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RESEARCH ARTICLE

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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 1–25 years showed that Barbary macaques sniffed, on average, 5.24 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 may play a role in male mating decisions, but the role of olfaction in sexual interactions warrants further investigations. In sum, results show that Barbary macaques routinely use olfaction during feeding, but also in a socio-sexual context, corroborating the relevance of the olfactory sense in the lives of catarrhine primates.

KEYWORDS

anogenital inspection, copulation, macaques, olfaction, sniffing

1 | INTRODUCTION

Primates, like other mammals, use various senses to gain information about their social and physical environment. Olfaction is one of the evolutionarily oldest senses, 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*], Sündermann et al., 2008) or mating (e.g., ring-tailed lemurs [*Lemur catta*], Boulet et al., 2010).

Abbreviations: CI, confidence interval; df, degrees of freedom; GLMM, generalized linear mixed model; ICC, intra-class correlation coefficient; LRT, likelihood ratio test; N, sample size; *SD*, standard deviation; *SE*, standard error.

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Optic convergence and stereoscopic vision represent significant parts of primate evolution, accompanied by a relative shrinking of the olfactory apparatus (Kay, 2018). Olfaction was thus long assumed to be of little relevance in taxa with advanced visual capabilities and 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, odor plays an important role in strepsirrhine sociality by providing information about sex, age or group membership (Janda et al., 2019; Scordato & Drea, 2007), and in their foraging behavior (Cunningham et al., 2021; Rushmore et al., 2012). However, it has become increasingly evident that also diurnal, haplorrhine primates may rely strongly on olfaction in various contexts. Platyrrhine primates routinely use active olfaction (i.e., sniffing) in feeding situations, whereby sniffing rates may be modulated by visual information about food items (Hiramatsu et al., 2009; Laska et al., 2007b; Nevo & Heymann, 2015). Olfaction also plays a role in the sociality of platyrrhines, including mating. For instance, anogenital odor secretions of female common marmosets (*Callithrix jacchus*) vary across the ovarian cycle and males inspect peri-ovulatory odors more intensely than odor samples from follicular and luteal phases (Kücklich et al., 2019).

Catarrhine primates have trichromatic vision in both sexes. With only half as many olfactory receptor genes and relatively smaller olfactory bulbs compared to strepsirrhines (Niimura et al., 2018), the notion of "microsmatic" catarrhines has persisted over decades (Smith & Bhatnagar, 2004). However, a more recent viewpoint suggests that features like the number of olfactory receptor genes or olfactory bulb size do not always predict olfactory abilities (Laska et al., 2007a; Matsui et al., 2010; Smith & Bhatnagar, 2004) and that olfactory behavior is prevalent in many species (Jänig et al., 2018; Vaglio et al., 2021).

Evidence for the importance of olfaction in catarrhine sociality and ecology has accumulated in recent years (Matsumoto-Oda et al., 2007; Rigaill et al., 2022; Setchell et al., 2010; Vaglio et al., 2021). For instance, rhesus macaques (*Macaca mulatta*) as well as chimpanzees (*Pan troglodytes*) differentiate between odors of group and non-group members (Henkel & Setchell, 2018; Henkel et al., 2015). Mandrills (*Mandrillus sphinx*) infected with parasites had a different fecal odor than non-infected individuals, and healthy individuals avoided feces of infected conspecifics and groomed these conspecifics less (Poirotte et al., 2017). Chimpanzees sniff food and conspecifics, whereby females sniffed food more frequently than males, while males sniffed more often in a socio-sexual context than females (Jänig et al., 2018; Matsumoto-Oda et al., 2007). Despite such evidence the number of studies and investigated species remains low, restricting our understanding of the role of olfaction in catarrhine lives.

The present study investigated the natural sniffing behavior of Barbary macaques (*Macaca sylvanus*), a primarily herbivorous (Fooden, 2007) catarrhine species native to northern Africa and Southern Europe. Like many other catarrhines, Barbary macaques live in multi-male, multi-female groups with a promiscuous mating system (Modolo & Martin, 2008). They are sexually active year-round, but increase 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 of the cycle (Brauch et al., 2007). Males inspect anogenital swellings by looking, sniffing and touching, but do not appear to discriminate between fertile and post-conception maximal swellings (Young et al., 2013).

