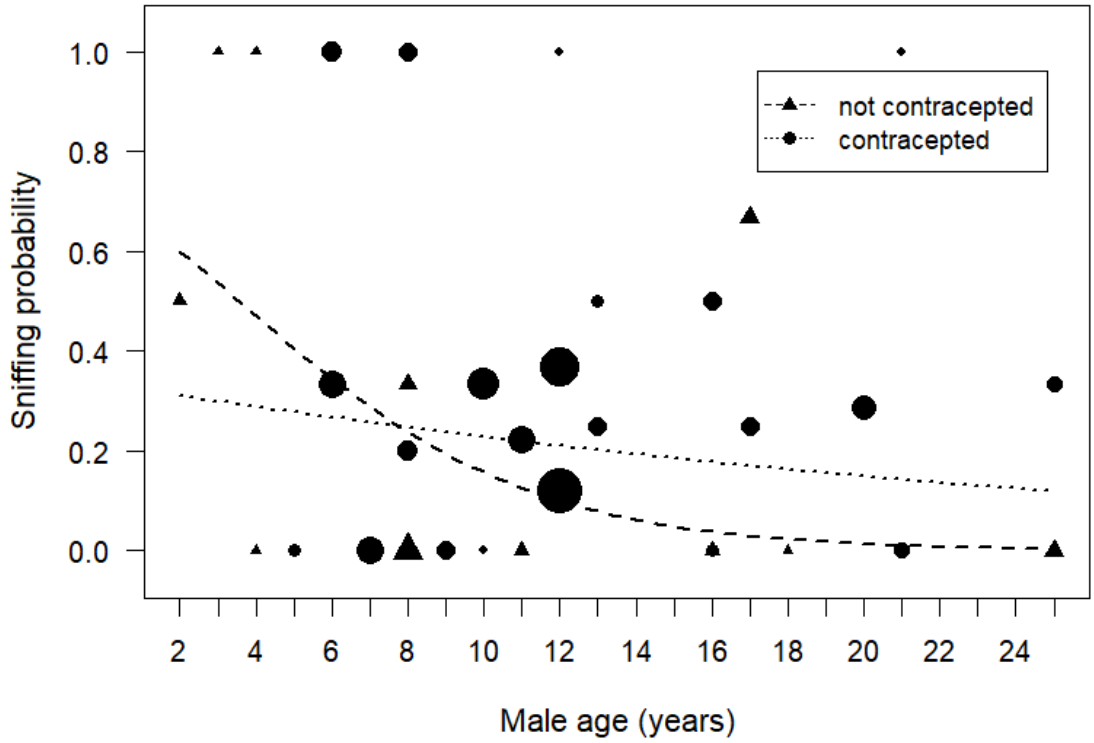

Fig. 3 Sniffing probability during an anogenital inspection as a function of male age and female contraception (triangles: non-contracepted, circles: contracepted females). The lines represent the model estimate when all other predictors are at their average (dashed line: non-contracepted females, dotted line: contracepted females). Symbols are scaled relative to sample size (range 1-25 inspections).

Model C: Genital inspections and copulation

Whether genital inspections were followed by a copulation was significantly affected by the suite of test predictors in model C (after excluding interactions from model due to stability issues (see methods), LRT, N = 176, $\chi 2 = 31.951$, df = 4, $P < 0.001$, marginal $R^2 = 0.357$, conditional $R^2 = 0.513$). In particular, olfactory inspection of the swelling significantly decreased the probability of copulation after inspection (Tab. 5). In fact, only 2 of the 51 visual *and* olfactory inspections were followed by a copulation, while copulation followed genital inspection in 44 of the 125 solely visual genital inspections. Furthermore, female age also influenced the copulation

probability, with copulations more likely after inspections of younger females than older females (Tab. 5).

