Chemical signatures of social information in Barbary macaques

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Abstract

Primates are well-known for their complex social lives and intricate social relationships, which requires them to obtain and update social knowledge about conspecifics. The sense of smell may provide access to social information that is unavailable in other sensory domains or enhance the precision and reliability of other sensory cues. However, the cognition of social information in catarrhine primates has been studied primarily in the visual and auditory domain. We assessed the social information content of body odor in a catarrhine primate, the Barbary macaque (*Macaca sylvanus*), in three semi-free ranging groups at Affenberg Salem, Germany. In particular, we related socially relevant attributes (identity, genetic relatedness, rank, sex, age, group membership) to chemical profiles of body odor. We applied non-invasive active sampling via thermal desorption tubes, and analyzed samples by gas chromatography–mass spectrometry. We found robust evidence for olfactory individual signatures, and limited support for kin signatures. Chemical profiles were also related to group membership, but little to rank, sex or age. The detected associations between chemical profiles and socially relevant attributes form the theoretical foundations for olfactory information transfer, highlighting the potential of body odor to provide valuable social information in this highly visually oriented primate.

Keywords: individual signature, catarrhine primate, relatedness, social information, body odor

Introduction

The development and maintenance of social relationships requires animals to acquire and update social information about conspecifics. For instance, animals that form stable relationships need to be able to recognize the unique features of other individuals, and indeed, individual recognition is widespread in the animal kingdom (e.g. Rendall et al., 1996; Scheiber et al., 2011; reviewed in Tibbetts and Dale, 2007). Additionally, social animals may interact differently with each other depending on attributes such as sex, rank, group membership or genetic relatedness (Ward and Webster, 2016). Primates are particularly well-known for forming intricate social relationships and frequently show strong and long-lasting relationships among kin (reviewed in Silk, 2001), but also with unrelated individuals (e.g. Goffe et al., 2016; Ostner and Schülke, 2014). Representations of these social relationships are based on the recognition of traits such as identity, rank and kinship (Seyfarth et al., 2005). For instance, rhesus macaques (*Macaca mulatta)* discriminate individuals, and familiar as well as unfamiliar kin (Pfefferle et al., 2014a, 2014b; Rendall et al., 1996). Various macaque species also appear to categorize individuals according to their relationships with others (see overview in Cheney and Seyfarth, 1999). Similarly, baboons discriminate individuals according to their identity and rank, and they also appear to recognize third-party relationships (Cheney et al., 1996; Cheney and Seyfarth, 1999; Seyfarth et al., 2005).

The social information underlying differentiated interactions can be emitted and received via different sensory modalities (Moreira et al., 2013; Yorzinski, 2017). Olfaction is among the evolutionarily oldest of the animal senses (Wyatt, 2014), and social communication is considered as one of its major functions (Stevenson, 2010). Indeed, social interactions are mediated via olfaction in numerous mammals (e.g. African elephants, *Loxodonta africana*, Bates et al., 2008; black rhinoceros, *Diceros bicornis*, Linklater et al., 2013), including primates. For instance, many strepsirrhine (lemurs, lorises and galagos) and platyrrhine (South American) primates show pronounced scent-marking behavior (e.g. delBarco-Trillo et al., 2012; Janda et al., 2019; Scordato and Drea, 2007). Observational, experimental and chemical studies suggest that primate scent marks as well as odors

emanating directly from the body may convey a wealth of information about a sender such as identity, sex, age, rank or reproductive state (e.g. Drea and Scordato, 2008; Fontani et al., 2022; Janda et al., 2019; Kücklich et al., 2019), and that scent marks primarily function in intra-sexual competition and mediating reproductive behavior (Drea and Scordato, 2008; Heymann, 2006a; Moreira et al., 2013).

Notably, vision has gained more and more importance during primate evolution (see overview in Veilleux et al., 2022), and catarrhine (African and Asian) primates, in particular, are highly visually oriented animals (Kawamura, 2016). Scent-marking, on the other hand, is uncommon in catarrhines (Freeman et al., 2012), and in contrast to evolutionarily older primates, catarrhines lack a functional accessory olfactory system (the vomeronasal organ, VNO, Smith et al., 2014). Accordingly, catarrhine primates have long been regarded as little predisposed for olfactory communication (Drea, 2015). However, also the main olfactory system has an important part in the processing of cues relevant to social recognition, rendering the lack of a functional VNO of little significance for the communicative functions of olfaction (see Stevenson, 2010; Tang-Martinez, 2001). Furthermore, catarrhine olfactory sensitivity may be on par or even exceed those of other mammals (Laska and Seibt, 2002a, 2002b). Research on catarrhine olfaction has primarily focused on humans (Heymann, 2006b). Similar to other primates, human body odor has been associated with socially relevant information such as identity, sex, age, kinship or reproductive status (reviewed in Loos et al., 2023), although the latter is debated (see Zetzsche et al., 2024). Also in mandrills (*Mandrillus sphinx*), one of the few catarrhine species known to have scent glands, body odor has been related to sex, age, dominance status, group membership and, possibly, individual identity (Setchell et al., 2010; Vaglio et al., 2016). Results of recent studies further show that also the body odor of other catarrhine species contains information on socially relevant attributes such as sex, rank, female fertility, genetic relatedness or group membership may be recognized and acted upon by conspecifics (*M. mulatta*: Henkel et al., 2015; Weiß et al., 2018a; *Pan troglodytes*: Henkel and Setchell, 2018; *Papio anubis*: Vaglio et al., 2021; *M. fuscata*: Rigaill et al., 2022). Nonetheless, with the exception of a few species such as

humans or mandrills, olfaction remains severely understudied in catarrhine primates (Drea, 2015). This is particularly true for chemical profiles of body odors (i.e. the presence/absence and relative abundance of chemical compounds), which restricts our understanding of which olfactory cues may be available to conspecifics within catarrhines at all. To reduce this gap, we assessed the social information content of (i.e. potential olfactory cues in) body odor in a catarrhine primate by relating chemical profiles of body odor to socially relevant attributes of Barbary macaques living in natural social structures under semi-free conditions at Affenberg Salem, Germany.

Like other macaque species, Barbary macaques live in multi-male, multi-female groups with female philopatry and male dispersal (Kuester and Paul, 1999; von Segesser et al., 1999). Matrilineal kin (especially mother-offspring and maternal half-sibling dyads) form strong bonds throughout their lives and are therefore highly familiar with each other (Roubová et al., 2015; Silk, 2001). Patrilineal kin (e.g. father-offspring or paternal half-sibling dyads), on the other hand, typically are less closely associated and may even reside in different groups so that they can be expected to be less familiar with each other(see Kuester et al., 1994; Widdig, 2007). Females show matrilineal rank acquisition in which female relatives take similar ranks (Paul and Kuester, 1987; Prud'homme and Chapais, 1993). Adult males form dominance hierarchies in which older males tend to rank higher, but males beyond their prime (i.e. older than 14-16 years) are subordinate to prime age males due to being in inferior physical condition (Berghänel et al., 2011b). Male Barbary macaques also form strong, enduring affiliative relationships often referred to as "friendships" (Young et al., 2014), whereby triadic interactions between two males and an infant represent an important form of male affiliative interaction (Paul et al., 1996).

Various studies suggest that Barbary macaques can discriminate individuals, sexes, age classes and group members using visual or acoustic cues (Fischer, 2004; Ritter, 2022; Schell et al., 2011). They further distinguish familiar maternal kin from non-kin (acoustic cues: Hammerschmidt and Fischer, 1998). However, Barbary macaques, which are considered to be particularly promiscuous (Small, 1990), do not seem to differentiate between unfamiliar kin and non-kin either in a mating context

(Kuester et al., 1994) or in infant care (Paul et al., 1996, 1992). It remains unclear whether this is due to i) a lack of kin-related cues, ii) monkeys not being able to recognize available cues or iii) monkeys recognizing kin-related cues but not acting upon them. Kin-related cues in body odor composition have been shown in a closely related species (rhesus macaques, Weiß et al., 2018a), and Barbary macaques also use olfaction in social contexts (Simon et al., 2024), but systematic studies on olfactory kin signatures or other socially relevant information in Barbary macaque body odor are, to date, absent.