We aimed to investigate sniffing behavior in Barbary macaques in different contexts (feeding, social and non-social) and in relation to sex and age. We hypothesized that individuals who benefit more from olfactory information in a given context than others would sniff more frequently (model A). Similar to a study in chimpanzees (Jänig et al., 2018), we predicted that (1) males sniff more in the social context than females because of intrasexual competition for the access to fertile females, for which olfactory information would be beneficial. We further predicted (2) that females would sniff edible items more frequently than males, because females are energetically more constrained (chimpanzees: Matsumoto-Oda et al., 2007), and more stringent food inspection may improve female reproductive success by lowering contamination risks (Poirotte et al., 2019; Rolff, 2002). With regard to age, we predicted (3) that younger individuals would sniff more frequently than older ones irrespective of the context. Infants and juveniles still need to learn about their environment and conspecifics, for which olfactory information could be beneficial (great apes: Jänig et al., 2018). We also assessed the role of olfaction in inspections of the female sexual swelling (models B and C). We hypothesized that olfactory information would be involved in male mating decisions, as male Barbary macaques appear to assess not only swelling size visually but also other sensory information about swellings (Young et al., 2013). In particular, we predicted (4) that sniffing in the sexual context is influenced by male age, with olfactory inspections being more prevalent in younger males which may lack the experience in visually assessing anogenital swellings and may therefore be more prone to attend to additional cues. Furthermore, female fertility and reproductive success vary with age, with higher variability in interbirth intervals in young females and a decline in reproductive performance from middle age to old age (Campos et al., 2022; Paul et al., 1993). Accordingly, we also predicted (5) that olfactory inspections are affected by female age, being aimed more often towards young and old females whose fertility status may be more uncertain compared to females of prime age. Finally, olfactory inspections were frequently followed by copulations in olive baboons (*Papio anubis*), when females were in their fertile phase but not when they were post-fertile (Rigaill et al., 2013). Accordingly, we expected (6) that olfactory inspections would affect copulatory behavior in Barbary macaques, although we were not able to address this aspect in as much detail as by Rigaill et al. (2013) given that we did not have systematic data on the fertile state of the females.

2 | METHODS

2.1 | Study site

We conducted the study at Affenberg Salem, Germany, where ~200 Barbary macaques live in 20 hectares of fenced forest year-round under near-natural conditions (see de Turckheim & Merz, 1984). The park opens 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. The monkeys have access to water at several ponds and water troughs ad libitum and feed on natural vegetation and insects. They receive daily supplements of fruits, vegetables and wheat, which are distributed widely on and around the clearings and meadows. The park is home to three naturally formed social groups, each consisting of 50–70 individuals. All monkeys are individually identifiable by tattoos and natural markings. To control population size, about two thirds of the adult females receive subcutaneous hormonal implants (Implanon NXT), which inhibit ovulation by reducing the luteinising hormone level and impede entry of sperm into the uterus. Implanted females show cyclical changes in anogenital swelling size and have sexual interactions qualitatively similar to non-contracepted females (B.M.W., personal observation). 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, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

2.2 | Behavioral observations

Author M.S. observed sniffing behavior between October 17, 2020 and December 6, 2020, i.e., 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 (Table S1), and thus covered all age classes, from juveniles (up to 2.5 years old, $N = 6$) and subadults (up to 4.5 years old, $N = 9$) to adults (5 years and older, $N = 33$, Kuester et al., 1995; Paul & Kuester, 1990). A total of 13 of 18 adult focal females had hormone implants. We observed each focal animal six times for 20 min over the study period (total observation time = 48 × 2 h = 96 h), with three of the six observations conducted in a feeding context (defined as at least 10 min of feeding per protocol) and three in a non-feeding context. For each focal subject, we spread observations randomly across the available daylight hours from 08:00 a.m. to 05:00 p.m., and as equally as possible over the study period by observing the majority of individuals once before moving on to the next set of observations. We further alternated contexts between observations for a given individual whenever possible. During focal protocols we recorded all instances of sniffing as well as details about the targets of sniffing. Because our study involved focal animals in the field, it was not possible to record data blind.

TABLE 1 Ethogram of observed behavior in this study.

Behavior	Description
Sniff	Individual brings their nose ≤3 cm towards an object/conspecific/themselves or touches an object with the hand and then brings the hand towards the nose
Visual inspection	Male focuses on the female anogenital swelling from a close range ≤1 m
Olfactory inspection	A sniff (as defined above) directed at the female anogenital swelling
Copulation	Male mounts female with thrusting

We recorded all focal observations with a digital video camera (Panasonic HC-V180). If the recorded subject moved out of sight during filming, we usually discarded the video, but combined two shorter videos as one observation (11 cases), because some individuals were less approachable and more difficult to observe for 20 min continuously. We combined videos only if both were recorded in a similar behavioral context, on the same day (<30 min to 4.5 h apart) and were long enough to amount to 20 min. We scored sniffs using the recorded video image as well as commentaries verbally recorded onto the video during the focal observations (see Table 1 for ethogram). We followed Jänig et al. (2018) in assigning sniffs to one of three target categories: food, social (directed at a conspecific or its excretions) or other (directed at the environment, human-made objects and self-sniffs). We also noted the target object of each observed sniff and the behavior of the individual after the sniff. Author M.S. coded all videos. An additional person, trained by M.S., also analyzed five percent of the data (without audio-track to avoid bias) to assess interobserver reliability. The intraclass correlation coefficient (ICC), calculated from numbers of observed sniffs, revealed good reliability (ICC = 0.86; Koo & Li, 2016).