Table 5 Results of the binomial GLMM (model C) investigating the probability of a copulation following a genital inspection (N = 176 inspections). Values in parentheses indicate trait levels relative to the respective reference level. SE = standard error, CI = confidence interval. χ^2 and P values are derived from Likelihood Ratio Tests to determine the significance of the individual test predictors

Term	Estimate	SE	CI 2.5	CI 97.5	χ2	P
Intercept	-0.280	0.705	-2.452	1.701	†	†
test predictors						
olfactory inspection (yes)	-3.330	1.020	-31.929	-2.326	22.169	<0.001
male age	-0.104	0.287	-1.061	0.671	0.120	0.729
female age	-0.862	0.339	-2.550	-0.182	5.268	0.022
contraception (yes)	-0.708	0.810	-3.506	1.311	0.660	0.417
control predictors						
Julian day	-0.486	0.314	-1.478	0.266	1.860	0.173
daytime (morning)	-0.516	0.467	-2.184	0.651	1.001	0.317
group (2)	0.411	0.645	-0.968	2.558	0.321	0.571

† not presented because of having a very limited interpretation

Discussion

This study contributes to understanding the sniffing behavior of Barbary macaques and thereby, catarrhine primates in general. In particular, we show that the frequency of sniffs varied with sex, age and context, in line with the hypothesis that individuals who benefit more from olfactory information than others sniff more frequently.

With an average of 5.3 sniffs per hour and individual, Barbary macaques sniffed at similar rates as some guenon species (*Cercopithecus diana, neglectus* and *hamlyni*) observed in captivity (6.1 sniffs/h, Zschoke & Thomsen 2014). In contrast, sniffing rates reported for chimpanzees in captivity were considerably lower (0.2 sniffs/h, Jänig et al. 2018) and even lower for chimpanzees observed in the wild (0.04 - 0.11 sniffs/h

470 depending on season, Matsumoto-Oda et al. 2007). Furthermore, sniffing frequencies
471 in Barbary macaques were not constant, but decreased over the course of the study.
472 Along with different sampling conditions (wild *vs.* captivity, focal *vs.* group sampling)
473 and the sparse availability of similar studies with different primate species, this makes
474 meaningful comparisons between species difficult, calling for more studies on a wider
475 range of species to assess interspecific patterns.
476
477 Influence of context & target
478 In our study, the vast majority of sniffs were directed at food, which parallels
479 findings for great apes (Jänig et al. 2018), guenons (Zschoke & Thomsen 2014) as well
480 as mandrills and olive baboons (Laidre 2009). Primates have been suggested to steadily
481 rely on olfactory cues to find and identify ripe food (e.g., Nevo & Heymann 2015),
482 obtain information about nutritional value (Dominy et al. 2001), determine food safety
483 and notice possible contamination (Sarabian et al. 2020). Hence, it comes as no
484 surprise that an almost exclusively herbivorous species like the Barbary macaque
485 shows frequent olfactory assessment of edible items. We were unable, however, to
486 systematically assess why certain items were sniffed and others were not. Captive
487 squirrel monkeys (*Saimiri sciureus)* and spider monkeys (*Ateles geoffroyi*) were
488 described to rely mostly on visual cues when assessing familiar food items whereas
489 novel food was more likely to prompt olfactory inspections (Laska et al. 2007b). In line
490 with this suggestion, we observed a disproportional number of sniffs at hay and a
491 chestnut provided by the park (data not shown), both of which were only rarely
492 available to the monkeys. However, we did not systematically collect data on how