In the present study we aimed to i) identify variation in body odor composition (i.e. presence and abundance of chemicals) that is systematically associated with socially relevant information about individuals, and ii) to pinpoint potential semiochemicals (i.e. compounds and compound mixtures involved in chemical interactions between organisms, Wyatt 2014) associated with the respective traits. Our particular focus was on traits that form the basis for differentiated social relationships, i.e. individual identity, genetic relatedness between and rank of individuals. We further assessed effects of sex, age and group membership while statistically controlling for potential seasonal and methodological variation in the chemical profiles of body odors. We hypothesized that the odorants emanating from the skin and fur of Barbary macaques contain socially relevant information. In particular, we expected the similarity between chemical profiles to be greater within than between individuals, and higher among related than among unrelated individuals. Because maternal kin are in frequent physical contact and may exchange odors from the environment or share more of the odor-producing microbiome, we expected maternal kin to exhibit stronger kin signatures than paternal kin, for whom kin signatures should primarily result from similarities in their genetic architecture. We also expected individuals of similar rank to have more similar chemical profiles and/or to show rank-related differences in the relative abundance of particular compounds (as also suggested in Burgener et al., 2009), because individuals of similar rank may have similar hormonal profiles (e.g. androgens or glucocorticoids), access to food resources and/or space use (see Majolo et al., 2012; Mehta and Josephs, 2010; Naud et al., 2016; Schoof et al., 2011). Finally, given the comprehensive evidence for

135 olfactory differences with respect to sex, age and group membership in other primates, we also
136 expected similarities between chemical profiles and/or the relative abundance of compounds to be
137 associated with these traits.

138

139 Methods

140 *Study animals*

141 The study was conducted at Affenberg Salem, Germany, home to ~ 200 Barbary macaques in three
142 social groups roaming year-round within a 20 ha forested enclosure. The monkeys are well-
143 habituated to humans, as the park is open to visitors from spring to autumn, and to researchers year-
144 round (see de Turckheim and Merz, 1984 for details on the park). The monkeys' diet consists of
145 plants and insects found naturally within the park as well as fruit, vegetables and grain that is
146 provided daily by park staff. Ponds and water troughs are distributed throughout the park and grant
147 *ad libitum* access to water. Individuals differ in facial pigmentation patterns, coat color and stature
148 and have an alphanumeric code tattooed on the inner thigh, which makes them well distinguishable
149 for experienced observers. Park staff monitor the groups on a near-daily basis and record major life
150 history events such as births, deaths or group changes. About two thirds of the adult females receive
151 hormonal implants (Implanon NXT) to control population size.

152 We collected odor samples from a total of 72 focal males and females from all three groups ("C", "F"
153 & "H") and across all ages (2 - 27 years, mean ± SD = 10.5 ± 5.4 years) that were most suitable to
154 address the main study questions. Focal animals included 13 females without and 18 females with
155 hormonal contraception throughout the study period; two females received contraception for part of
156 the study period (see supplement 2). To address individual signatures, we included particularly well-
157 habituated reproductively mature individuals (> 4 years) that could be sampled frequently (10
158 samples per ID, Pollard et al. 2010). To address kinship, we included mothers/fathers and their
159 offspring (> 2 years, because younger individuals could not be reliably habituated to sampling yet).

For rank of males and females, we selected individuals from the highest- and lowest-ranking adults in their respective groups.

Odor sampling

One experimenter (B.M.W.) collected 476 odor samples from the focal animals (mean ± SD = 6.6 ± 2.6 samples per ID) in five sampling periods between October 2020 and April 2022. Sampling took place in spring, summer and autumn, but, for logistic reasons, not during the peak of the mating season in the months of November, December and January. As Barbary macaques, like other macaque species, do not appear to have specialized scent glands, we non-invasively collected the airborne volatile and semi-volatile compounds emanating from the skin or fur of the animals across different parts of the body (see below). We employed active sampling with thermal desorption (TD) tubes (stainless steel, Supelco), which contained two adsorbent polymers (Tenax TA and XAD-2, Sigma Aldrich) that trap a wide range of chemical compounds (Kücklich et al., 2017). The tubes were connected to a silently operating air pump (BiVOC2, Holbach) via a silicone hose (Weiß et al., 2018b). To be able to trap the air in the immediate vicinity of the animals (1 to 15 cm, mean ± SD = 3.5 ± 2.6 cm), monkeys were habituated to retrieve pieces of peanuts from a pipe collar (7.5 cm diameter) strapped to a horizontal branch or rail while the experimenter stood next to the setup and pointed a wooden stick with the TD tube mounted at its end towards the monkey. Once a monkey calmly started to retrieve the peanuts, the experimenter opened the TD tube, positioned it close to the monkey and started the air flow through the tube with the flow rate set to 1 L/min. Sampling was resumed until an air volume of 0.5 – 1 L was collected. If the animal moved away before the sample was completed, the pump was immediately stopped, the tube closed, the volume already sampled noted and sampling resumed as soon as possible onto the same TD tube (mean ± SD = 2.3 ± 1.5 subsamples). A sample was typically completed with < 5 min between subsamples, except for 10 of the 476 samples in which the sample was completed on different days (see supplement 3). Samples were collected from body parts that could be reliably sampled without disturbing the animals, which

primarily constituted the shoulders, flanks or outer thighs (54 % of samples being collected exclusively from these regions, and 86 % of samples included these regions). Whenever possible we avoided sampling the hands, feet or facial area, which were the body parts most likely contaminated with food, feces or other items from the environment. To be able to statistically control for potential variation arising from the sampled body parts we grouped them into 4 categories: "upper" constituted samples collected from the upper part of the body (i.e. arms, shoulders and/or the back of the head), "central" the middle part of the body (i.e. flanks, central back or chest), and "lower" the lower part of the body (i.e. hips, thighs and legs). Finally, we grouped all samples collected from multiple regions of the body (i.e. upper, central and/or lower) into the category "mixed" (see supplement 3).

We avoided sampling when conspecifics were within 3 m of the target animal or higher-ranking individuals were within sight, when animals had body contact with group members less than 5 minutes before, when the monkeys were wet or when it was very windy. To avoid disturbances during sampling and contamination with human scents, we did not collect any samples when visitors or park staff were within 15 m. All equipment was handled wearing disposable gloves. The experimenter wore a medical mouth-nose cover during sampling and avoided the use of perfumed products or strongly smelling foods before and on sampling days.

To control for chemical compounds originating from the sampling material and sampling environment *per se*, we further collected samples of air in the absence of animals (N = 17), TD tubes mounted for sampling in the absence of animals but without drawing air through the tube (N = 6) and TD tubes taken to the field but remaining closed at all times (N = 9) as blanks. Before each use, we cleaned the TD tubes in a thermal conditioner (TD Clean-Cube, Scientific Instruments Manufacturer) under a constant stream of nitrogen for 120 minutes. When not in use, the tubes were closed tightly with Swagelok brass caps, wrapped in aluminum foil and stored in airtight bags at ambient temperature.

212

213 *Chemical analysis & profiling*

214 Samples were analyzed with gas chromatography – mass spectrometry (GC-MS) on a Shimadzu
215 TQ8040 GC-MS coupled to a thermal desorption unit (TD-20) with a scan range from 30 to 500 *m/z*
216 following established GC-MS protocols for the analysis of TD tube samples (Kücklich et al., 2017;
217 Weiß et al., 2018b). In the process, the trapped organic compounds were entirely desorbed from the
218 tube, which then was conditioned and re-used for sampling. To remove any potential residues from
219 previous measurements from the column, we ran three blank samples at the start and end of each
220 batch as well as after every tenth sample.