We also collected ad libitum data about sniffs outside the focal observations for focal and non-focal animals, and for inspections of female swellings. For the latter we recorded male and female identity (ID), group, date, time, whether visual and/or olfactory inspection occurred and which was first, and if a copulation followed (Table 1).

2.3 | Statistical analysis

We conducted three sets of generalized linear mixed models (GLMM), which allow accounting for repeated observations of the same individuals (Bates et al., 2015). We fitted all models in R version 4.0.3 [R Core Team (2020)] by using the function "glmer" from the package "lme4" version 1.1-31 (Bates et al., 2015).

2.3.1 | Model A: Sniffing frequencies

With model A we investigated the influence of sex, age and context on sniffing frequencies to test our first three predictions. 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 from each 20 min focal observation: the number of sniffs at food, the number of sniffs at social targets and the number of sniffs at other targets ($N = 288$ focal protocols × 3 target categories = 864 sniffing frequencies). We did not use data collected ad libitum in this model. Test predictors (fixed effects) included sex, age (years), observational context ("feeding" or "non-feeding") and target category ("food," "social," or "other"). Target category refers to the object that was actually sniffed at, irrespective of whether the observational context was "feeding" or "non-feeding." We also included group, time of day ("morning" until 12:30 p.m., "afternoon" after 12:30 p.m.) and Julian day (to control for the progress of the mating season) as control predictors (fixed effects). We further included several two-way interactions: (i) sex and target category to address the prediction that males sniff more in a social setting and females more on food; (ii) sex and Julian day, to account for differences in the effect of sex on sniffing across the observation period; (iii) observational context and target category, because the contexts "feeding" or "non-feeding" presumably influence the probable targets of sniffing; (iv) age and target category, to account for the possibility that age affects which objects the monkeys sniff, and (v) time of day and target category, as we expected more sniffs at fresh food in the morning when it was distributed. We included individual ID and the ID of the observational protocol as random effects. For 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 time of day × target category within individual ID, and target category within protocol ID.

2.3.2 | Model B: Olfactory inspection of females

With model B we investigated 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 thus our predictions 4 and 5. 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. We fitted female age (linear and squared, to account for potential non-linear age effects on fertility) and male age, female contraception status, and Julian day as test predictors, along with time of day and group as control predictors. We included the two-way interactions of male age and female age (linear and squared), respectively, to account for the possibility that an effect of male age on olfactory inspection could be modulated by the female's age in a linear or non-linear fashion: the fertility status of young and old females may be more uncertain to an inspecting male compared to prime-aged females, particularly to young, inexperienced males. We also included an interaction between male age and contraception status in case inexperienced males would be more prone to gather additional cues about female fertility. We included female and male ID as random effects. For the random effect of male ID we incorporated the random slopes of Julian day, female age and contraception, and for female ID, the random slopes of Julian day and male age.

2.3.3 | Model C: Genital inspections and copulation

Using focal and ad libitum data as described for model B, we fitted model C with a binominal error distribution to investigate the influence of female and male characteristics and the occurrence of olfactory inspection on whether a genital inspection was followed by a copulation ($N = 176$ genital inspections), thus testing prediction 6. We fitted female and male age, contraception (yes/no) and olfactory inspection (yes/no) as test predictors and time of day, group and Julian day as control predictors. We initially included 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, and we therefore removed the interactions from the model, after which the stability issues vanished. We included female and male ID as random effects, with Julian day, olfactory inspection, contraception and female age as random slopes for male ID, and Julian day, olfactory inspection and male age as random slopes for female ID.

2.4 | General model procedures

For all models, we z-transformed covariates to facilitate interpretation of model coefficients and model convergence (Schielzeth, 2010). We computed variance inflation factors (VIF) ("vif" function of the package "car," (Fox & Weisberg, 2019) to check for collinearity of predictors (Quinn & Keough, 2002). With largest VIFs of 1.08 (model A), 1.3 (model B) and 1.1 (model C), we detected no collinearity issues. We tested all models for over- and underdispersion, with resulting dispersion parameters of 0.12 (model A), 0.87 (model B), and 0.65 (model C). As models A and C were underdispersed, the computed *p* values should be considered as conservative (i.e., potentially biased towards higher *p* values). We assessed model stability by excluding levels of random effects one at a time. None of the models showed stability issues, except model C when fitted with interactions (as noted above).

