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 catarrhine primate species. We therefore observed the sniffing behavior of semi-free ranging Barbary macaques, *Macaca sylvanus*, at Affenberg Salem, Germany, to assess how frequently macaques use olfaction and in which contexts, and how olfaction 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 used olfaction more often than older ones. Females sniffed more often on food than males did, while males used olfaction more often in a social context than females did. Sniffs at conspecifics primarily occurred 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, Melin et al. 2019), predator avoidance (e.g. mouse lemurs, Suendermann et al. 2008) or mating (e.g. ring-tailed lemurs, 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, resulting in a paucity of olfactory studies in several primate taxa. Many strepsirrhine primates are nocturnal and possess bigger-sized main and accessory olfactory bulbs and less specialized vision than other primate taxa (Barton 2006). Accordingly, the role of olfaction in their ecology and social lives has been studied more intensely than in other taxa. For example, it is well-established that odor plays an important role in their sociality by providing information about, e.g., sex, age or group (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 also diurnal primates, as found in many haplorrhine primates, may rely strongly on olfaction in a range of contexts. Particularly in platyrrhine primates, studies in several species have shown that they actively use olfaction in feeding situations, and that the use of olfaction is modulated by the available visual information. For example, white-faced capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi)* sniff more on fruits that give cryptic visual cues about their ripeness (Nevo & Heymann 2015; Hiramatsu et al. 2009). Moreover, olfaction also plays a role in the

64 sociality of platyrrhine species, including the context of mating. For instance, anogenital
65 odor secretions of female common marmosets (*Callithrix jacchus*) vary with fertile phases
66 and males inspected peri-ovulatory odors more intensely than odor samples from other
67 fertile phases (Kücklich et al. 2019).

68 Catarrhine primates show trichromatic vision in both sexes along with only half the
69 number of olfactory receptor genes and relatively smaller olfactory bulbs compared to
70 strepsirrhine primates (Niimura et al. 2018). In this taxonomic group, the assumption of
71 'microsmatic' primates has persisted over decades. However, a more recent viewpoint
72 suggests that features like the number of olfactory genes are not always predictive of e.g.
73 olfactory sensitivity (Laska et al. 2007a) or olfactory behavior (Jänig et al. 2018).
74 Furthermore, the importance of proportionally smaller olfactory bulbs has been questioned,
75 since the mere proportional correlation of body size to organ size and, therefore, function
76 may not apply in olfactory systems (Smith & Bhatnagar 2004). In addition, the traditionally
77 assumed separation of the main and the accessory olfactory system appears to be vaguer
78 than previously thought (Sipos et al. 1995; Petrulis et al. 1999). Hence, it is not surprising
79 that research has also started to focus on the involvement of olfaction in catarrhine sociality
80 and ecology (Matsumoto-Oda et al. 2007; Setchell et al. 2010; Vaglio et al. 2021; Rigaill et al.
81 2022). For instance, rhesus macaques (*Macaca mulatta*) as well as chimpanzees (*Pan*
82 *troglodytes*) were shown to differentiate between group and non-group members when
83 presented with samples of body odor (Henkel et al. 2015; Henkel & Setchell 2018). In
84 mandrills (*Mandrillus sphinx*), group members infected with parasites were discovered to
85 have a different fecal odour than non-infected members, whereby healthy individuals
86 avoided the fecal matter of infected conspecifics and avoided grooming them (Poirotte et al.
87 2017). Both in the wild and in captivity, chimpanzees were observed to sniff at food as well

as at conspecifics. While females used olfaction to inspect food more frequently than males did, males were observed to sniff more often in a social and sexual context than females, which was attributed to their fission-fusion society and the high level of male competition (Matsumoto-Oda et al. 2007; Jänig et al. 2018). Hence, evidence is accumulating that also catarrhine primates rely on olfaction in a range of contexts, but the number of studies and species investigated remains low, thereby hampering a more general understanding of the role of olfaction in catarrhine lives.

To contribute to closing the knowledge gap regarding olfaction in catarrhine species, the present study investigated the natural sniffing behavior of Barbary macaques (*Macaca sylvanus*), a catarrhine species native to northern Africa and Southern Europe. Their diet consists of various plants as well as insects (Fooden 2007). Like many other catarrhine species, Barbary macaques live in multi-male, multi-female groups and show a promiscuous mating system (Modolo & Martin 2008). They are sexually active year-round, but show increased sexual behavior during the mating season from late autumn to late winter (Kuester & Paul 1992). Females show a conspicuous visual fertility signal, the anogenital swelling, which is directly linked to estrogen levels and reaches its maximum size during the most fertile phase (Brauch et al. 2007). Nonetheless, observations of genital inspections by looking, sniffing and touching, as well as mating behavior suggest that males may have more than visual information available to determine female fertility (Young et al. 2013).

Hence, we aimed to investigate the use of olfaction (i.e. sniffing behavior) in Barbary macaques in different contexts (feeding, social and non-social), and to examine possible variation in the use of olfaction related to sex and age. Similar to a study in chimpanzees (Jänig et al. 2018), we hypothesized that 1) male Barbary macaques sniff more in the social context than females, with males sniffing particularly at females, given that the anogenital

swelling was suggested to be a reliable cue of fertility (Brauch et al. 2007). On the other hand, we expected 2) females to sniff more at edible items than males, as females are energetically more constrained than males. With regard to age, we expected 3) younger Barbary macaques to sniff more frequently than older individuals irrespective of the context. Infants and juveniles are in a process of learning about their environment and conspecifics surrounding them. Hence, olfaction could be used more often to explore and gain experience in all contexts, as observed in great apes (Jänig et al. 2018). We also assessed the role of olfaction in inspection behavior of the female sexual swelling. In particular, we hypothesized that olfaction in the sexual context is influenced by 4) male age and experience, with olfactory inspections being more prevalent in younger, more inexperienced males and by 5) female age and fertility status, with olfactory inspections being aimed more often towards older females, whose fertility status may be uncertain to the respective male.

