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Comparative chemical analysis of body odor in great apes

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Abstract

Olfaction is important across the animal kingdom for transferring information on, for example, species, sex, group membership, or reproductive parameters. Its relevance has been established in primates including humans, yet research on great apes still is fragmentary. Observational evidence indicates that great apes use their sense of smell in various contexts, but the information content of their body odor has not been analyzed. Our aim was therefore to compare the chemical composition of body odor in great ape species, namely Sumatran orangutans (*Pongo abelii* (Lesson, 1827), one adult male, five adult females, four nonadults), Western lowland gorillas (*Gorilla gorilla gorilla* (Savage, 1847), one adult male, two adult females, one nonadult), common chimpanzees (*Pan troglodytes* (Blumenbach, 1775), four adult males, nine adult females, four nonadults), and bonobos (*Pan paniscus* (Schwarz, 1929), two adult males, four adult females, two nonadults). We collected 195 samples (five per individual) of 39 captive individuals using cotton swabs and analyzed them using gas chromatography mass spectrometry. We compared the sample richness and intensity, similarity of chemical composition, and relative abundance of compounds. Results show that species, age, and potentially sex have an impact on the variance between odor profiles. Richness and intensity varied significantly between species (gorillas having the highest, bonobos the lowest richness and intensity), and with age (both increasing with age). Richness and intensity did not vary between sexes. Odor samples of the same species were more similar to each other than samples of different species. Among all compounds identified some were associated with age ($N = 7$), sex ($N = 6$), and species-related ($N = 37$) variance. Our study contributes to the basic understanding of olfactory communication in hominids by showing that the chemical composition of body odor varies across species and individuals, containing potentially important information for social communication.

KEYWORDS
GC-MS, hominids, odor profiles, scent, species discrimination

1 | INTRODUCTION

Olfaction is one of the oldest senses in animals (Wilson, 1970) and of particular importance for social communication. It is distinct from other sensory channels such as vision or somatosensation as odor traces can be perceived by a recipient in the presence or absence of the sender. Body odor can contain various information, for instance, species, sex, and female reproductive state (spotted *Crocuta crocuta* (Erxleben, 1777), and striped hyenas, *Hyaena hyaena*; Linnaeus, 1758; Theis et al., 2013), individual identity (humans; Penn et al., 2007), or age (Iberian wolves, *Canis lupus signatus*; Latorre, 1907; Martín, Barja, & López, 2010). Regarding primates, previous research focused mainly on Strepsirrhines, which often scent-mark using odorous gland secretions for social communication (e.g., in ring-tailed lemurs, *Lemur catta*; Linnaeus, 1758; Boulet, Charpentier, & Drea, 2009; Scordato, Dubay, & Drea, 2007). In Catarrhines and especially

non-human great apes, olfaction has been far less examined, possibly because it was long thought to be of minor relevance in those species (Heymann, 2006).

To our knowledge, the chemical composition of hominid body odor has not been investigated, whereas the few observational and experimental studies suggested that olfaction indeed influences social communication of great apes. Chimpanzees (*Pan troglodytes*), for instance, use their olfactory sense to investigate food and their environment, but also group members or themselves (Matsumoto-Oda et al., 2007). Gorillas (*Gorilla gorilla gorilla*) produce an individual body odor which could be distinguished by human raters (Hepper & Wells, 2010), and they use the strength of their body odor as a flexible tool in interunit communication (Klailova & Lee, 2014). Furthermore, sniffing behavior of four species of great apes was influenced by species, sex, and age (Jänig, Weiß, & Widdig, 2018).