We assessed the effect of test predictors on the response variable using a likelihood ratio test (LRT) to compare the full model to a null model without the test predictors (Dobson, 2002; Forstmeier & Schielzeth, 2011). If this comparison was significant ($p < 0.05$) or a trend ($p < 0.1$), we determined the *p* values of the individual predictors using LRTs (function "drop1," package "lme4" version 1.1-31, 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 (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, we removed interactions with a $p > 0.1$ from the final models (Engqvist, 2005), but only after conducting the respective full-null model comparison to ensure that predictions were tested with all predictors included. We report final models (excluding non-significant interactions) in the main text and, if different from final models, full models in the supplementary information (Tables S2 and S3). We computed 95% confidence intervals for all terms in the final model with parametric bootstrapping ($n = 1000$ simulations) using the "bootMer" function from the package "lme4" version 1.1-31.

3 | RESULTS

In total, we observed 503 sniffs across all focal observations (96 h), with 1.7 ± 1.3 (mean ± *SD*) sniffs per individual per 20 min observation period (5.2 sniffs per hour). Females sniffed a total of 306 times (mean ± *SD*: 6.4 ± 4.8 per hour) and males 197 times (mean ± *SD*: 4.1 ± 2.3 per hour, Table 2). The vast majority of sniffs (83%) during focal observations were directed at food items, while 8% and 9% were directed at social or other targets, respectively (Table 2).

In the target context "food," monkeys sniffed 49 identifiable types of edible items (Table S4). In 288 (69%) of the 420 cases, the monkeys consumed the item after sniffing it, while they discarded the item in the remainder.

Female swellings were the target of 70% (28/40) of social sniffs (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) and one at a juvenile male by a subadult male. Of the 43 sniffs at "other" targets, monkeys sniffed themselves 23 times (e.g., their hand), the environment (e.g., tree branch or ground) 14 times and human-made objects (e.g., camera trap) 6 times.

In addition, we observed 136 sniffs ad libitum, of which 70 were directed at food, 44 at conspecifics and 22 at other targets. Of the 136 sniffs, we observed 41 by infants too young to identify and 87 by identifiable individuals, with distributions across sex and age classes similar to data recorded during focal observations. Females directed 36 of 52 sniffs at food, 8 at conspecifics (mostly infants), and 13 at themselves or the environment. Males directed 16 of 30 sniffs at food, 10 at conspecifics and four at themselves or the environment. We also observed 17 cases of infants sniffing their mother's mouth (and in one case the grandmother's mouth) while she was feeding.

TABLE 2 Number of sniffs directed to different targets for 48 focal animals in 96 h of focal observations.

Sniffer sex	Food	Social	Other	Sum
Male	150	29	18	**197**
Female	270	11	25	**306**
Sum	**420**	**40**	**43**	***503***

Note: Bold values indicate sums per category, the value in italics the overall sum.

3.1 | 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, $N = 864$, $\chi^2 = 195.95$, $df = 14$, $p < 0.001$, marginal $R^2 = 0.322$, conditional $R^2 = 0.851$). Specifically, sniffing frequencies differed between the sexes, but the sex effect 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, while males sniffed more often at social targets than females (Tables 2 and 3, Figure 1). We observed more sniffs during feeding than non-feeding focal follows. Furthermore, younger individuals sniffed more often than older individuals (Table 3, Figure 2).

Of the control predictors, Julian day and time of day significantly affected sniffing frequencies (Table 3). In particular, we observed more sniffs earlier in the season and in the morning versus afternoon. No other predictors had a significant influence on sniffing frequencies.

3.2 | Model B: Olfactory inspection of females

Data on male inspections of sexual swellings showed that 51 of 176 visual inspections were accompanied by an olfactory inspection of the swelling. The parameters investigated in model B tended to affect the occurrence of olfactory inspections (LRT, $N = 176$, $\chi^2 = 15.262$, $df = 8$, $p = 0.054$, marginal $R^2 = 0.212$, conditional $R^2 = 0.411$). Specifically, the interaction between male age and contraception tended to influence the probability of an olfactory inspection (Table 4), whereby younger males generally tended to sniff slightly more during an inspection than older ones, but this effect was more pronounced when inspecting non-contracepted females (Figure 3).

3.3 | 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 (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 (Table 5). In fact, only 2 of 51 visual *and* olfactory inspections were followed by a copulation, while copulation followed genital inspection in 44 of 125 solely visual inspections. Female age also influenced the copulation probability, with copulations more likely after inspections of younger versus older females (Table 5).

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 × 3 target categories = 864).