Methods

Study site

The study was conducted at Affenberg Salem close to Lake Constance, Germany, which is home to ~ 200 Barbary macaques living in 20 hectares of fenced forest year-round under near-natural conditions. The park is open to visitors from March to November. Visitors are restricted to a path in one third of the enclosure, while the monkeys can roam freely across the entire area. For more details on the park, see de Turckheim & Merz (1984). The monkeys feed on food found throughout the park and receive daily supplements of fruits and vegetables. Furthermore, wheat is distributed widely on and around the feeding grounds. Water is accessible at several ponds and water troughs *ad libitum*. The park is home to three naturally formed social groups, each consisting of 50-70 individuals of both

sexes and all age classes. All monkeys are individually identifiable by tattoos and natural markings. To control population size, about two thirds of the adult females receive hormonal implants (Implanon NXT). This study was purely observational and in accordance with the legal requirements of Germany, all national and institutional guidelines for the care and use of animals.

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). Out of the 24 females observed, 13 had contraception implanted. Each focal animal was observed six times á 20 minutes over the study period (total observation time = 48*2 hours = 96 hours). Out of the six observations per focal animal, three were conducted in a feeding context (defined as at least ten minutes of feeding per protocol) and three were recorded in a non-feeding context. During the focal protocols all instances of sniffing as well as details about the targets of sniffing were recorded. Observations were randomly distributed between the available daylight hours from 08:00 am to 05:00 pm. Since 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 combined as one

observation, since the respective individuals proved themselves to be harder to record. If the first video was longer than ten minutes, observations continued as soon as the individual was visible again. Sniffs were scored from the videos using the recorded video image as well as commentaries verbally recorded onto the video during the focal observations (see Tab. 1 for ethogram). Each sniff recorded in the videos was assigned to one of three target categories: food, social (sniffs directed at a conspecific or its excretions) or other (sniffs directed at the environment, human-made objects and self-sniffs) following Jänig et al. (2018). For each observed sniff, the target object was specified and the behavior of the monkey after the sniff was noted. All videos were analyzed by one observer (M.S.), however, five percent of the data were also analyzed by an additional observer trained by M.S. to check for inter-observer reliability. The audio-track of the video was unavailable to the second coder to avoid bias. By comparing the respective observed sniffs, the intra-class correlation coefficient (ICC) was calculated and revealed good reliability (ICC=0.86; Koo & Li 2016).

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	males bringing their nose </= 3cm towards female anogenital swelling
copulation	male mounting female and thrusting

Besides the focal video protocols, *ad libitum* data were collected for every sniff that was observed outside the focal observations for focal and non-focal animals. 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).

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- 26 (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 hypotheses 1), 2) and 3). Accordingly, the number of sniffs per 20min focal observation and target category (‘food’, ‘social’ or ‘other’) was used as the response variable, fitted with a Poisson error distribution (N = 288 observations x 3 target categories = 864). Data collected *ad libitum* was not used in this model. Sex, birth year, observational context and target category (‘food’, ‘social’ or ‘other’) were fitted as fixed effects test predictors. Observational context referred to the context ‘feeding’ or ‘non-feeding’ in which each protocol was recorded, while target category referred to the object that was actually sniffed at, irrespective of whether the general observational context was feeding or not. Group, daytime and Julian day were fitted as fixed effects control predictors. Daytime was coded as morning (until 12:30 pm) or afternoon (after 12:30pm). Julian day was included to control for the progress of the mating season. Several two-way interactions were included in the model: I) sex and target category to

address the hypothesis that males sniff more in a social setting and females more on food; II) sex and Julian day, since the observational period started at the early beginning of the mating season and ended at its height. Therefore, male and female sniffing behavior could show different patterns from the beginning to the end of the observation period; III) observational context and target category, because the observational contexts 'feeding' or 'non-feeding' presumably influence the probable targets of sniffing; IV) birth year and target category, to account for the possibility that age affects which objects the monkeys sniff at, and V) daytime and target category, as fresh food got distributed every morning at 08:00 and we accordingly expected more sniffs at edible items in the morning than in the afternoon. ID was included as a random effects control predictor. To achieve more reliable p-values (Barr et al. 2013), we fitted random slopes of all predictors showing sufficient variation within ID, i.e., the random slopes of Julian day, context*target category, and daytime*target category.

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 hypotheses 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. Female and male birth year, 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 interaction of female and male birth year, respectively, was 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. Female and male ID were included as random effects control predictors. For the random effect of male ID, the random slopes of Julian day, female birth year and contraception were incorporated. For female ID, the random slopes of Julian day and male birth year were included.

Model C: Genital inspections and copulation

Using focal and *ad libitum* data, 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, further test our hypotheses 4) and 5). Female and male birth year, 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 birth year and male birth year; II) female birth year 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 predictors. For the random effect of male ID, we included Julian day, olfactory inspection, contraception and female birth year as random slopes. For female ID, we included Julian day, olfactory inspection and male birth year 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 0.59 (model A), 0.91 (model B), and 0.62 (model C). As model A and C were moderately underdispersed, the computed p-values should be considered as conservative. 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 1.1-26 (Bates et al. 2015). To facilitate interpretation of the main terms, non-significant interactions were removed from the models.