221 GC-MS data were processed following an established, semi-automated procedure (Kücklich et al.,
222 2017; Weiß et al., 2018b), in which a preliminary compound library was created through automated
223 peak detection and alignment of peaks by retention time using AMDIS (version 2.71, Stein 1999). We
224 manually corrected this library by taking into account characteristic mass-to-charge ratios of peaks in
225 addition to retention times. For the 264 compounds in this library, we extracted the peak areas for
226 the highest ion not present in adjacent peaks using the Shimadzu GCMS Browser software. In a
227 subsequent data cleaning step we excluded 81 compounds consistently found in blanks with peak
228 areas higher than in the animal samples from further analysis, as they are unlikely to have derived
229 from the target animal (detailed in Weiß et al., 2018b), and performed statistical analyses using the
230 remaining 183 compounds. Furthermore, we assigned undetected peaks, peaks with a signal to noise
231 ratio < 1 and with a peak area below the noise threshold (visually determined to be at 1000) a peak
232 area of 0, because these peaks were not reliably separable from background noise. We tentatively
233 identified compounds statistically related to particular traits (see below) by comparing their mass
234 spectra with the best matches of the NIST Mass Spectral Library (NIST14; National Institute of
235 Standards and Technologies, Gaithersburg, MD, USA).

236

237 *Parentage analysis*

238 Pregnancies and births have been monitored consistently by Affenberg staff since the 1970s, so that
239 partial pedigrees could be built tracing back maternal relatedness over 5-6 generations for most
240 individuals based on these long-term observational records.

241 For genetic parentage analysis we used DNA extracted from blood, tissue, hair or feces of 144
242 individuals (including 68 of the 72 odor-sampled animals, see supplement 1 for details on genetic
243 samples). These included 28 offspring from cohorts 2017-2019 (for 22 of which we also collected
244 odor samples), their mothers and potential sires. Because Barbary macaques may also reproduce
245 with extra-group partners (Brauch et al., 2008), we considered all males in the population that were
246 alive and at least 4 years of age at the onset of the respective mating season as potential sires. For
247 animals born in cohort 2017 we were able to obtain samples for 96 %, and for cohorts 2018-2019,
248 97 % of all potential sires.

249 We genotyped the DNA samples using a panel of up to 23 polymorphic microsatellite markers
250 established for the study population by (Westphal, 2020), whereby we eventually focused on the 16
251 markers with the lowest dropout rate, that were most reliable, scorable and combinable in
252 polymerase chain reactions (PCR, see Table S1). To increase the amount of host DNA in the samples
253 we used the two-step multiplex approach for PCR amplification (Arandjelovic et al., 2009) by running
254 a first PCR with all markers simultaneously, followed by a second set of PCRs containing diluted
255 multiplex products as amplification templates and 4 – 6 fluorescently labelled primers with different
256 allele ranges. PCRs were conducted in a Mastercycler® vapo.protect thermal cycler (Eppendorf,
257 Hamburg, Germany) following the protocols of Westphal (2020). We performed fragment analysis on
258 an *ABI 3730* sequencer. For allele calling we used the Peak Scanner 2 software (Applied Biosystems®).

259 We typed all individuals at an average of 16.7 ± 2.8 loci. For 27 of the 28 offspring born 2017 – 2019
260 the observed mothers showed no mismatches to their offspring. For one offspring we could not
261 confirm the observed mother genetically, probably due to poor sample quality. In this case we

262 considered the observed mother to be the biological mother, but excluded the offspring from
263 paternity analysis. We could also genetically confirm the observed mother for 38 females and males
264 initially sampled as mothers or potential sires.

265 We used confirmed maternities in the paternity analysis, applying a combination of exclusion and
266 likelihood methods for mother-offspring-putative father trios with the programs Findsire and Cervus
267 following established criteria (e.g. Minkner et al., 2018; Ruiz-Lambides et al., 2018) (see supplement
268 1 for details).

269 We were able to assign fathers to 23 of the 28 offspring from cohorts 2017-2019 with high certainty
270 (see supplement 1 for details). Furthermore, we accepted fathers assigned with high confidence for
271 18 individuals initially sampled as mothers or potential sires in the present study and born between
272 2011 and 2016. For these cohorts, 58-87 % of potential sires were genotyped. We did not accept
273 fathers assigned to older individuals due to the increasingly lower proportion of potential sires
274 sampled. For the 68 odor-sampled and genotyped individuals, we were able to genetically confirm 25
275 fathers and 41 mothers.

276 Based on the genetic analysis and maternal pedigree data from long-term records, we calculated
277 pedigree relatedness (r) per kin line (maternal or paternal/mixed) for each possible dyad in our study
278 using the software TRACE (version 0.1.0, Westphal et al., 2023). Maternal r reflected genetic
279 relatedness exclusively via female ancestors, while paternal/mixed r (hereafter just called "paternal")
280 reflected any connections involving at least one paternal link between two given individuals. As input
281 we used genetically confirmed mothers whenever available, and observed mothers (based on
282 observational records from the field) for all remaining subjects, as well as all available paternity data.
283 Given that mother-offspring dyads are available from long-term observational records, our value of
284 pedigree relatedness for maternal relatedness can be considered as highly precise, reflecting close
285 maternal ($r > 0.125$) but also distant maternal kin ($r \leq 0.125$). However, because no genetic samples
286 could be obtained for potential sires deceased before the onset of the study, paternities could only

be reliably determined for the younger cohorts, and therefore our values of pedigree relatedness for the paternal line are likely underestimated in this analysis.

Dominance and rank

At the onset of the study, we asked experienced park staff to classify individuals from low to high-ranking, and to identify the alpha male and female in each group based on observed agonistic interactions and priority of access to resources. This initial judgement was used to pre-select focal individuals for habituation to the sampling setup. We further conducted dynamic Elo-rating (Newton-Fisher, 2017) using *ad libitum* observations of agonistic interactions (as defined in Berghänel et al., 2011a) throughout all sampling periods. Dynamic Elo-rating allows for incorporating intensities of interactions as well as prior knowledge and therefore requires fewer observed interactions and interacting dyads than unmodified Elo-rating (Neumann et al., 2011) or matrix methods to obtain robust rank estimates (Newton-Fisher, 2017). We used the initial classification by park staff, supplemented by a classification by B.M.W., to define starting values for Elo-rating, and updated this information with 462 female-female and 240 male-male interactions of varying intensities observed between October 2020 and April 2022. We computed ranks separately per sex and group, using the observations during the first two sampling periods as a "burn-in" phase, and extracted the ranks of the focal individuals at the ends of the second to fifth sampling period for further analysis.

Ethical note

The study was approved by Affenberg Salem. All samples collected specifically for this study (i.e. odor and fecal samples) were collected non-invasively and the animals participated in the odor sampling procedure voluntarily. In line with the animal protection law in Germany, we therefore required no further animal ethics approval.

Statistical analysis

General procedures

We conducted all analyses in R (version 4.3.3., R Core Team, 2024).

To investigate chemical similarity between samples, we performed permutational multivariate analyses of variance (perMANOVAs) using the function "adonis2" from the package "vegan" (version 2.6-4, Oksanen et al., 2022). These analyses relate pairwise chemical (dis)similarities between all samples entered into a given analysis to (dis)similarities between traits using distance matrices automatically assembled from the sample-specific information provided. As measure of distance (or dissimilarity) we used Bray-Curtis indices calculated from standardized, log(x+1)-transformed peak areas (Stoffel et al., 2015; Weiß et al., 2018b). Depending on the investigated trait(s) we used different data subsets and predictor variables as described for the different traits below. Unless noted otherwise, we set ID as stratum to account for repeated measures per individual. For perMANOVAs with multiple test predictors we first conducted a full-null model comparison by setting the argument "by" to "NULL", and only if this was significant ($p < 0.05$) we investigated the effects of the single predictor variables by setting the argument "by" to "margin". In case of non-significant interactions, we re-ran the marginal model without the interaction to be able to assess the effect of the respective main terms. We ran all perMANOVAs with the default of 999 iterations.