Term	Estimate	*SE*	CI 2.5	CI 97.5	χ^2	*p*
Intercept	−0.114	0.228	−0.532	0.329	[a]	[a]
Test predictors						
Sex (male)	−0.570	0.209	−0.976	−0.158	[a]	[a]
Target category (other)	−6.972	1.519	−8.457	−6.524	[a]	[a]
Target category (social)	−6.187	1.202	−8.524	−6.146	[a]	[a]
Age	−0.365	0.109	−0.544	−0.161	10.357	0.001
Observ. context (non-feeding)	−1.138	0.212	−1.473	−0.693	29.040	<0.001
Control predictors						
Group (2)	0.093	0.207	−0.274	0.479	0.155	0.694
Julian day	−0.303	0.112	−0.490	−0.085	7.184	0.007
Time of day (morning)	0.757	0.194	0.346	1.064	12.058	<0.001
Interactions						
Target category × sex					4.720	0.094
Target category (other) × sex (male)	0.506	2.222	−0.245	1.490		
Target category (social) × sex (male)	1.727	1.440	0.322	2.147		

Note: Terms in parentheses indicate trait levels relative to the respective reference level. χ^2 and *p* values are derived from likelihood ratio tests to determine the significance of the individual test predictors.

Abbreviations: CI, confidence interval; GLMM, generalized linear mixed model; *SE*, standard error.

[a] Not presented because of having a very limited interpretation.

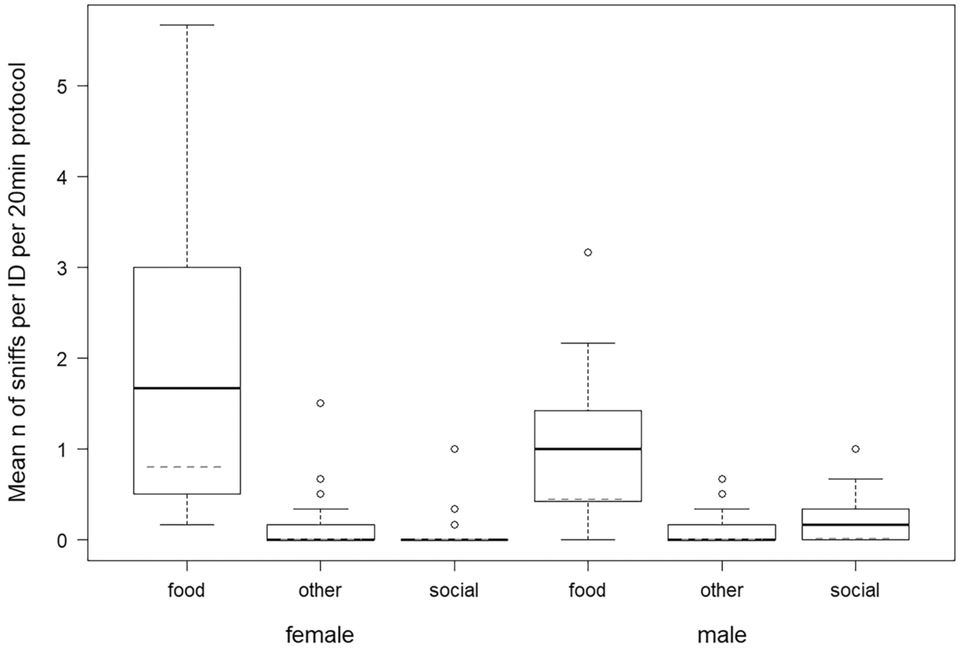

FIGURE 1 Mean number of sniffs per individual per 20 min focal observation for both sexes divided into the target categories food, other and social. Boxes represent medians and first and third quartiles, while the whiskers represent 1.5 times the interquartile range. Outliers are represented by points.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