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 135 (32%) of 423 cases, the edible item was discarded after sniffing it, while it was eaten after sniffing 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, with distributions across sex and age classes similar to data recorded during focal observations. 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 per individual per observation (LRT, N = 864, $\chi2 = 111.8$, df = 12, $P < 0.001$). Specifically, sniffing frequencies differed between the sexes, whereby the effect of sex depended on the target of the sniff. In particular, more sniffs were observed by females at food and 'other' targets compared to males. Males, on the other hand, sniffed slightly 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 investigating sniffing frequency (number of sniffs) per focal animal, observation period and target category as response variable with Poisson error distribution (model A, N = 288 observations x 3 target categories = 864). Terms in parenthesis indicate trait levels relative to the respective reference level. Values for the non-significant interactions (daytime*target, context*target and birth year*target) represent values before removal of the respective terms from the model. SE = standard error. χ^2 and P values are derived from Likelihood Ratio Tests to determine the significance of the individual test predictors

term	Estimate	SE	χ2	P
Intercept	-0.042	0.259	†	†
test predictors				
sex (male)	-0.368	0.267	†	†
target category (other)	-2.630	0.568	†	†
target category (social)	-3.545	0.591	†	†
birth year	0.297	0.137	4.502	**0.034**
observ. context (non-feeding)	-1.255	0.204	31.479	**<0.001**
control predictors				
group (2)	0.111	0.268	0.159	0.690
Julian day	-0.308	0.097	9.103	**0.003**
daytime (morning)	0.862	0.164	†	†
interactions				
target category*sex			7.368	**0.025**
target category (other)*sex (male)	0.159	0.785		
target category (social)*sex (male)	1.780	0.678		
daytime*target category			15.085	**<0.001**
daytime(morning)*target (other)	-2.592	0.775		
daytime(morning)*target (social)	-0.994	0.455		
observ. context*target category			2.480	0.289
context (non-feeding)*target (other)	1.342	0.765		
context (non-feeding)*target (social)	-0.739	0.703		
birth year*target category			0.602	0.740
birth year*target (other)	0.193	0.346		
birth year*target (social)	0.25	0.402		
sex (male)*Julian day	-0.193	0.198	-0.974	0.329

† not presented because of having a very limited interpretation

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

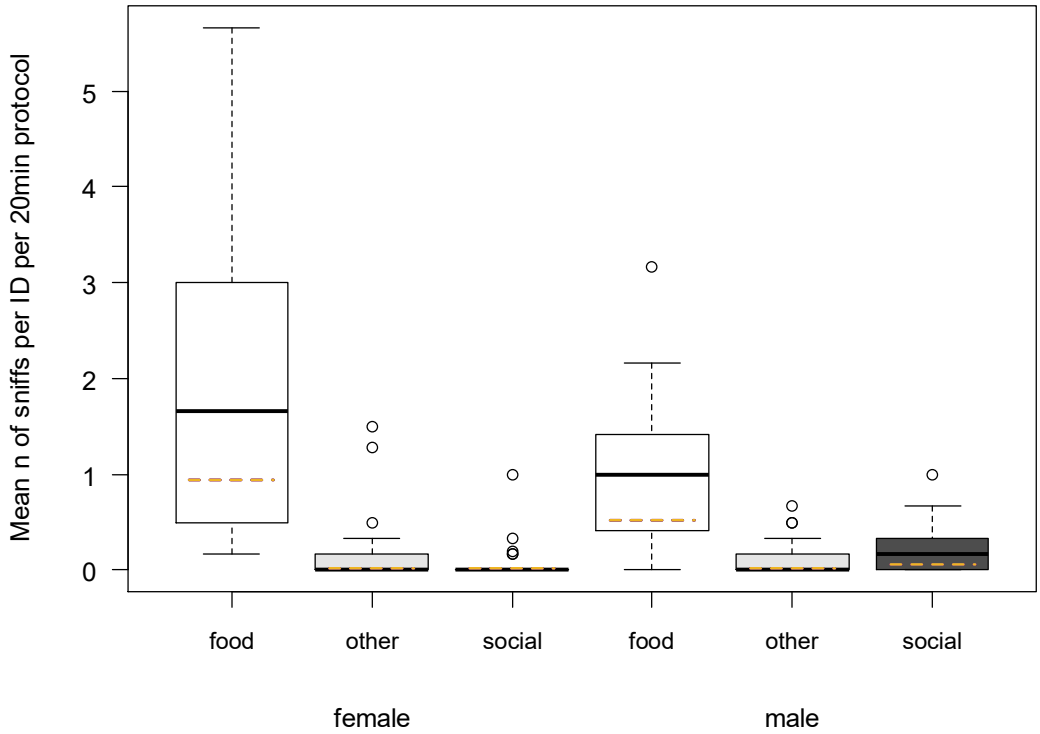

Fig. 1 Mean number of sniffs per individual per 20 min focal observation for both sexes divided into the target categories food, other and social. Boxes represent medians and first and third quartiles, while the whiskers represent 1.5 times the interquartile range. Outliers are represented by data points.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