When the analysis of chemical (dis)similarities involved predictor variables describing pairs of samples (e.g. pedigree relatedness) and/or required the selection of specific pairs of samples (which is not possible with the perMANOVA), we further conducted multi-membership models. Multi-membership models extend multilevel models by allowing to fit data with multiple membership structures that are not purely hierarchical (Chung and Beretvas, 2012), such as terms whose levels are present in more than one variable (e.g. ID in either sample 1 or sample 2 of a given pair-wise comparison). For these models we computed Bray-Curtis dissimilarities from standardized, log(x+1)-transformed peak areas using the package "vegan" and, for easier interpretation, transformed them

into similarities by subtracting the dissimilarity scores from 1. We fitted these models with chemical similarity as response variable and various test and control predictors as described below. As similarity scores follow a beta distribution, we computed the models using a Bayesian approach in the package "brms" (version 2.21.0, Bürkner, 2017), which is the only package we are aware of that implements multi-membership models with beta distribution. We used the default settings for priors, i.e. uninformative priors.

We further conducted compositional mixed model analyses, suitable for data whose components are constrained to sum to a constant value, for a detailed analysis of chemical profiles that considers the peak areas of all compounds per sample rather than overall (dis)similarities between samples, and may therefore aid in detecting (suites of) compounds associated with particular traits. For this purpose, we vectorized the data matrix and included the matrix rows and columns (i.e. the samples and compounds) as random intercepts to avoid pseudo-replication and heteroscedastic variance (Jamil et al., 2013; Weiß et al., 2018b). As response variable we used standardized peak areas. Because standardized areas are bound between 0 and 1 and sum up to 1 per sample, we applied a centered log-ratio (clr) transformation (Boogaart and Tolosana-Delgado, 2013) and modelled the transformed values with a Gaussian error distribution. As effects of interest in this analysis we modelled the interactions between the predictors and compound, i.e. the random slopes & random interactions of fixed effects test predictors within compound (see Weiß et al., 2018b). To follow a consistent modelling approach, we also performed this model in the package brms.

In all mixed models we z-transformed continuous predictor variables to a mean of 0 and an SD of 1 prior to fitting the model to facilitate convergence and interpretation of model estimates (Schielzeth, 2010). We assessed collinearity between predictor variables using the function "vif" from the R package "car" (version 3.1-2 Fox and Weisberg, 2019), whereby we considered values < 4 as unproblematic. To assess model convergence we inspected rhat values and effective sample sizes (ESS), with rhat values deviating from 1 by less than 0.01and ESS values > 400 indicating satisfactory convergence (Vehtari et al., 2021).

363 We present model results most relevant for the interpretation of the test predictors in the main text,
364 and full model results, including rhat and ESS values, in supplement 1 (Tables S2-S5).

365

366 Individual identity

367 To investigate individual signatures, we analyzed distance matrices using a perMANOVA with ID as
368 test predictor while controlling for sex, age (in years), group and season of the year (spring, summer
369 or autumn). Because ID was the test predictor, we did not set ID as stratum. For this analysis we used
370 data from 24 individuals (12 males, 12 females) sampled 10 times each. As individual signatures
371 commonly result from the unique combination and abundance of compounds (i.e. the overall
372 similarity between chemical profiles) rather than certain compounds that vary consistently between
373 all individuals (see Smith, 2006; but see Rigaill et al., 2022), we did not conduct a more detailed
374 analysis of chemical profiles (compositional models) for individual identity.

375

376 Genetic relatedness

377 Similar to ID, kin signatures should result from similarities in the overall composition of compounds
378 rather than specific compounds. We therefore assessed whether the chemical (dis)similarities
379 between samples are explained by genetic relatedness. In the first of two sets of analyses, we
380 computed perMANOVAs using only samples of genetically confirmed units of close kin. Each kin unit
381 comprised 2 – 4 individuals in up to 3 generations and as such, parent-offspring, grandparent-
382 grandchild and/or half-sibling dyads, reflecting close kin with relatedness coefficients ranging from
383 0.25 to 0.5. We ran the perMANOVAs separately per kin line, using the maternal or paternal kin unit
384 (i.e. belonging to the same or a different kin unit) as test predictor, while controlling for sex, age and
385 season of the year (spring, summer or autumn). All individuals used in these analyses were sampled
386 for odor at least 5 times. For maternal kin we used 220 samples from 31 individuals and for paternal
387 kin 179 samples from 29 individuals in 12 kin units per kin line (see supplement 2). Maternal/paternal

388 relatedness between individuals from different units ranged from 0 to 0.125, reflecting distant or
389 non-kin.

390 While belonging to a certain kin unit was genetically confirmed in this first set of analyses, it treated
391 relatedness categorically as belonging to a given kin unit or not, but lacked the possibility to
392 differentiate the pair-wise degree of relatedness. In a second analytical approach we therefore
393 conducted a multi-membership model to relate pair-wise chemical similarities between samples to
394 kinship while accounting for a variety of fixed and random predictor variables. For the multi-
395 membership model we used the data from all genotyped and odor-sampled individuals (N = 68),
396 irrespective of whether their maternities or paternities were genetically solved. We fitted dyadic
397 Bray-Curtis similarities as beta-distributed response variable and relatedness between members of a
398 dyad as two separate test predictors: one reflecting maternal kinship (i.e. individuals linked
399 exclusively via the maternal line) and one reflecting paternal & mixed kinship (i.e. containing at least
400 one male linking two individuals, which breaks the familiarity between maternal kin typical for
401 matrilineally structured primate groups). To control for other sources of biological variation we also
402 fitted the age and rank difference between the two individuals in a given dyad, the number of days
403 between the two samples and the difference in the time of day the sample was collected. We further
404 included whether or not the two individuals were of the same sex, belonged to the same group, were
405 sampled in the same season of the year and from the same body region. To control for variation in
406 sampling and measurement we included the difference in sampling distance, sampling volume, the
407 number of subsamples needed to complete a sample and whether or not samples were analyzed in
408 the same GC-MS batch. To account for repeated measures we fitted the sample, the individual and
409 the dyad (i.e. the unique combination of individuals) and random intercepts, whereby sample and
410 individual were fitted as multi-membership terms because a given sample or individual could occur in
411 either of the two columns describing the elements of a dyad. For a more accurate estimation of fixed
412 effects, we further included all technically possible random slopes of fixed effects within the random

intercepts of individual and dyad. Using 9000 post-warmup draws, the model converged with all rhat values deviating from 1 by < 0.01 and all ESS > 400 (see Table 1).

Dominance and rank

To address potential dominance and rank-related signatures, we first conducted a perMANOVA with rank as a categorical test predictor (high/low) in interaction with sex while controlling for age, group and season of the year. For this analysis we used 260 samples from 34 individuals sampled at least 5 times each and classified as particularly high- or low-ranking in their respective groups based on judgements of staff and confirmed with behavioral data (high-ranking: 9 females & 8 males, low-ranking: 8 females & 9 males). To keep confounds between dominance class and kinship arising from matrilineal rank acquisition to a minimum, we chose no more than two females from the same matriline, so that the 17 females used for this analysis represented 12 different matrilines.

We further conducted a multi-membership model using chemical data and rank as a continuous measure (i.e. Elo scores) using 476 samples from all 72 sampled individuals. We only considered same-sex dyads for this analysis, because Barbary macaque males outrank females and Elo scores were thus computed separately per sex. We fitted dyadic Bray-Curtis similarities as beta-distributed response variable and the difference in Elo scores and its interaction with sex as test predictors. Similar to the model on genetic relatedness we also controlled for potential sources of biological and technical variance by fitting dyad-specific overall relatedness and differences in age, sampling day, time of day, group, season of the year, body region, sampling distance, sampling volume, number of subsamples and GC-MS batch. As above we fitted sample and individual as multi-membership terms as well as dyad as random intercepts, and all technically possible random slopes within individual and dyad. We subsequently removed the interaction between the difference in Elo scores and sex because it explained no variance (estimate 0.0004 +- 0.0028, lower/upper CI -0.005 – 0.006) and

437 fitted both as main terms instead. Using 12000 post-warmup draws, the model without interaction
438 converged with all rhat values deviating from 1 by < 0.01 and all ESS > 400 (see Table 2).