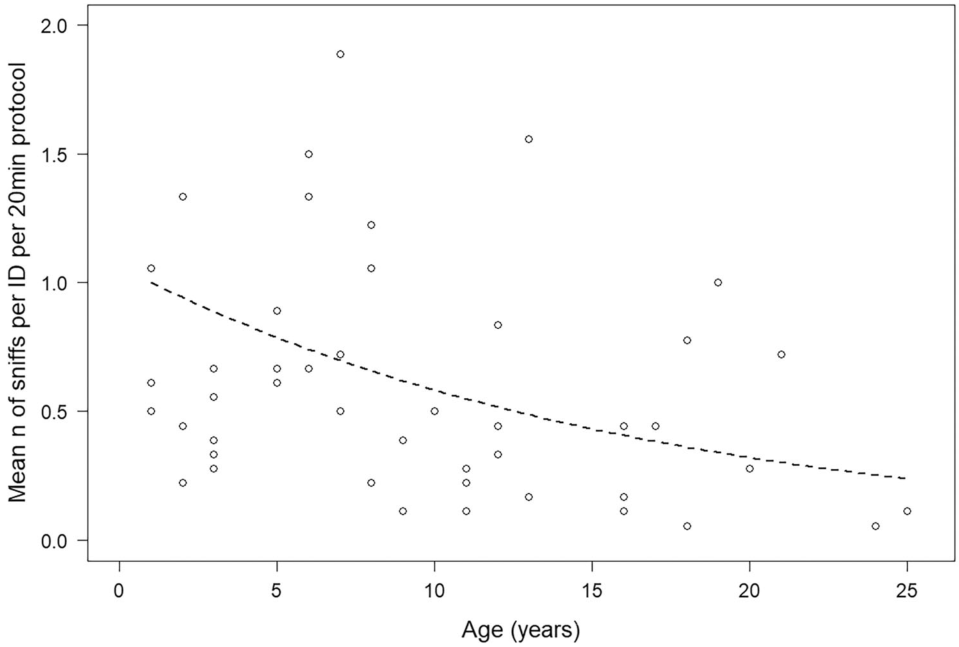

FIGURE 2 Mean number of sniffs per individual per 20 min focal observation across age. Dashed line represents the model estimate when all other predictors are at their average values.

TABLE 4 Results of the binomial GLMM (model B) investigating the probability of an olfactory inspection during genital inspections ($N = 176$ inspections).

Term	Estimate	*SE*	CI 2.5	CI 97.5	χ^2	*p*
Intercept	−1.739	0.726	−5.981	−0.505	[a]	[a]
Test predictors						
Male age	−1.269	0.525	−4.826	−0.563	[a]	[a]
Female age	0.425	0.263	−0.071	1.271	2.461	0.117
Female age^2	0.254	0.171	−0.163	0.861	2.041	0.153
Contraception (yes)	0.747	0.771	−0.762	4.872	[a]	[a]
Control predictors						
Julian day	−0.151	0.244	−0.854	0.445	0.355	0.552
Time of day (morning)	0.222	0.413	−0.757	1.181	0.271	0.603
Group (2)	−0.715	0.575	−2.208	0.677	1.269	0.260
Interactions						
Male age × contraception (yes)	1.014	0.599	0.01	4.366	2.998	0.083

Note: Values in parentheses indicate trait levels relative to the respective reference level. χ^2 and *p* values are derived from likelihood ratio tests to determine the significance of the individual test predictors.

Abbreviations: CI, confidence interval; GLMM, generalized linear mixed model; *SE*, standard error.

[a] Not presented because of having a very limited interpretation.

4 | DISCUSSION

This study contributes to understanding the sniffing behavior of Barbary macaques and thereby, catarrhine primates in general. 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 sniff more frequently.

With an average of 5.2 sniffs per hour, Barbary macaques sniffed at similar rates as some guenon species (*Cercopithecus diana*, *neglectus*, and *hamlyni*) observed in captivity (6.1 sniffs/h, Zschoke

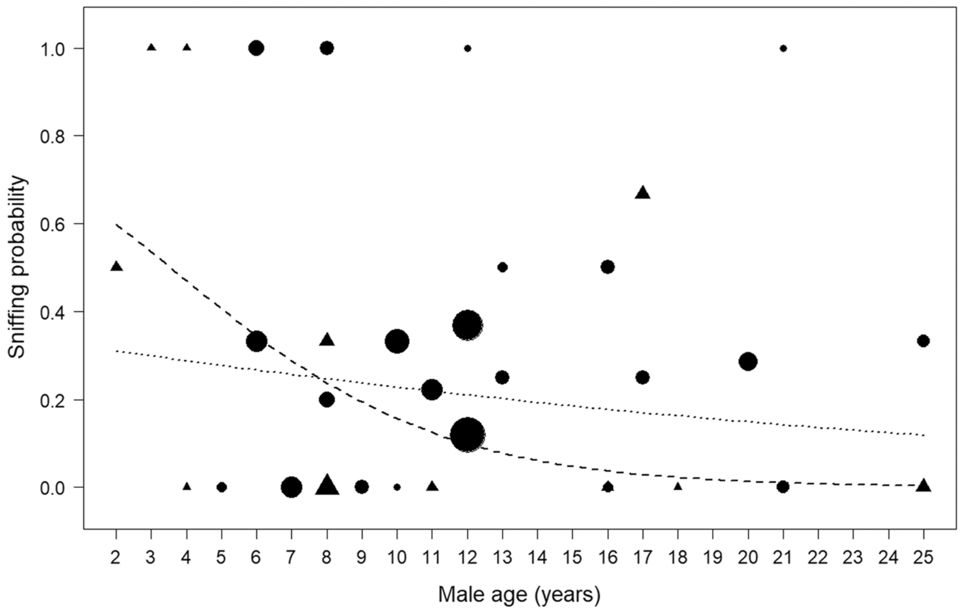

FIGURE 3 Sniffing probability during an anogenital inspection as a function of male age and female contraception. Triangles represent non-contracepted females, circles contracepted females. Lines represent the model estimate when all other predictors are at their average value (dashed line: non-contracepted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

TABLE 5 Results of the binomial GLMM (model C) investigating the probability of a copulation following a genital inspection ($N = 176$ inspections).