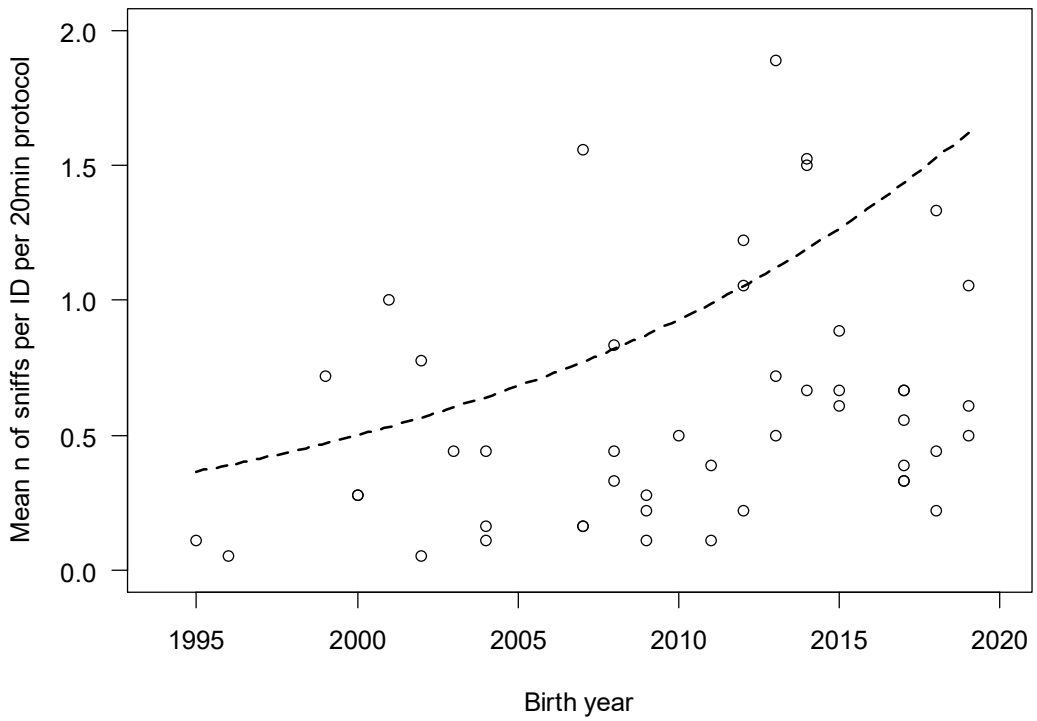

Fig. 2 Mean number of sniffs per individual per 20 min focal observation across birth years. The dashed line represents the model estimate when all other predictors are at their average

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 only a weak trend (LRT, N = 176, $\chi 2$ =16.111, df = 10, P = 0.09). With this trend in mind, we found that solely the interaction between female and male birth year significantly influenced the probability of an olfactory inspection (Tab. 4). Younger males tended to sniff more often while older females were sniffed at more often by males.

350 **Table 4** Results of the binomial GLMM investigating the probability of an olfactory inspection during
351 genital inspections (model B, N = 176 inspections). Values in parenthesis indicate trait levels relative
352 to the respective reference level. SE = standard error. χ^2 and P values are derived from Likelihood
353 Ratio Tests to determine the significance of the individual test predictors (notably after the full-null
354 comparison showed only a weak trend)

	Estimate	**SE**	**χ2**	**P**
Julian day	-0.176	0.217	0.571	0.450
male birth year	0.648	0.290	†	†
female birth year	-0.421	0.224	†	†
contraception (yes)	0.774	0.754	1.050	0.306
daytime (morning)	0.292	0.403	0.499	0.480
group (2)	-0.744	0.599	1.478	0.224
male birth year*female birth year	0.417	0.200	4.512	**0.034**

† not presented because of having a very limited interpretation

355

356 *Model C: Genital inspections and copulation*

357 Whether or not genital inspections were followed by a copulation was significantly
358 affected by the suite of test predictors in model C (after excluding interactions from model
359 due to stability issues, LRT, N = 176, χ2 = 22.142, df = 4, P < 0.001). In particular, olfactory
360 inspection of the swelling significantly decreased the probability for copulation after
361 inspection (Tab. 5). In fact, only 2 out of the 51 visual *and* olfactory inspections were
362 followed by a copulation, while copulation followed genital inspection in 44 of the 125 solely
363 visual genital inspections. Furthermore, the female birth year also impacted the copulation
364 probability, with copulations more likely after inspections of younger females than older
365 females (Tab. 5).

366

367 **Table 5** Results of the binomial GLMM investigating the probability of a copulation following a genital
368 inspection (model C, N = 176 inspections). Values in parenthesis indicate trait levels relative to the

respective reference level. SE = standard error. χ^2 and P values are derived from Likelihood Ratio Tests to determine the significance of the individual test predictors

	Estimate	**SE**	**χ2**	**P**
Julian day	-0.508	0.301	2.212	0.137
olfactory inspection (yes)	-3.287	1.014	21.987	**<0.001**
male birth year	0.101	0.291	0.111	0.739
female birth year	0.874	0.345	5.221	**0.022**
contraception (yes)	-0.490	0.747	0.393	0.531
daytime (morning)	-0.492	0.466	0.919	0.338

Discussion

This study contributes to understanding the sniffing behavior of Barbary macaques and thereby, catarrhine primates in general. In particular, we show that most sniffs occurred when assessing edible items, with females sniffing more at food than males did. Males used olfaction in the social context more than females did, and sniffing generally decreased with increasing age. 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/hour depending on season, Matsumoto-Oda et al. 2007). Hence, sniffing frequencies of Barbary macaques appear to be more alike to those of species traditionally considered to use olfaction more often, however, different sampling conditions (wild *vs.* captivity, focal *vs.* group sampling) and the sparse availability of similar studies with different primate species make reliable comparisons difficult.