439 To consider the possibility that rank information could be encoded by a few specific compounds
440 (rather than or additional to overall similarities), we further included rank as predictor in a
441 compositional mixed model as described in the analyses of sex, age and group below.

442

443 Sex, age and group

444 To address potential signatures of sex, age or group membership we conducted a perMANOVA with
445 these terms as test predictors while controlling for season of the year. For this analysis we used all
446 476 samples from 72 individuals.

447 To assess to what extent specific (suites of) compounds may encode information about individual
448 traits, we further computed a compositional mixed model. As fixed effects predictors we fitted sex,
449 age, group and rank (Elo scores) along with season of the year, the sampled body part, time of day,
450 sampling distance, sampling volume and the number of subsamples. As random terms we fitted the
451 intercepts of sample, compound, individual, date, GC-MS batch and TD tube used for sampling, as
452 well as all technically possible random slopes, but no random correlations to avoid an overly complex
453 model. Using 8000 post-warmup draws, the model converged with all rhat values deviating from 1 by
454 < 0.01 and all ESS > 400 (see Table 3).

455

456 <u>Results</u>

457 *Individual identity*

458 Odor samples from the same individuals were significantly more similar than samples from different
459 individuals, with ID explaining ~ 20 % of the variance in Bray-Curtis indices (perMANOVA, $r^2 = 0.203$,
460 df = 21, F = 3.838, p = 0.001, example chromatograms in supplement 1, Fig. S1). An individual

chemical signature was further supported by the posterior mean estimates for ID in the multi-membership models on genetic relatedness and rank (see Tables 1 and 2).

Genetic relatedness

Odor samples from close maternal kin were significantly more similar than samples from different kin units (perMANOVA, $r^2 = 0.099$, df = 11, F = 2.537 , p = 0.001). Furthermore, individuals from the same paternal kin unit tended to have more similar chemical profiles than individuals from different kin units (perMANOVA , $r^2 = 0.132$, df = 11, F = 2.772 , p = 0.067).

Table 1: Estimates for fixed effects and random intercepts from the multi-membership model on genetic relatedness. Terms of primary interest are indicated in italics. CrI = Credible Interval. ESS = effective sample size.

fixed terms	**Estimate**	**Est.Error**	**2.5 % CrI**	**97.5 % CrI**	**Rhat**	**bulk ESS**	**tail ESS**
Intercept	0.1419	0.0264	0.0891	0.1935	1.0017	1592	2884
maternal r	*0.0001*	*0.0010*	*-0.0018*	*0.0020*	*1.0000*	*9718*	*7456*
paternal/mixed r	*-0.0016*	*0.0015*	*-0.0048*	*0.0012*	*1.0003*	*6365*	*5522*
d_elo score	-0.0002	0.0010	-0.0022	0.0018	1.0001	10551	7505
d_sex (same)	-0.0018	0.0018	-0.0053	0.0017	1.0001	9026	7614
d_age	-0.0010	0.0016	-0.0042	0.0022	1.0003	6827	6459
d_group (same)	0.0120	0.0055	0.0009	0.0229	1.0014	2163	3956
d_season (same)	-0.0244	0.0119	-0.0480	-0.0010	1.0032	562	1399
d_date	-0.3204	0.0095	-0.3391	-0.3013	1.0075	528	944
d_time	0.0005	0.0013	-0.0019	0.0030	0.9999	4987	6121
d_bodyregion (same)	0.0026	0.0028	-0.0028	0.0082	1.0005	4418	5675
d_s.distance	0.0043	0.0023	-0.0002	0.0088	1.0006	3783	5261
d_s.volume	0.0065	0.0051	-0.0035	0.0164	1.0032	984	1902
d_subsamples	-0.0072	0.0020	-0.0112	-0.0034	1.0007	4902	6101
d_batch (same)	0.1994	0.0154	0.1690	0.2302	1.0011	1051	1941
random terms							
sample (Intercept)	0.3994	0.0144	0.3724	0.4293	1.0031	1074	2166
ID (Intercept)	0.1490	0.0277	0.0960	0.2037	1.0033	471	973
dyad (Intercept)	0.0189	0.0013	0.0164	0.0214	1.0010	1690	3502

When relatedness was treated as a continuous variable (i.e. using pedigree r) across all genotyped individuals in the data set, neither maternal nor paternal relatedness affected similarities in chemical profiles (Table 1).

Dominance and rank

The interaction between dominance classes (high vs. low) and sex (male vs. female) had no significant effect on the similarity between chemical profiles (perMANOVA, $r^2 = 0.003$, df= 1, F = 0.932 , p = 0.982), but individuals from the same dominance class had slightly more similar chemical profiles than individuals from different dominance classes (perMANOVA, $r^2 = 0.002$, df = 1, F = 0.879, p = 0.008). When treated as a continuous variable across all individuals in the data set, rank (Elo score) had no effect on similarities between chemical profiles (Table 2).

Also the specific composition of chemical profiles showed no pronounced variation in relation to rank (see random slope of Elo score within compound in Table 4).

Table 2: Estimates for fixed effects and random intercepts from the multi-membership model on rank. Terms of primary interest are indicated in italics. CrI = Credible Interval. ESS = effective sample size.

fixed term	**Estimate**	**Est.Error**	**2.5 % CrI**	**97.5% CrI**	**Rhat**	**bulk ESS**	**tail ESS**
Intercept	0.1544	0.0394	0.0756	0.2315	1.0010	2680	5074
d_Elo score	*-0.0001*	*0.0014*	*-0.0027*	*0.0026*	*1.0002*	*19102*	*9841*
total r	-0.0021	0.0014	-0.0049	0.0007	1.0002	18584	8977
sex (male)	-0.0228	0.0526	-0.1265	0.0798	1.0014	2879	5192
d_age	0.0013	0.0021	-0.0030	0.0054	1.0001	14446	9510
d_group (same)	0.0159	0.0070	0.0022	0.0297	1.0001	5497	7723
d_season (same)	-0.0267	0.0108	-0.0484	-0.0059	1.0015	2736	4694
d_date	-0.3250	0.0104	-0.3456	-0.3053	1.0023	1088	2508
d_time	0.0005	0.0012	-0.0019	0.0030	1.0002	15821	9039
d_bodyregion (same)	0.0041	0.0033	-0.0024	0.0107	1.0002	11941	8932
d_s.distance	0.0054	0.0025	0.0006	0.0103	1.0007	11074	9460
d_s.volume	0.0081	0.0054	-0.0026	0.0187	1.0014	2684	3564
d_subsamples	-0.0070	0.0021	-0.0113	-0.0029	0.9999	15094	10231
d_batch (same)	0.1838	0.0182	0.1477	0.2188	1.0011	2652	5513
random term							
sample (Intercept)	0.3952	0.0141	0.3684	0.4239	1.0016	2096	4665
ID (Intercept)	0.1509	0.0282	0.0988	0.2076	1.0058	891	1598
dyad (Intercept)	0.0189	0.0019	0.0152	0.0226	1.0016	2254	4976

Sex, age and group

When testing sex, age and group membership, the set of predictor variables significantly affected chemical similarities (perMANOVA, $r^2 = 0.213$, df = 6, F = 21.145, p = 0.001). In particular, sex, age as well as group explained significant, albeit small proportions of the variance in Bray-Curtis indices (3.5 – 5 %, Table 3). In comparison, season of the year (included as a control predictor) explained more variance than sex, age and group together (14.5 %, Table 3).

Table 3: Results of the perMANOVA investigating effects of sex, age and group on chemical similarities.