Term	Estimate	*SE*	CI 2.5	CI 97.5	χ^2	*p*
Intercept	−0.280	0.705	−2.452	1.701	[a]	[a]
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
Time of day (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

Note: Values in parentheses indicate trait levels relative to the respective reference level. χ^2 and *p* values are derived from likelihood ratio tests to determine the significance of the individual test predictors.

Abbreviations: CI, confidence interval; GLMM, generalized linear mixed model; *SE*, standard error.

[a] Not presented because of having a very limited interpretation.

& 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 wild chimpanzees (0.04–0.1 sniffs/h depending on season, Matsumoto-Oda et al., 2007). Furthermore, sniffing frequencies in Barbary macaques were not constant, but decreased over the course of the study towards the height of the mating season. Different sampling conditions (wild *vs*. captivity, focal *vs*. group sampling) and the sparse availability of similar studies with different primate species make meaningful comparisons between species difficult, calling for more studies on a wider range of species to assess interspecific patterns.

4.1 | Influence of context and target

In our study, most sniffs were directed at food, which parallels findings for great apes (Jänig et al., 2018), guenons (Zschoke & Thomsen, 2014) as well as mandrills and olive baboons (Laidre, 2009).

Primates have been suggested to rely on olfactory cues to find and identify ripe food (e.g., Nevo & Heymann, 2015), obtain information about nutritional value (Dominy et al., 2001) and possible contamination (Sarabian et al., 2020). We were unable, however, to assess systematically why the macaques in our study sniffed certain items but not others.

4.2 | Influence of sex and age

In support of prediction 1, we found an effect of sex on sniffing frequencies that tended to be modulated by the target (food, social or other) of a sniff, although the result was not very robust. In chimpanzees (Jänig et al., 2018; Matsumoto-Oda et al., 2007) and owl monkeys (*Aotus nancymaae*; Spence-Aizenberg, 2017), males also sniffed more than females in a socio-sexual context. Socio-sexual sniffs might help males to accurately assess female fertility, which may be particularly beneficial in societies with high levels of male–male competition such as chimpanzees (Jänig et al., 2018; Matsumoto-Oda et al., 2007). In line with this idea, adult Barbary macaque males directed almost all social sniffs at female sexual swellings and only one at another adult male. Olfactory inspection may therefore play a role in modulating male-female socio-sexual relationships, potentially related to male mate choice and mating decisions. In contrast, sniffing does not seem as important for males to gather direct information about other males. Similarly, we observed a female sniff another female's anogenital swelling only twice. Intrasexual assessment of potential competitors may not be particularly relevant in a promiscuous species like the Barbary macaque, or other sensory modalities may be more important, such as a male competitor's size or female condition (visual cues: Setchell et al., 2008; Tschoner, 2015, auditory cues: Engelhardt et al., 2012; Pfefferle et al., 2008). We also cannot rule out that monkeys may have perceived conspecific odors just by being nearby, without the need for an active sniff.

Female Barbary macaques sniffed food more than males, supporting prediction 2 and corresponding to observations of female chimpanzees (Matsumoto-Oda et al., 2007). Female primates tend to be more wary than males of parasitic or bacterial contamination through food that is rotten or spoiled with feces (Poirotte et al., 2019; Sarabian & MacIntosh, 2015; Sarabian et al., 2020), as evident from more olfactory inspection and manipulation of contaminated food (Sarabian et al., 2020). Similar contamination risk avoidance might apply to Barbary macaques, but a systematic analysis of parasite loads in both sexes would be needed to assess this possibility.

Comparable to great apes (Jänig et al., 2018), younger Barbary macaques sniffed more often than older ones, supporting prediction 3. These findings agree with the consensus that young animals inspect their environment more closely than older ones because they are still in the process of learning about food, conspecifics or their general environment. Because the decrease of sniffing events with age in Barbary macaques appears quite linear and starts already in young adults rather than showing a sharp drop at old age (Figure 2), it is unlikely that it is primarily caused by a loss of olfactory capability at old age. Rather, this decrease may reflect changes in experience and/or individual requirements. Particularly in the context of food assessment, sniffing frequencies may decrease as animals gain experience with different foods and learn to assess food quality based on visual or tactile cues. Additionally, older females reaching post-reproductive age may not need to be as careful of contamination risks as females who are still reproducing.