Sniffing frequencies significantly decreased when the mating season intensified. Food abundancy and availability were consistent, however, agonistic interactions within the

390 groups increased (M.S., personal observation), with especially males being more focused on
391 social dynamics than before. Hence, males may have redirected temporal resources from
392 food assessment to finding suitable females and observing their competitors.
393
394 Influence of context & target
395 In our study, the vast majority of sniffs were directed at food, which parallels findings
396 for great apes (Jänig et al. 2018), guenons (Zschoke & Thomsen 2014) as well as mandrills
397 and olive baboons (Laidre 2009). Species that depend mostly on fruits and other plant parts
398 as their diet were suggested to steadily rely on olfactory cues to find and identify ripe food
399 (e.g., Nevo & Heymann 2015), get information about the nutritional value (Dominy et al.
400 2001), determine food safety and notice possible contamination (Sarabian et al. 2020).
401 Hence, it comes as no surprise that an almost exclusively herbivore species like the Barbary
402 macaque shows frequent olfactory assessments of edible items. The collected data,
403 however, did not provide suitable information to assess why certain items were sniffed at
404 and others not. While food ripeness can be implied for all items fed at the park, nutritional
405 value, safety and contamination with, e.g., soil or feces, are more complicated to assess for
406 an observer. Additionally, in an environment with a regular feeding routine, primates may
407 learn to rely on food safety and habituate to the produce available, which could lead to a
408 decrease in the importance of olfactory inspection (Laska et al. 2007b). Captive squirrel
409 monkeys (*Saimiri sciureus)* and spider monkeys (*Ateles geoffroyi*) were described to rely
410 mostly on visual cues when assessing familiar food items whereas novel food was more likely
411 to prompt olfactory inspections (Laska et al. 2007b). In line with this suggestion, we
412 observed a disproportional number of sniffs at hay and a chestnut provided by the park
413 (data not shown), both of which were only rarely available to the monkeys. However, we did

not systematically collect data on how often which types of food and other plants were available and therefore cannot address whether Barbary macaques really sniffed more frequently at novel or rare food items in this study. However, it should be kept in mind that seasonality and varying geographical availability of food sources could potentially lead to a different performance of olfactory inspection of food at other times or in other Barbary macaque populations.

Influence of sex and age

The significant interaction between sex and age on sniffing probability supports hypothesis 1) that male Barbary macaques sniff more often in a social context than females do. This imbalance in social sniffs was also observed in other primate species such as chimpanzees (Jänig et al. 2018; Matsumota-Oda et al. 2007) and owl monkeys (*Aotus nancymaae*; Spence-Aizenberg 2017). Chimpanzees live in multi-male multi-female groups with fission-fusion dynamics and high levels of male-male competition for access to fertile females, enhancing the need for olfaction in the social context (Jänig et al. 2018; Matsumota-Oda et al. 2007). For Barbary macaques, which also live in multi-male multi-female groups, almost all social sniffs by adult males were observed to be directed at female sexual swellings and only one at another adult male. Thus, olfaction likely plays a role in male sexual competition for fertile females by, for example, providing information about the ovarian cycle, in addition to the visual signal of swelling size. However, it does not seem as important for males to gather direct information about other males through olfaction. Female Barbary macaques, on the other hand, sniffed more at food than males, supporting hypothesis 2). This corresponds to observations of female chimpanzees (Matsumota-Oda et al. 2007). Moreover, female primates of various species tend to be more wary of

contamination risks for parasites or bacteria through food that is rotten or spoiled with feces (Sarabian et al. 2015; Sarabian et al. 2020; Poirotte et al. 2019), as evident from more olfactory inspection of contaminated food, followed by food manipulation (Sarabian et al. 2020). This behavior was rewarded by lower infection rates of females (Poulin 1996; Rolff 2002; Poirotte et al. 2019), suggesting that more visual or olfactory inspections, even though potentially costly, maximize the health, and therefore, also reproductive success of females. Similar mechanisms might apply to Barbary macaques, but a systematic analysis of parasite occurrence in both sexes would be needed to assess this possibility.

Furthermore, our hypothesis 3) of young individuals sniffing more often than older ones was supported with our data. These findings agree with the consensus that young animals inspect their environment more closely than older individuals since they are still in the process of learning to evaluate food, conspecifics or their general environment, and are comparable to observations in great apes (Jänig et al. 2018). Since the decrease of sniffing events with age in Barbary macaques appears to be quite linear (see Fig. 2), it is likely that it is primarily caused by increased experience and not by a loss of olfactory capability at older age. Together, 18 out of 22 social sniffs that were observed for infant monkeys during *ad libitum* data collection were directed at the feeding mother's, or in one case the grandmother's, mouth. In each case the infants appeared to observe the eating behavior and tried to inspect the item visually. They were not chased off and the mothers reacted with indifference to the inspection attempt of their infant. This ‘muzzle-muzzle’ behavior has been observed in different mammals, including primates, and may enable the individuals to smell the breath of their conspecifics while they are eating (Nord et al. 2021; Arakawa et al. 2013; Laidre 2009). In this way they may gather information on which food has been deemed safe and valuable to eat by their conspecific.

462

463 Olfaction in sexual interactions

464 Most social sniffs occurred in a sexual context and were directed at the female
465 anogenital swelling. However, not every inspection observed included olfaction. Hence, we
466 tried to assess which circumstances led to an olfactory inspection, but were not able to
467 robustly pinpoint any predictor we tested. It has to be noted though, that in the present
468 study we did not track changes in female swelling size or other transient individual attributes
469 over time, and thus could not assess whether the salience of the visual fertility signal
470 affected whether or not males additionally used olfaction to inspect females.