493 often which types of food and other plants were available and therefore cannot
494 address whether Barbary macaques really sniffed more frequently at novel or rare
495 food items in this study.
496
497 Influence of sex and age
498 The tendency that an effect of sex on sniffing probability is modulated by the
499 target of a sniff supports prediction 1) that male Barbary macaques sniff more often in
500 a social context than females do. Such an imbalance in social sniffs was also observed
501 in other primate species such as chimpanzees (Jänig et al. 2018; Matsumota-Oda et al.
502 2007) and owl monkeys (*Aotus nancymaae*; Spence-Aizenberg 2017). Chimpanzees live
503 in multi-male multi-female groups with fission-fusion dynamics and high levels of
504 male-male competition for access to fertile females, enhancing the need for olfaction
505 in the social context (Jänig et al. 2018; Matsumota-Oda et al. 2007). For Barbary
506 macaques, which also live in multi-male multi-female groups, almost all social sniffs by
507 adult males were observed to be directed at female sexual swellings and only one at
508 another adult male. Thus, olfaction likely plays a role in male sexual competition for
509 fertile females by, for example, providing information about the ovarian cycle, in
510 addition to the visual signal of swelling size. However, sniffing does not seem as
511 important for males to gather direct information about other males. Similarly, only in
512 two instances a female was observed to sniff another female's anogenital swelling. In
513 both males and females, it could therefore be argued that an intra-sexual assessment
514 of potential competitors either is not particularly relevant in such a highly promiscuous
515 species, or that such an assessment is achieved using other sensory modalities.

516 Possibly, aspects such as a male competitor's size or female condition are more readily
517 assessable using visual (Setchell et al. 2008; Tschoner 2015) or auditory cues (Pfefferle
518 et al. 2008; Engelhardt et al. 2012).

519 Female Barbary macaques, on the other hand, sniffed more at food than males,
520 supporting prediction 2). This corresponds to observations of female chimpanzees
521 (Matsumota-Oda et al. 2007). Moreover, female primates of various species tend to be
522 more wary than males of contamination risks for parasites or bacteria through food
523 that is rotten or spoiled with feces (Sarabian et al. 2015; Sarabian et al. 2020; Poirotte
524 et al. 2019), as evident from more olfactory inspection of contaminated food, followed
525 by food manipulation (Sarabian et al. 2020). This behavior was rewarded by lower
526 infection rates of females (Poulin 1996; Rolff 2002; Poirotte et al. 2019), suggesting
527 that more visual or olfactory inspections, even though potentially costly, maximize the
528 health, and therefore, also reproductive success of females. Similar mechanisms might
529 apply to Barbary macaques, but a systematic analysis of parasite occurrence in both
530 sexes would be needed to assess this possibility.

531 Furthermore, our prediction 3) of young individuals sniffing more often than
532 older ones was supported with our data. These findings agree with the consensus that
533 young animals inspect their environment more closely than older individuals because
534 they are still in the process of learning to evaluate food, conspecifics or their general
535 environment, and are comparable to observations in great apes (Jänig et al. 2018).
536 Because the decrease of sniffing events with age in Barbary macaques appears to be
537 quite linear rather than showing a sharp drop at old age (see Fig. 2), it is unlikely that it
538 is primarily caused by a loss of olfactory capability at older age. Rather, this decrease

539 may be caused by changes in experience and/or individual requirements. Particularly
540 in the context of food assessment, sniffing frequencies may decrease as animals gain
541 experience with different food items and conditions and learn to assess food quality
542 based on visual or tactile cues. Additionally, it could be assumed that older females
543 reaching post-reproductive age do not need to be as careful of contamination risks as
544 females who still experience pregnancy and rear their young.

545 Together, 18 of 22 social sniffs that were observed for infant monkeys during
546 *ad libitum* data collection were directed at the feeding mother's, or in one case the
547 grandmother's, mouth. In each case the infants appeared to observe the eating
548 behavior and tried to inspect the item visually. They were not chased off and the
549 mothers reacted with indifference to the inspection attempt of their infant. This
550 'muzzle-muzzle' behavior has been observed in different mammals, including primates,
551 and may enable the individuals to smell the breath of their conspecifics while they are
552 eating (Nord et al. 2021; Arakawa et al. 2013; Laidre 2009). In this way they may gather
553 information on which food has been deemed safe and valuable to eat by their
554 conspecific.