Term	Df	SumOfSqs	R^2	F	P
sex	1	0.466	0.004	2.332	0.001
age	1	0.425	0.004	2.124	0.001
group	2	6.106	0.051	15.273	0.001
season	2	17.225	0.145	43.083	0.001
Residual	469	93.756	0.787		
Total	475	119.117	1		

This pattern was similar when considering chemical profiles in detail. Slope estimates from the compositional model suggest that the effects of sex, age and group on relative peak areas differed between chemical compounds, whereby the variance was close to 0 for age, only slightly higher for sex and more pronounced for group. Again, variance related to control predictors such as season of the year was considerably higher than for sex, age and group (see Table 4).

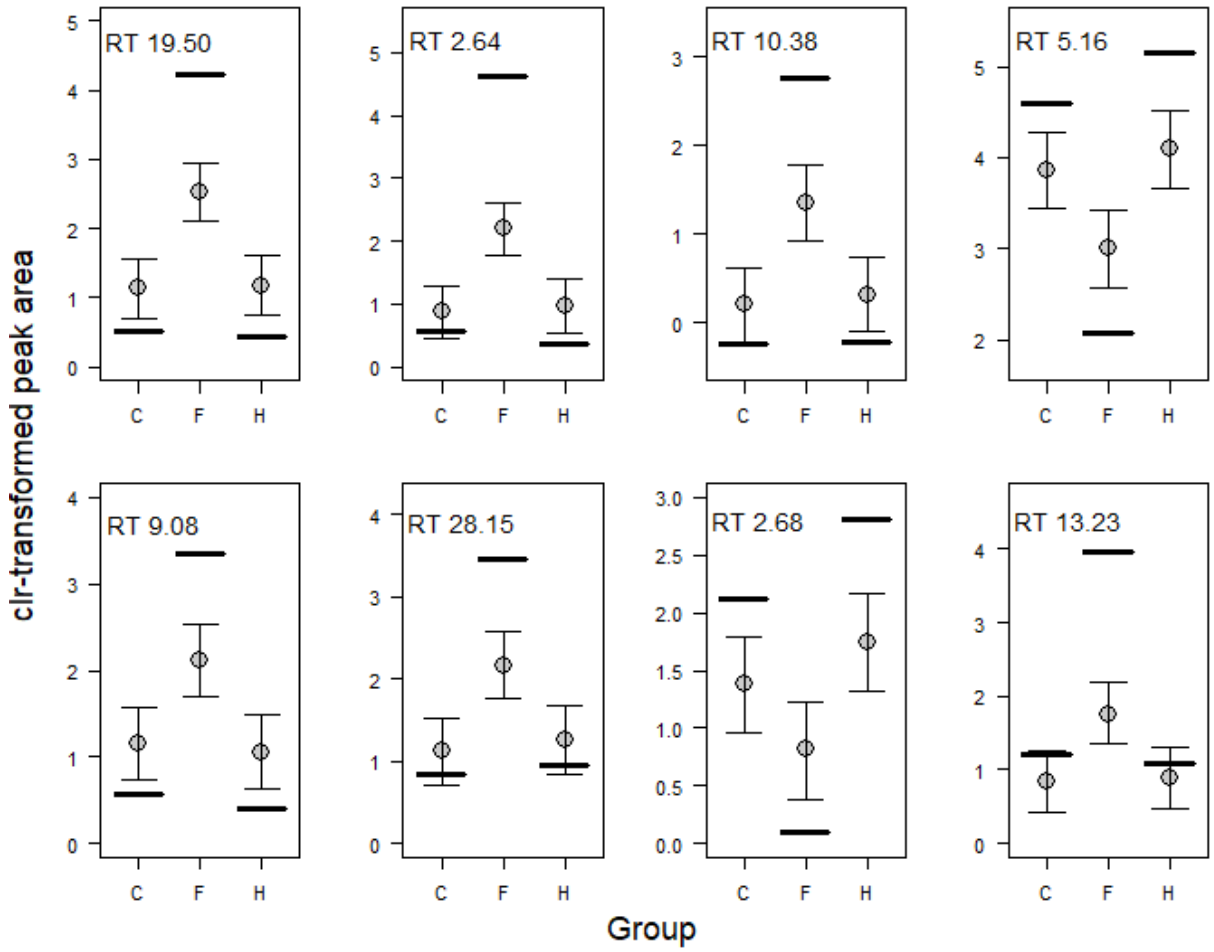
Table 4: Estimates for random slope terms within the random intercept of compound for the compositional model. Terms of primary interest are indicated in italics. CrI = Credible Interval. ESS = effective sample size.

slope in compound	Estimate	Est.Error	2.5 % CrI	97.5% CrI	Rhat	bulk ESS	tail ESS
Elo score	*0.0166*	*0.0118*	*0.0007*	*0.0435*	*1.0020*	*3304*	*3855*
sex	*0.1023*	*0.0191*	*0.0626*	*0.1380*	*1.0006*	*2819*	*3082*
age	*0.0524*	*0.0175*	*0.0121*	*0.0831*	*1.0017*	*1709*	*1218*
group	*0.2901*	*0.0157*	*0.2606*	*0.3214*	*1.0012*	*3772*	*4889*
season	1.0605	0.0417	0.9822	1.1461	1.0019	2698	4371
time	0.0397	0.0182	0.0041	0.0724	1.0032	1657	2624
bodyregion	0.1333	0.0176	0.0987	0.1672	1.0009	2690	3865
s.distance	0.2624	0.0177	0.2290	0.2983	1.0003	2989	5028
s.volume	0.8104	0.0420	0.7341	0.8990	1.0015	1140	2388
subsamples	0.1280	0.0147	0.0993	0.1569	0.9999	3441	5449

When investigating the compound-specific estimates per test predictor, the credible intervals for all compound-specific age and sex estimates overlapped 0. The group estimates for 8 compounds did

512 not overlap between at least 2 of the 3 groups, suggesting that the peak areas of these compounds
513 differ distinctly between groups (Fig. 1, supplementary Table S6). We tentatively identified 5 of these
514 compounds as a ketone, a carboxylic acid, an alcohol, an aromatic hydrocarbon and a catechol
515 derivate (Table 5).

516



517

518 Figure 1: Group differences (C, F and H) in peak areas (centered log-ratio transformed) of 8
519 compounds with retention times in [min] as indicated in the upper left corner of each graph.
520 Compounds are sorted by order of importance as derived from their compound-specific slope
521 estimates. Vertical lines show mean peak areas per group, points the estimates per group (with all
522 other predictors at their average) and whiskers the 95 % Credible Intervals.

523

524

525 Table 5: Compounds associated with group differences in chemical profiles of Barbary macaque

526 samples. RT = retention time (in min.), base peak describes the largest mass fragment of the peak. SI

527 = similarity index (from 0 - 100) for the match between mass spectra and their respective best hit in

528 the NIST library.

RT	base peak	best NIST library hit	SI	substance class	found in
2.64	43	2-Pentanone, 3-methyl-	91	ketone	humans [1,2], Japanese macaques[3]
2.68	43	Acetic acid	94	carboxylic acid	various mammals [1,4-9]
5.16	149	unidentified	< 80		
9.08	73	3-Pentanol, 2,4-dimethyl-	81	alcohol	*human excretions [1,2]
10.38	79	unidentified	< 80		
13.23	115	1H-Indene, 3-methyl-	92	aromatic hydrocarbon	unknown
19.50	179	4-tert-Butylcatechol, dimethyl ether	87	catechol derivate	** beaver castoreum 6
28.15	91	unidentified	< 80		

529

530 [1] Costello et al (2014), [2] Garner et al (2007), [3] Rigaill et al 2022, [4] Bernier et al (2000), [5] Smith et al
531 (2001), [6] Burger (2005), [7] Gallagher et al (2008), [8] Vaglio et al (2016), [9] Marneweck et al (2017)
532

533 * these studies identified a different derivate (3-Pentanol, 3-methyl)

534 ** this study identified two different catechol derivates

535

536 Discussion

537 In the present study, we investigated to what extent the chemical composition of Barbary macaque

538 body odor is related to socially relevant traits and might thus have the potential to convey social

539 information. Our analyses support the existence of olfactory individual signatures, while support for

540 kin signatures differed between our analytical approaches. Chemical profiles were also related to

541 group membership, but we found little to no support that rank, sex or age affect chemical similarity

542 or detailed composition of scents emanating from the skin and fur of Barbary macaques.