471 Surprisingly, if an olfactory inspection of the swelling occurred, this almost exclusively
472 led to no subsequent copulation. This may indicate that, although swelling size was
473 suggested to closely reflect female ovarian function in Barbary macaques (Brauch et al.
474 2007; Tschoner 2015), an olfactory cue may provide additional information that deters
475 males from engaging in costly mating behavior. This may be particularly relevant in single
476 mounting species like the Barbary macaque, which are able to ejaculate in one mount (Taub
477 1982), however, in this study we did not check if observed copulations actually led to
478 ejaculation or not. Furthermore, an inspection – whether or not it involved olfaction –
479 resulted in fewer copulations in older than in younger females. It would be interesting to
480 assess whether female age and olfactory inspection interacted in their effects on copulation
481 probabilities, but unfortunately the low number of olfactory inspections that led to
482 copulation did not allow us to address this question. The same applies to a potential effect of
483 hormonal contraception. While we could not observe any apparent influence on the size of
484 the anogenital swelling of contracepted female monkeys (M.S., B.M.W. personal
485 observations), studies on other primate species report differences in mating behavior due to

486 hormonal contraception. In Japanese macaques (*M. fuscata*), contracepted females showed
487 less interest in mating, they mated with fewer partners and for shorter periods of times,
488 while males were less likely to mate with contracepted females compared to non-
489 contracepted females and approached contracepted females less often (Leca et al. 2018).
490 Furthermore, in ring-tailed lemurs (*Lemur catta*) contraceptives changed the olfactory
491 signals released by females, with males preferring the scent of contraceptive-free females
492 (Crawford et al. 2011). On the other hand, owl monkeys (*Aotus nancymaae*) showed no
493 change in the released chemical profiles of females with contraception and no difference in
494 the ability of females to form new pair bonds with males (Spence-Aizenberg et al. 2018).
495 There is no available data yet on a potential influence of contraceptives on the chemical
496 profile or the behavior of female Barbary macaques and our results provide no indication
497 that female contraception affected either the likelihood of males to sniff at the anogenital
498 female swelling nor the likelihood of a copulation after inspection. But again, we were not
499 able to test whether an effect of olfactory inspection on copulatory behavior may have
500 differed between contracepted and non-contracepted females due to the low number of
501 olfactory inspections that indeed led to copulation. Furthermore, differences in the
502 administered contraceptives need to be considered when comparing studies. More detailed
503 studies on, e.g., whether a copulation was ejaculatory or not, or if males later returned to
504 inspect and/or copulate with the respective female will help to better understand the role of
505 olfaction in Barbary macaque mating interactions. This, however, would require more
506 systematic focal observations of sexual interactions, including an assessment of female
507 fertility based on hormonal data, that were beyond the scope of this study.
508 In conclusion, Barbary macaques routinely used olfaction in different contexts and its
509 use 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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Ethics statement

This study was purely observational and in accordance with the legal requirements of Germany, all national and institutional guidelines for the care and use of animals.

Conflict of Interest

The authors declare that they have no conflict of interest.

References

Arakawa, H., Kelliher, K. R., Zufall, F., & Munger, S. D. (2013). The receptor guanylyl cyclase type d (Gc-d) ligand uroguanylin promotes the acquisition of food preferences in mice. Chemical Senses, 38(5), 391–397. doi.org/10.1093/chemse/bjt015

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language, 68(3), 255–278. doi.org/10.1016/j.jml.2012.11.001

Barton, R. A. (2006). Olfactory evolution and behavioral ecology in primates. American Journal of Primatology, 68(6), 545–558. doi.org/10.1002/ajp.20251

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1). doi.org/10.18637/jss.v067.i01

Boulet, M., Crawford, J. C., Charpentier, M. J., & Drea, C. M. (2010). Honest olfactory ornamentation in a female-dominant primate. Journal of Evolutionary Biology, 23(7), 1558–1563. doi.org/10.1111/j.1420-9101.2010.02007.x

Brauch, K., Pfefferle, D., Hodges, K., Möhle, U., Fischer, J., & Heistermann, M. (2007). Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. Hormones and Behavior, 52(3), 375–383. doi.org/10.1016/j.yhbeh.2007.06.001

Crawford, J. C., Boulet, M., & Drea, C. M. (2011). Smelling wrong: hormonal contraception in lemurs alters critical female odour cues. Proceedings of the Royal Society B: Biological Sciences, 278(1702), 122–130. doi.org/10.1098/rspb.2010.1203

Cunningham, E. P., Edmonds, D., Stalter, L., & Janal, M. N. (2021). Ring-tailed lemurs (*Lemur catta*) use olfaction to locate distant fruit. American Journal of Physical Anthropology, 175(1), 300–307. https://doi.org/10.1002/ajpa.24255

de Turckheim, G., & Merz, E. (1984). Breeding Barbary macaques in outdoor open enclosures. In J. E. Fa (Ed.), The Barbary macaque: A case study in conservation (pp. 241– 261). Plenum Publishing Corporation. doi.org/10.1007/978-1-4613-2785-1_10

Dobson, A. J. (2002). An introduction to generalized linear models (2nd ed). Chapman & Hall/CRC.

Dominy, N. J., Lucas, P. W., Osorio, D., & Yamashita, N. (2001). The sensory ecology of primate food perception. Evolutionary Anthropology: Issues, News, and Reviews, 10(5), 171–186. doi.org/10.1002/evan.1031

Fooden, J. (2007). Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). Fieldiana Zoology, 113(1), 1. doi.org/10.3158/0015-0754(2007)113[1:SROTBM]2.0.CO;2

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. Behavioral Ecology and Sociobiology, 65(1), 47–55. doi.org/10.1007/s00265-010-1038-5

Fox, J. & Weisberg, S. (2019). An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Henkel, S., Lambides, A. R., Berger, A., Thomsen, R., & Widdig, A. (2015). Rhesus macaques (*Macaca mulatta*) recognize group membership via olfactory cues alone. Behavioral Ecology and Sociobiology, 69(12), 2019–2034. doi.org/10.1007/s00265-015-2013-y

Henkel, S., & Setchell, J. M. (2018). Group and kin recognition via olfactory cues in chimpanzees (*Pan troglodytes*). Proceedings of the Royal Society B: Biological Sciences, 285(1889), 20181527. doi.org/10.1098/rspb.2018.1527