555

556 <u>Olfaction in sexual interactions</u>

557 Most social sniffs occurred in a sexual context and were directed at the female
558 anogenital swelling, whereby about one third of inspections observed included
559 sniffing. In line with prediction 4, younger males tended to sniff more frequently
560 during an inspection than older ones, particularly if the inspected female was not
561 contracepted. Although we observed contracepted females to show similar swelling

562 sizes and patterns of tumescence and detumescence as non-contracepted ones (M.S.,
563 B.M.W. personal observations), this suggests that there may have been subtle
564 differences in the visual appearance of the swellings that males could pick up upon.
565 The nature of these differences and how they modulated sniffing behavior in an age-
566 dependent fashion warrants further investigation. In contrast to prediction 5, however,
567 we did not observe an effect of female age on the propensity of an olfactory
568 inspection.

569 In line with prediction 6, the occurrence of an olfactory inspection affected
570 subsequent sexual behavior. In particular, instances of sniffing the anogenital swelling
571 almost exclusively led to no subsequent copulation. This may indicate that sniffing
572 provides additional information about female fertile states or indicators of male
573 competitors such as sperm remains that deters males from engaging in costly mating
574 behavior, although male Barbary macaques were suggested not to be able to
575 distinguish between fertile and non-fertile maximum swelling phases (Young et al.
576 2013). By inhibiting some males from inspecting their anogenital swelling close range,
577 females may even manipulate the degree of access to olfactory information depending
578 on the characteristics of the male.

579 Our assessment of olfactory inspections and their consequences (and thus of
580 addressing prediction 4, 5 and 6) was certainly limited, because we did not track
581 changes in female swelling size, ovarian hormone levels or whether observed
582 copulations actually led to ejaculation. Additionally, female odor cues could potentially
583 be gathered by males from a greater distance than what we defined as a sniff in this
584 study. It is possible that the active sniffs we scored were associated with situations in

585 which olfactory cues were so subtle that they required bringing the nose close to the
586 odor source, while at other times, olfactory cues may have been strong enough to be
587 perceivable from a greater distance, requiring no movement towards the odor source
588 that is visible to the observer. We therefore are not able to entirely rule out that what
589 we scored as visual inspections were truly multimodal ones that included a potential
590 olfactory component. Whether this could be the case is not assessable from
591 observations alone, and would require an experimental approach. As we only ever
592 observed an active protruding out of the nose from a very close distance to an object
593 and not from further away, however, we believe that our definition covers the vast
594 majority of instances of active olfactory sampling.

595 Unfortunately, the low number of olfactory inspections that led to copulation
596 did not allow us to address whether aspects such as female age or hormonal
597 contraception modulated an effect of olfactory inspection on copulation probabilities.
598 Studies on other primate species report differences in mating behavior or olfactory
599 signals related to hormonal contraception (Japanese macaques, *M. fuscata*, Leca et al.
600 2018, ring-tailed lemurs *Lemur catta*, Crawford et al. 2011). By contrast, owl monkeys
601 (*Aotus nancymaae*) showed no change in the released chemical profiles of females
602 with contraception and no difference in the ability of females to form new pair bonds
603 with males (Spence-Aizenberg et al. 2018). Our results provide no indication that
604 female contraception affected the likelihood of a copulation after inspection, but the
605 limitations indicated above prevent us from drawing more detailed conclusions about
606 the role of sniffing in Barbary macaque mating interactions, which would require more
607 comprehensive focal observations of sexual interactions, including an assessment of

female fertility based on hormonal data. A greater focus on sniffing in a social context along with data on dominance and other social interactions further would open up possibilities to address the role of olfaction in intra-sexual competition.

In conclusion, Barbary macaques routinely sniff in different contexts and sniffing behavior was modulated by individual attributes such as sex and age. These findings are in line with current research in other (catarrhine) primates and add to the growing evidence about the importance of olfaction across primate species. Subsequent research is needed to thoroughly interpret sniffing behavior at food or conspecifics in the light of visual or other available sensory information, with this study serving as a basis. As such, this study represents a first step towards understanding the use and importance of olfaction in the social lives of Barbary macaques.