To discriminate individuals of the same species from those of other species is essential for animals especially in regards of mate choice, however, species differences in scent are an underrepresented topic, especially in primates (as discussed in delBarco-Trillo, Sacha, Dubay, & Drea, 2012). Tufted capuchins (*Cebus apella*; Linnaeus, 1758) were able to discriminate the scent of urine samples from three species of New World monkeys in a behavioral experiment but failed to discriminate between two species of Old World monkeys, suggesting effects of sympatry and allopatry (Ueno, 1994). The only studies analyzing species differences in the chemical composition of scent samples were conducted in the genus *Eulemur*. Closely related lemur species had more similar urinary chemical profiles, suggesting a gradual signal evolution (delBarco-Trillo, Burkert, Goodwin, & Drea, 2011). Comparing the scent of eight species of *Eulemur* also revealed that chemical richness (number of compounds) was influenced by the complexity of their social system, with more compounds found in species forming multimale multifemale groups than in pair-bonded species (delBarco-Trillo & Drea, 2014). Furthermore, in species with codominance between males and females, male samples were chemically richer than females', whereas in female-dominant species, female samples had a higher richness than males' (delBarco-Trillo et al., 2012). Differences in the social complexity of the species and therewith variance in the significance and frequency of social information transfer thus appear to predictably result in a different amount of chemical compounds used for communication (similar to vocal communication in Cercopithecines; Bouchet, Blois-Heulin, & Lemasson, 2013). Hominids are an interesting taxon in this respect as they developed substantial differences in their social systems. These range from semisolitary orangutans (*Pongo* spp.; Te Boekhorst, Schürmann, & Sugardjito, 1990), over mainly one-male units in gorillas (Robbins et al., 2004) to multimale multifemale groups in bonobos (*Pan paniscus*), and chimpanzees (Goodall, 1986; Kano, 1982).

For social animals, cues of individual attributes such as identity, sex or age are a prerequisite for effectively managing social interactions and communication. By assessing fertility, health, age, rank, and/or strength, intraspecific variation in odors may allow conspecifics to find the best mating partner or to decide when to invest in contest competition. Within species, odor can vary due to various aspects such as sex (for review see Drea, 2015) and age. For example, tamarins are able to discriminate between sexes using olfactory cues (*Saguinus fuscicollis*; Spix, 1823; Epple, 1978 and *Saguinus labiatus*; Geoffroy Saint-Hilaire, 1812; Smith & Gordon, 2002). Analyses of odor samples with gas chromatography mass spectrometry (GC-MS) revealed sex differences in the chemical composition of scents for example in *Aotus spp*. (Spence-Aizenberg, Kimball, Williams, & Fernandez-Duque, 2018), *Eulemur*; Simons and Rumpler, 1988; delBarco-Trillo et al., 2012), mandrills (*Mandrillus sphinx*; Linnaeus, 1758; Setchell et al., 2010; Vaglio et al., 2016), and rhesus macaques (*Macaca mulatta*; Zimmermann, 1780; Weiß, Kücklich, et al., 2018). In human body odor, variance was also found between the sexes (Penn et al., 2007; Zeng, Leyden, Spielman, & Preti, 1996). Age had an effect on body odor in Owl monkeys (*Aotus nancymaae*; Hershkovitz, 1983), where young individuals had less complex chemical profiles than old ones (MacDonald, Fernandez-Duque, Evans, & Hagey, 2008). In humans, body odor of older individuals is perceived as less intense and less unpleasant than odor of younger individuals (Mitro, Gordon, Olsson, & Lundström, 2012). However, a large gap remains in understanding the chemical composition and information content of body odor in great apes.

The main aim of this study thus was to establish fundamental knowledge of hominid body odor composition using different measures of chemical complexity of samples analyzed with GC-MS: richness (i.e., the number of compounds per chromatogram), intensity (i.e., sum of the areas of all compounds detected in a chromatogram), whole profile composition, and relative abundance of specific compounds. In particular, we aimed at investigating, first, species differences in the scents of four species of great apes (Sumatran orangutans, Western lowland gorillas, Common chimpanzees, and bonobos), and second, intraspecific variation related to sex and age.

Given the differences in sociality across species, we first hypothesized that the body odor differs in chemical complexity, with semisolitary orangutans having least complex chemical profiles, gorillas expressing intermediately rich profiles, and bonobos and chimpanzees as species living in complex multimale multifemale groups having the most complex body odor samples. Second, based upon phylogenetic distances we hypothesized that bonobos and chimpanzees have more similar chemical profiles compared to gorillas and orangutans since they diverged last from the line leading to hominins (Prado-Martinez et al., 2013).

Third, based upon the results of delBarco-Trillo et al. (2012), we hypothesized that body odor varies between sexes. Since great apes either express male dominance (orangutans, chimpanzees, and gorillas) or codominance between the sexes (bonobos), we expected richer chemical profiles in males than females. Fourth, we hypothesized that age affects body odor variability. We here expected older individuals to have richer profiles, as levels of reproductive competition should be higher in adult individuals, suggesting more complex social networks that may require more frequent or more extensive communication (Freeberg, Dunbar, & Ord, 2012) and thus, more compounds.