We also observed several infant monkeys sniffing their mother's (or grandmother's) mouth during feeding. In each case the infants appeared to observe the eating behavior and tried to inspect the item visually. This “muzzle-muzzle” behavior has been observed in different mammals, including primates, and may enable the individuals to smell the breath of their conspecifics and gather information on which food has been assessed as safe and valuable to eat by conspecifics (Arakawa et al., 2013; Laidre, 2009; Nord et al., 2021).

4.3 | Olfaction in sexual interactions

Most social sniffs occurred in a sexual context and were directed at the female anogenital swelling, whereby about one-third of inspections included sniffing. In line with prediction 4, younger males tended to sniff more frequently during an inspection than older ones, particularly if the inspected female was not contracepted. Although contracepted females showed similar swelling sizes and patterns of tumescence and detumescence as non-contracepted ones (M.S., B.M.W. personal observations), males may have detected subtle differences in the visual appearance of the swellings. The nature of these differences and how they modulated sniffing behavior in an age-dependent fashion warrants further investigation. In contrast to prediction 5, however, we did not observe an effect of female age on the likelihood of olfactory inspections.

In line with prediction 6, the occurrence of an olfactory inspection affected subsequent sexual behavior. Sniffing the anogenital swelling usually led to no subsequent copulation, which may indicate that sniffing provides additional information about female fertility or indicators of male competitors such as sperm remains that deters males from engaging in costly mating behavior. By inhibiting some males from inspecting their anogenital swelling at close range, females may even manipulate access to olfactory information depending on the characteristics of the male. However, although male Barbary macaques in Morocco inspected female swellings more frequently during pre-fertile and fertile versus post-fertile states, males mated at similar rates with females in fertile and non-fertile maximum swelling phases (Young et al., 2013). The results of Young et al. (2013) thus seem to contradict our interpretation, but the two studies addressed slightly differed aspects. We assessed whether inspections using different senses were followed by a copulation, but did not record copulations occurring without prior inspection, which may also explain why we did not find an effect of Julian day on the likelihood of copulations. Young et al. (2013) related inspection and mating rates to fertile states of females, but did not directly relate the occurrence of copulations to prior inspections. Bringing these aspects together in future studies may help to better understand how fertility cues in different modalities inform male mating decisions.

Our assessment of olfactory inspections and their consequences (addressing prediction 4, 5, and 6) was certainly limited, because we did not track changes in female swelling size, ovarian hormone levels or whether observed copulations actually led to ejaculation. Additionally, female odor cues could potentially be gathered from a greater distance than what we defined as a sniff in this study. It is possible that active sniffs occurred only in situations in which olfactory cues were subtle and required bringing the nose close to the odor source, while at other times, odors may have been perceivable from a greater distance, requiring no movement towards the odor source that is visible to an observer. We therefore cannot rule out entirely that what we scored as visual inspections were actually multimodal ones that included a potential olfactory component detectable from a greater distance. As we only observed animals actively protruding their nose from a very close distance to an object and not from further away, however, we believe that our definition covers the vast majority of instances of active olfactory sampling.

Unfortunately, the low number of olfactory inspections that led to copulation did not allow us to address whether aspects such as female age or hormonal contraception modulated an effect of olfactory inspection on copulation probabilities. Studies on other primate species report differences in mating behavior or olfactory signals related to hormonal contraception (Japanese macaques, *M. fuscata*, Leca et al., 2018, ring-tailed lemurs *Lemur catta*, Crawford et al., 2011). By contrast, contracepted female owl monkeys (*Aotus nancymaae*) showed no change in chemical profiles or in the ability to form new pair bonds with males (Spence-Aizenberg et al., 2018). Our results provide no indication that female contraception affected the likelihood of a copulation after inspection, but the available data do not allow us to assess whether contracepted females were inspected less than non-contracepted ones. More comprehensive focal observations of sexual interactions along with a hormonal assessment of female fertility would be needed to draw further conclusions about the role of sniffing in Barbary macaque mating interactions. 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 lives of Barbary macaques.

AUTHOR CONTRIBUTIONS

Miriam Simon: data curation (lead); formal analysis (equal); visualization (lead); writing—original draft (lead); writing—review & editing (equal). **Anja Widdig**: conceptualization (supporting); resources (lead); supervision (supporting); writing—review & editing (equal). **Brigitte M. Weiß**: conceptualization (lead); formal analysis (equal); funding acquisition (lead); methodology (lead); project administration (lead); supervision (lead); writing—original draft (supporting); writing—review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data on sniffs recorded during focal observations and anogenital inspections are available as Supporting Information material.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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