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838 Table S1: Overview of observed sniffs for 48 focal animals, including their birth year,
839 sex, group, total sniffs and distribution of sniffs in feeding, social or other contexts.
840 Asterisk notes female on contraception.
841

Birthyear	ID	Sex	Group	Sniffs Total	Food	Social	Other
1995	M1	Male	1	2	2	0	0
1996	F1	Female	1	1	1	0	0
1999	M2	Male	2	13	13	0	0
2000	M3	Male	2	5	4	1	0
2000	F2	Female	2	5	5	0	0
2001	F3	Female*	2	18	18	0	0
2002	F4	Female*	2	14	12	0	2
2002	F5	Female*	1	1	1	0	0
2003	F6	Female*	2	8	8	0	0
2004	M4	Male	2	3	1	0	2
2004	M5	Male	1	2	1	0	1
2004	M6	Male	1	8	8	0	0
2007	M7	Male	1	3	3	0	0
2007	F7	Female*	2	28	28	0	0
2007	F8	Female*	2	3	2	0	1
2008	M8	Male	2	6	5	1	0
2008	M9	Male	2	8	0	6	2
2008	F9	Female*	1	15	12	2	1
2009	M10	Male	1	2	2	0	0
2009	F10	Female*	2	4	4	0	0
2009	F11	Female*	1	5	4	1	0
2010	M11	Male	1	9	7	2	0
2011	M12	Male	2	7	6	0	1
2011	F12	Female	1	2	2	0	0

2012	M13	Male	2	4	3	1	0
2012	F13	Female*	2	19	18	0	1
2012	M14	Male	1	22	19	3	0
2013	M15	Male	2	9	9	0	0
2013	M16	Male	2	13	13	0	0
2013	F14	Female*	2	34	34	0	0
2014	M17	Male	1	12	7	4	1
2014	F15	Female*	1	27	21	6	0
2014	F16	Female	1	32	23	0	9
2015	M18	Male	2	11	10	1	0
2015	F17	Female*	2	12	12	0	0
2015	F18	Female	1	16	16	0	0
2017	M19	Male	2	10	5	2	3
2017	M20	Male	1	12	11	1	0
2017	M21	Male	1	7	6	1	0
2017	F19	Female	2	12	2	1	9
2017	F20	Female	2	5	4	1	0
2017	F21	Female	1	6	6	0	0
2018	M22	Male	1	8	2	2	4
2018	F22	Female	2	4	2	0	2
2018	F23	Female	2	24	23	0	1
2019	M23	Male	2	11	6	4	1
2019	M24	Male	1	9	6	0	3
2019	F24	Female	1	19	16	0	3

Table S2: Identified edible items focal animals sniffed at and the respective number of observed sniffs. Not included were unidentifiable objects.

Item	No. Sniffs
Potato	30
Leaf	26
Carrot	23
Pineapple	22
Apple	21
Salad	17
Tomato	16
Leek	15
Grape	14
Hay	11
Popcorn	11
Parsley	10
Capsicum	8
Green onion	8
Beech nut	7
Chestnut	7
Stems	7
Celery	6
Orange	6
Seed	6
Tree branch	6
Mushroom	5
Broccoli	4
Cucumber	4
Fennel	4
Mango	4
Basil	3
Brussel sprout	3
Cabbage	3
Chinese cabbage	3
Honey melon	3
Potato "Vitelotte"	3
Banana	2

Item	No. Sniffs
Black radish	2
Pear	2
Pomegranate	2
Walnut	2
Wheat	2
Avocado	1
Beetroot	1
Chives	1
Clover	1
Eggplant	1
Fern	1
Grass	1
Pellet ("monkey chow")	1
Red cabbage	1
Thyme	1