Hiramatsu, C., Melin, A. D., Aureli, F., Schaffner, C. M., Vorobyev, M., & Kawamura, S. (2009). Interplay of olfaction and vision in fruit foraging of spider monkeys. Animal Behaviour, 77(6), 1421–1426. doi.org/10.1016/j.anbehav.2009.02.012

Janda, E. D., Perry, K. L., Hankinson, E., Walker, D., & Vaglio, S. (2019). Sex differences in scent-marking in captive red-ruffed lemurs. American Journal of Primatology, 81(1), e22951. doi.org/10.1002/ajp.22951

Jänig, S., Weiß, B. M., & Widdig, A. (2018). Comparing the sniffing behavior of great apes. American Journal of Primatology, 80(6), e22872. doi.org/10.1002/ajp.22872

Kay, R. F. (2018). 100 years of primate paleontology. American Journal of Physical Anthropology, 165(4), 652–676. doi.org/10.1002/ajpa.23429

Koo, T. K., & Li, M. Y. (2016). A Guideline of Selecting and Reporting Intraclass Correlation Coefficients for Reliability Research. Journal of Chiropractic Medicine, 15(2), 155–163. doi.org/10.1016/j.jcm.2016.02.012

Kücklich, M., Weiß, B. M., Birkemeyer, C., Einspanier, A., & Widdig, A. (2019). Chemical cues of female fertility states in a non-human primate. Scientific Reports, 9(1), 13716. doi.org/10.1038/s41598-019-50063-w

Kuester, J., & Paul, A. (1992). Influence of male competition and female mate choice on Male mating success in Barbary macaques (*Macaca sylvanus*). Behaviour, 120(3–4), 192–216. doi.org/10.1163/156853992X00606

Kuester, J., Paul, A. & Arnemann, J. (1995). Age-related and individual differences of reproductive success in male and female barbary macaques (*Macaca sylvanus)*. Primates 36, 461–476. doi.org/10.1007/BF02382869

Laidre, M. E. (2009). Informative breath: Olfactory cues sought during social foraging among old world monkeys (*Mandrillus sphinx, M. Leucophaeus,* and *Papio anubis*). Journal of Comparative Psychology, 123(1), 34–44. doi.org/10.1037/a0013129

Laska, M., Bautista, R. M. R., Höfelmann, D., Sterlemann, V., & Salazar, L. T. H. (2007a). Olfactory sensitivity for putrefaction-associated thiols and indols in three species of non-human primate. Journal of Experimental Biology, 210(23), 4169–4178. doi.org/10.1242/jeb.012237

Laska, M., Freist, P., & Krause, S. (2007b). Which senses play a role in nonhuman primate food selection? A comparison between squirrel monkeys and spider monkeys. American Journal of Primatology, 69(3), 282–294. doi.org/10.1002/ajp.20345

Leca, J. B., Gunst, N., Shimizu, K., Huffman, M. A., Takahata, Y., & Vasey, P. L. (2018). Hormonal contraceptive affects heterosexual but not homosexual behavior in free-ranging female Japanese macaques over 17 mating seasons. Hormones and Behavior, 105, 166–176. doi.org/10.1016/j.yhbeh.2018.08.009

Matsumoto-Oda, A., Kutsukake, N., Hosaka, K., & Matsusaka, T. (2007). Sniffing behaviors in Mahale chimpanzees. Primates, 48(1), 81–85. doi.org/10.1007/s10329-006-0006-1

Melin, A.D., Nevo, O., Shirasu, M., Williamson, R. E., Garrett, E. C., Endo, M., Sakurai, K., Matsushita, Y., Touhara, K., & Kawamura, S. (2019). Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. Nature Communications 10, 2407. doi.org/10.1038/s41467-019-10250-9

Modolo, L., & Martin, R. D. (2008). Reproductive success in relation to dominance rank in the absence of prime-age males in Barbary macaques. American Journal of Primatology, 70(1), 26–34. doi.org/10.1002/ajp.20452

Nevo, O., & Heymann, E. W. (2015). Led by the nose: Olfaction in primate feeding ecology. Evolutionary Anthropology: Issues, News, and Reviews, 24(4), 137–148. doi.org/10.1002/evan.21458

Niimura, Y., Matsui, A., & Touhara, K. (2018). Acceleration of olfactory receptor gene loss in primate evolution: Possible link to anatomical change in sensory systems and dietary Transition. Molecular Biology and Evolution, 35(6), 1437–1450. doi.org/10.1093/molbev/msy042

Nord, C. M., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2021). Tolerance of muzzle contact underpins the acquisition of foraging information in vervet monkeys (*Chlorocebus pygerythrus*). Journal of Comparative Psychology, 135(3), 349–359. doi.org/10.1037/com0000258

Paul, A., & Kuester, J. (1990). Adaptive significance of sex ratio adjustment in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem. Behavioral Ecology and Sociobiology, 27(4), 287–293.