543 Individual identity showed the strongest and most robust signature related to social information in

544 Barbary macaque body odor. Our results are in line with the extensive evidence for individually

545 distinct body odor across a range of mammals (e.g. Buesching et al., 2002; Caspers et al., 2008; Kwak
546 et al., 2008), including primates (e.g. Kulahci et al., 2014; Palagi and Dapporto, 2006; Rigaill et al.,
547 2022; Spence-Aizenberg et al., 2018; Scordato et al., 2007; reviewed in Smith, 2006). While the
548 majority of evidence thus far has come from scent-marking species, our results, along with studies in
549 Japanese macaques (Rigaill et al., 2022) and on human axillary odor (Penn et al., 2007), indicate that
550 individually distinct odors may also be present in catarrhine primates that do not show apparent
551 scent-marking. Individual identity explained only slightly less variance (r^2 of 0.2) in the chemical
552 profiles of Barbary macaques than in Japanese macaque urine (r^2 of 0.25) or vaginal secretions (r^2 of
553 0.29). Although the comparison between Japanese and Barbary macaques certainly needs to be
554 viewed in light of different methodologies and a larger and more heterogeneous sample of
555 individuals in Barbary macaques, it strongly suggests that odor emitted from the body surface may
556 carry identity information of similar magnitude as potentially more intense odor sources.
557 Furthermore, the present study shows that individually distinct information can be conveyed by the
558 chemicals emitted from the body surface, not just by scents deposited in the environment in the
559 form of scent marks or excretions.

560 The comparison of close vs. distant or non-kin based on overall chemical similarities suggested
561 olfactory signatures of both maternal and paternal relatedness, although paternal signatures were
562 statistically less robust. Units of close kin also showed a more similar chemical composition in owl
563 monkeys (*Aotus nancymaae* MacDonald et al., 2008; but see Spence-Aizenberg et al., 2018) and
564 rhesus macaques (Weiß et al., 2018a). Similar to our results in Barbary macaques, kin signatures in
565 rhesus macaques were only statistically robust among maternal, but not paternal half-siblings (Weiß
566 et al., 2018a). These patterns suggest that similarities in body odor between maternal relatives may
567 to some extent be mediated by frequent physical contact and/or a shared environment, which could
568 result in an exchange of odor-producing microbes, as e.g. suggested for group signatures in hyenas
569 (Theis et al., 2012). However, when treating relatedness as a continuous variable as well as
570 accounting for more other potential sources of variation in body odor, we found no support

571 whatsoever for relatedness predicting chemical similarity between individual odors. Possibly,
572 chemical profiles of surface body odor allow only a coarse, but no fine-scaled differentiation of
573 relatedness. Alternatively, what appeared to be kin signatures in the perMANOVAs may actually have
574 been variation related to other predictors that could not be as accurately controlled for in these
575 analyses. Furthermore, kin signatures may only be robustly expressed in certain contexts or seasons,
576 when kin discrimination is particularly important. For instance, kin signatures in glandular secretions
577 of ring-tailed lemurs (*Lemur catta*) were robustly expressed only in the breeding season, when they
578 may aid in inbreeding avoidance (Boulet et al., 2009; Charpentier et al., 2008), but we did not collect
579 odor samples during the mating season for logistic reasons.

580 The lack of robust chemical information about kinship involving the paternal line (at least outside the
581 mating season) is especially interesting with respect to the triadic interactions and care that Barbary
582 macaque males frequently engage in with infants. Particularly, male-infant interactions have been
583 suggested to be independent of paternity to the respective infant (Paul et al., 1996), which may be
584 due to low phenotypic similarity between father and offspring when the offspring is still in its infancy.
585 Studies in rhesus macaques testing exclusively adult subjects suggest that unfamiliar, paternal kin
586 discriminate relatives based on visual or acoustic phenotypic cues (Pfefferle et al., 2014a, 2014b).
587 Moreover, humans rating the facial similarity of rhesus macaque parents and offspring performed
588 above chance level (Kazem and Widdig, 2013) and better if the offspring were older (Kazem et al.,
589 2018). The paternal kin units sampled in the present study indeed comprised cases in which the
590 offspring was still rather young (2 years old), but in half of the cases all members of a paternal kin
591 unit were reproductively mature (i.e. 4 years or older). Hence, the chemical data presented here do
592 not point towards olfactory signatures alone being robust enough to allow Barbary macaque males
593 to reliably distinguish between own and unrelated offspring.

594 Regardless of the analytical approach, we detected no robust support for chemical profiles being
595 related to dominance classes or rank. Although we found a significant effect of dominance class on
596 the similarity between chemical profiles, the association was very weak, and ranks across the entire

597 dominance hierarchy were associated with neither chemical similarity nor the abundance of specific
598 compounds. Dominance-related odors have been described in various mammals (e.g. Burgener et al.,
599 2009; reviewed in Scordato et al., 2007), including male mandrills (*Mandrillus sphinx*, Setchell et al.,
600 2010; Vaglio et al., 2016), but were not detected in ring-tailed lemurs (Scordato et al., 2007) or
601 female mandrills (Setchell et al., 2010). In female rhesus macaques, individual rank had no effect on
602 overall chemical similarities, but affected the relative abundance of certain compounds (Weiß et al.,
603 2018a). As pointed out by Smith (2006), olfactory communication of dominance requires either a
604 specific dominance-related odor or olfactory individual signatures that can be associated with other
605 dominance-related information. Evidence for the latter comes from a study in ring-tailed lemurs, in
606 which males discriminated between the scents of dominant and subordinate individuals, but only if
607 they were familiar with the odor donors (Scordato and Drea, 2007). Hence, while our results provide
608 no robust evidence for dominance-related odor in either male or female Barbary macaques, the
609 detected individual signatures certainly open the possibility for a more indirect olfactory
610 communication of dominance among familiar individuals.

611 Based on behavioral and/or chemical evidence, the scents of numerous primates and other
612 mammals convey sex-specific (sex: e.g. Kean et al., 2011; Leclaire et al., 2017; Linklater et al., 2013;
613 Spence-Aizenberg et al., 2018; Weiß et al., 2018a) and age-specific information (e.g. Buesching et al.,
614 2002; Jänig et al., 2019; Kean et al., 2011; Kücklich et al., 2019; MacDonald et al., 2008; Marneweck
615 et al., 2017), although this need not always be the case (Jänig et al., 2019; also see review in Drea,
616 2015). Age, for instance, was related to chemical profiles in one subset of individuals in rhesus
617 macaques, but not in another (Weiß et al., 2018a). In the present study, sex and age, although
618 significantly associated with chemical similarities, explained very little variation in chemical profiles,
619 and none of the chemical compounds distinctly differed in abundance between sexes or showed
620 consistent changes with age. It is possible that sex and age information may actually be more
621 pronounced in a different context (e.g. mating), in other scent sources (e.g. urine) or other body
622 parts (e.g. the ano-genital region), all of which, along with differences in sampling and analytical

methods, may affect the expression of chemical signatures or our ability to detect them (see Charpentier et al., 2008; Drea, 2015; Drea et al., 2013; Rigaill et al., 2022). Furthermore, sex differences may have been attenuated in the study population due to the use of contraceptives in 60 % of the adult females (see below).

Group membership explained about 5 % of the variance in chemical similarities and affected the relative abundance of 8 compounds. For most of these compounds, abundances were consistently higher or lower in group F, but similar in the other two groups. Olfactory group signatures have been described in a range of group-living mammals, including rhesus macaques (Henkel et al., 2015; Weiß et al., 2018a), mandrills (Vaglio et al., 2016) and chimpanzees (Henkel and Setchell, 2018), with explanations for the origins of these differences including the environment, diet and microbial differences between groups (e.g. Leclaire et al., 2017; Spence-Aizenberg et al., 2018; Theis et al., 2012). In species living in family groups, group signatures may further reflect relatedness among individuals (e.g. owl monkeys, MacDonald et al., 2008). Relatedness is an unlikely explanation for the group differences observed in the present study, because all groups comprised multiple matrilines and average relatedness among genotyped focal animals was low both within (r = 0.04) and between groups (r = 0.02, data not shown). The three groups also received the same supplemental food and had spatially (but not temporally) overlapping home ranges, but there are subtle differences in the vegetation in different areas of the park that could potentially affect natural food sources as well as background volatiles or substances the animals get into contact with. Several of the tentatively identified compounds could fit such an explanation. 3-methyl-2-pentanone and 2,4-dimethyl-3-pentanol, for instance, could be microbial or plant products metabolized by the mammalian body (see Charpentier et al., 2012) and similar compounds have been found in human feces before (Costello et al., 2014). Furthermore, indenes have been described in plants (e.g. Mansur et al., 2018), although we could not find a source specifically for 3-methyl-1H-indene, which was the best mass spectral library match for the compound at RT 13.23 min. Alternatively, group differences could be related to demographical and social differences between groups. The focal animals of group F

649 comprised a slightly higher proportion of females than groups C and H (57 % vs. 43 % and 32 %) and
650 were marginally younger (average age in group F 9.2 years vs. 11.7 and 11.3 yrs in groups C and H,
651 see supplement 2). However, because sex and age effects on body odor were very small (see above)
652 and statistically accounted for, they are unlikely to contribute much to the observed group
653 differences. Group F also is the largest and highest-ranking of the three groups, which could affect
654 stress levels or other physiological parameters (see overview in Dunbar, 2018) and thereby, body
655 odor (reviewed in Roberts et al., 2022), but we have no physiological data available to further assess
656 this possibility.

657 Main assets of our study certainly are the large numbers of samples and focal individuals, the semi-
658 natural environment and natural social conditions. We also were able to collect all samples non-
659 invasively, thereby greatly reducing the chance that odors were affected by sampling-related stress.
660 At the same time, the study faced several limitations, some of which we were able to account for
661 during data analysis, and others not. For instance, we collected samples from different body parts
662 that we could approach most easily, i.e. primarily the shoulders, flanks and thighs, and controlled for
663 the variation in sampled body regions during statistical analysis. However, it is difficult to assess how
664 relevant these body parts actually are for day-to-day information exchange. Recent observational
665 data in the study population suggests that sniffs directed at conspecifics frequently target the ano-
666 genital region of adult females in a mating context (Simon et al., 2024). The ano-genital region might
667 thus be a more appropriate sampling region at least for certain types of individuals and contexts, but
668 would have been feasible to sample only in a subset of very well-habituated females at frequent
669 intervals. As the social information detectable in animal scents may differ between scent sources,
670 even within species (see Drea, 2015; Rigaill et al., 2022), it is possible that results would have differed
671 if we had sampled other body regions or scent sources such as urine.

672 Our data collection periods spanned much of the year, but for logistic reasons we did not collect data
673 during most of the park's winter break, which corresponds to the peak of the mating season in the
674 study population. Indeed, the season of the year did affect chemical profiles, even more so than the

675 socially relevant variables investigated. In particular, seasonal variation may have affected the
676 volatile background in the environment, which we could at least in part account for by using
677 environmental control samples. Furthermore, aspects such as reproductive physiology, diet, ambient
678 temperature or state of the fur (winter vs. summer coat) may additionally affect the chemical
679 compounds emitted by the body and how readily they become available to recipients (or sampling
680 tube). Such aspects are likely to be at the base of the detected seasonal changes in chemical profiles,
681 and we statistically accounted for them in our analyses of socially related olfactory signatures by
682 using season of the year as a control variable. What remains open is whether any of the investigated
683 effects might have been more pronounced during the mating season, as shown, e.g., for kin
684 signatures in ring-tailed lemurs (Boulet et al., 2009; Charpentier et al., 2008).

685 Another aspect to consider is that the size of the study population is managed via hormonal
686 contraception, and 60 % of the sampled females received contraception during part or all of the
687 study period. Studies on the effects of hormonal contraception on primate body odor are scarce and
688 contradicting: hormonal contraception using medroxyprogesterone acetate has previously been
689 shown to alter the chemical composition of female scents in ring-tailed lemurs (Crawford et al., 2011)
690 but not in owl monkeys (Spence-Aizenberg et al., 2018). Male mandrills showed more flehmen
691 responses towards scent samples from cycling females than from females contracepted with
692 etonogestrel (Charpentier et al., 2013), which is the active ingredient of the implants used in the
693 studied Barbary macaques. However, while contraception also tended to modulate age-specific
694 differences in ano-genital sniffs by male Barbary macaques, it did not affect subsequent sexual
695 behavior in our studied population (Simon et al., 2024). As we did not assess individual attributes
696 immediately related to mating and female fertility, contraception might be considered as a source of
697 noise in the data. Unlike several other sources of noise, however, we could not account for
698 contraception statistically given that it applied only to a minority of samples and individuals. Overall,
699 it is thus possible that certain signatures, in particular those of sex, might have been more
700 pronounced in a sample without females receiving contraception.

701 Our results also suggest some variation in chemical profiles related to sampling and GC-MS
702 measurement, whereby different variables affected different aspects of the composition: chemical
703 similarities between samples were greater if samples were collected closer in time, and to a lesser
704 extent also when analyzed within the same GC-MS batch. In contrast, variables such as the sampling
705 distance, sampling volume or the sampled body part had little effect on chemical similarities of
706 samples, but appeared to have some effect on the relative abundance of certain compounds.
707 However, while we were unable to eliminate these sources of variation in the study design, we
708 statistically accounted for them in all mixed model analyses.

709 Finally, results need to be put into perspective of what we can measure vs. what animals can
710 perceive. Statistically detectable associations between chemical profiles and socially relevant traits
711 show the potential for olfactory information transfer, but we do not know if or how animals use this
712 information. Animal sensory systems have evolved for the detection of relevant information and may
713 thus be superior to even the most modern of our analytical techniques, at least for certain
714 compounds (reviewed in Maidodou et al., 2023). Accordingly, it may be possible that animals are
715 able to pick up upon even very subtle differences in odors, or differences that our analyses are
716 unable to pick up at all, especially as we are unlikely to sample and detect all chemical substances
717 emitted by an animal's body across the possible ranges of volatility, polarity etc. (Drea et al., 2013)
718 despite the constant improvements in sampling and analytical methods. Hence, future studies should
719 combine chemical data with (experimental) assessments of behavioral and physiological reactions
720 towards conspecific odors across a range of contexts to obtain a detailed understanding of the
721 complex role of olfaction in primate social interactions. Particularly under natural and semi-natural
722 conditions, controlled presentations of conspecific odors are challenging to implement (e.g. Ritter,
723 2022), as stimuli need to be presented in a manner that is salient and realistic enough to elicit
724 interest and closer inspection without leading to quick habituation. Promising next steps would be
725 multi-modal experiments and experimental manipulation of *in vivo* odors to investigate how
726 olfactory discrimination of social information falls into place between the other senses, i.e. whether

macaques are able to discriminate such information based on odors alone, and/or if olfactory signatures improve the reliability of other sensory cues.

In conclusion, our results add to the limited evidence that socially relevant information may not only be encoded in scent secretions and excretions, but also in the volatile and semi-volatile components emanating from the body surface of primates. Based on chemical profiles alone, i.e. without knowing what the monkeys can make of it, data suggest that Barbary macaque body odor could directly contribute to recognizing individuals and groups, while olfactory signatures may not be pronounced or robust enough to allow differentiating kinship, rank, sex or age of conspecifics from surface body odor alone. However, given the central role of individual recognition in forming and maintaining social relationships, surface body odor could potentially still contribute to managing social relationships, if monkeys associate social knowledge obtained via other sensory modalities or direct social interactions with olfactory individual signatures.

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