Petrulis, A., Peng, M., & Johnston, R. E. (1999). Effects of vomeronasal organ removal on individual odor discrimination, sex-odor preference, and scent marking by female hamsters. Physiology and Behavior, 66(1), 73–83. doi.org/10.1016/S0031-9384(98)00259-5

Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P. M., Kappeler, P. M., & Charpentier, M. J. E. (2017). Mandrills use olfaction to socially avoid parasitized conspecifics. Science Advances, 3(4), e1601721. doi.org/10.1126/sciadv.1601721

Poirotte, C., Sarabian, C., Ngoubangoye, B., MacIntosh, A. J. J., & Charpentier, M. (2019). Faecal avoidance differs between the sexes but not with nematode infection risk in mandrills. Animal Behaviour, 149, 97–106. doi.org/10.1016/j.anbehav.2019.01.013

Poulin, R. (1996). Sexual inequalities in helminth infections: A cost of being a male? The American Naturalist, 147(2), 287–295. doi.org/10.1086/285851

Quinn, G., & Keough, M. (2002). Experimental Design and Data Analysis for Biologists. Cambridge: Cambridge University Press. doi:10.1017/CBO9780511806384

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Rigaill, L., Vaglio, S., Setchell, J. M., Suda-Hashimoto, N., Furuichi, T., & Garcia, C. (2022). Chemical cues of identity and reproductive status in Japanese macaques. American Journal of Primatology, 84(8), e23411. doi.org/10.1002/ajp.23411

Rolff, J. (2002). Bateman's principle and immunity. Proceedings of the Royal Society B: Biological Sciences, 269(1493), 867–872. doi.org/10.1098/rspb.2002.1959

Rushmore, J., Leonhardt, S. D., & Drea, C. M. (2012). Sight or scent: lemur sensory reliance in detecting food quality varies with feeding ecology. PloS One, 7(8), e41558. doi.org/10.1371/journal.pone.0041558

Sarabian, C., & MacIntosh, A. J. J. (2015). Hygienic tendencies correlate with low geohelminth infection in free-ranging macaques. Biology Letters, 11(11), 20150757. doi.org/10.1098/rsbl.2015.0757

Sarabian, C., Ngoubangoye, B., & MacIntosh, A. J. J. (2020). Divergent strategies in faeces avoidance between two cercopithecoid primates. Royal Society Open Science, 7(3), 191861. doi.org/10.1098/rsos.191861

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. Methods in Ecology and Evolution, 1(2), 103–113. doi.org/10.1111/j.2041-210X.2010.00012.x

Scordato, E. S., & Drea, C. M. (2007). Scents and sensibility: information content of olfactory signals in the ringtailed lemur, *Lemur catta*. Animal Behaviour, 73(2), 301–314. doi:10.1016/j.anbehav.2006.08.006

Setchell, J. M., Vaglio, S., Moggi-Cecchi, J., Boscaro, F., Calamai, L., & Knapp, L. A. (2010). Chemical composition of scent-gland secretions in an old world monkey (*Mandrillus sphinx*): influence of sex, male status, and individual identity. Chemical senses, 35(3), 205–220. doi.org/10.1093/chemse/bjp105

Sipos, M. L., Wysocki, C. J., Nyby, J. G., Wysocki, L., & Nemura, T. A. (1995). An ephemeral pheromone of female house mice: Perception via the main and accessory olfactory systems. Physiology and Behavior, 58(3), 529–534. doi.org/10.1016/0031-9384(95)00089-2

Smith, T. D., & Bhatnagar, K. P. (2004). Microsmatic primates: Reconsidering how and when size matters. The Anatomical Record, 279B(1), 24–31. doi.org/10.1002/ar.b.20026

Spence-Aizenberg, A. M. (2017). Olfactory communication, mate choice, and reproduction in a pair bonded primate (*Aotus spp*.). Publicly Accessible Penn Dissertations. 2885.

Spence-Aizenberg, A., Kimball, B.A., Williams, L.E., & Fernandez-Duque, E. (2018). Chemical composition of glandular secretions from a pair-living monogamous primate: Sex, age, and gland differences in captive and wild owl monkeys (*Aotus spp.).* American Journal of Primatology 80:e22730. doi.org/10.1002/ajp.22730

Suendermann, D., Scheumann, M., & Zimmermann, E. (2008). Olfactory predator recognition in predator-naïve gray mouse lemurs (*Microcebus murinus*). Journal of Comparative Psychology, 122(2), 146–155. https://doi.org/10.1037/0735-7036.122.2.146

Taub D. M. (1982). Sexual behavior of wild Barbary macaque males (*Macaca sylvanus).* American Journal of Primatology, 2(1), 109–113. doi.org/10.1002/ajp.1350020112

Tschoner, S.E. (2015). Sexual swelling as honest signal for fertility in female Barbary macaques (*Macaca sylvanus*)? (Master Thesis) Universität Wien. Fakultät für Lebenswissenschaften.

Vaglio, S., Minicozzi, P., Kessler, S. E., Walker, D., & Setchell, J. M. (2021). Olfactory signals and fertility in olive baboons. Scientific Reports, 11(1), 8506. doi.org/10.1038/s41598-021-87893-6

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2013). Male mating behaviour in relation to female sexual swellings, socio-sexual behaviour and hormonal changes in wild Barbary macaques. Hormones and Behavior, 63(1), 32–39. doi.org/10.1016/j.yhbeh.2012.11.004

Zschoke, A., & Thomsen, R. (2014). Sniffing behaviours in guenons. Folia Primatologica, 85(4), 244–251. doi.org/10.1159/000363409

Table S1: Overview observed sniffs for all 48 focal animals. For each monkey, the total number of sniffs that was observed during the six focal observations as well as a breakdown of the sniffs that occurred in the context food, social or other are listed. Additionally, the respective birthyear, sex and group are noted. All females marked with an asterisk were contracepted during the study period.

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 (e.g. stems).

Item	No. Sniffs
Potato	30
Leave	26
Carrot	23
Pineapple	22
Apple	21
Salad	17
Tomato	16
Leek	15
Grape	14
Hay	11
Popcorn	11
Parsley	10
Capsicum	8
Escallion	8
Beechnut	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
Vitelotte	3
Banana	2

Item	No. Sniffs
Black raddish	2
Pear	2
Pomegranate	2
Walnut	2
Wheat	2
Avocado	1
Beetroot	1
Chives	1
Clover	1
Eggplant	1
Fern	1
Gras	1
Pellet	1
Red cabbage	1
Thyme	1
Bark	1