2 | METHODS

This study is in accordance with the legal requirements of Germany, all national and institutional guidelines for the care and use of animals, and was approved by the ethics commission of the Department of Psychology of the Max Planck Institute for Evolutionary Anthropology and the Leipzig Zoo. This study adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates.

2.1 | Subjects

We investigated body odor of four species of great apes: Sumatran orangutans, Western lowland gorillas, chimpanzees, and bonobos. Individuals were housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in the Leipzig Zoo (Germany). All species lived in groups and had separate indoor and outdoor enclosures as well as sleeping rooms. The enclosures of the different species are separated by solid walls preventing odor contamination between the species. All species were fed with fresh fruits, vegetables, lettuce and leaves, pellets, and seeds four to six times a day, and meat and eggs once a week. Water was available ad libitum.

Odor samples were taken from 39 individuals in total: eight bonobos (two adult males, four adult females, two nonadults; age 2–21 years, mean ± *SD* = 11.5 ± 6.9 years), 17 chimpanzees (from two social groups: four adult males, nine adult females, four nonadults; age 2–36, mean ± *SD* = 16.5 ± 10.4), four gorillas (one adult male, two adult females, one nonadult; age 5–30, mean ± *SD* = 21.0 ± 13.0), and 10 orangutans (one adult male, five adult females, four nonadults; age 2–31, mean ± *SD* = 12.1 ± 10.4, for more details on individuals and group composition see Table S1). We did not control for the reproductive state and menstrual cycle phases of individuals as not all species have obvious signs for their reproductive status. However, it should be kept in mind that female reproductive states may modify body odors (Havliček, Dvorakova, Bartoš, & Flegr, 2006; Michael, Keverne, & Bonsall, 1971).

2.2 | Sample collection and preparation

The general "body odor" is produced through the metabolization of sweat components by bacteria on the skin (Drea et al., 2013). Thus, semivolatile compounds are degraded to more volatile products which can act as perceivable olfactory cues (fermentation hypothesis; Charpentier, Barthes, Proffit, Bessière, & Grison, 2012; Theis et al., 2013). Eccrine and apocrine sweat glands are distributed over the whole body but concentrated in the axillary organ (Ellis & Montagna, 1962; Montagna & Yun, 1963). Body odor (i.e., chemicals on the skin) was collected by rubbing a cleaned (baked) cotton pad (60% cotton wool, 20% microfiber from polyester, and 15% polyester; for details see also Birkemeyer et al., 2016) over the skin/fur of the animal for approx. 20 s. Samples were stored in glass vials (washed with methanol and diethyl ether) at −80°C within a few hours after sampling. Because of regular cognitive studies at the Research Centre, individuals were used to come close to the grid and participated voluntarily. Given the restriction when working with great apes, SJ sampled whatever body part the individuals preferably presented. This resulted in 92 arm samples, 25 leg samples, five back samples, 33 neck samples, and 40 belly/breast samples with no obvious bias of body parts towards a given species. We collected samples early in the morning before behavioral experiments took place to reduce the impact of stress, food, and so forth on body odor. Furthermore, we considered only samples of individuals showing no obvious signs of infections or illness. We collected all samples in June and July 2013 and included five samples per individual (195 samples in total). In general, intraindividual variance between samples was lower than interindividual variance (see Table S2). Additionally, we collected blank samples (pure cotton pad exposed to ambient air) at each sampling day.

2.3 | Chemical analysis and data processing

We extracted the cotton swab samples with 1.2 ml of n-hexane (Sigma Aldrich, Steinheim, Germany) for GC-MS analysis. After concentrating the solution stepwise to a volume of 60 µl, we injected 4 µl into the GC-MS (HP6890 Series GC System with the Mass Selective Detector HP-MSD 5973; Agilent, Waldbronn, Germany). Further details on the GC-MS analysis are provided in the Supporting Information.

For each chromatogram, we detected peak retention time (RT) and area (intensity) automatically with the program AMDIS v. 2.65 (Stein, 1999) with the following adjustments: Resolution—Medium, Sensitivity—Medium, Shape requirements—Low. Richness of a sample was assessed by the number of peaks detected per chromatogram and the overall intensity of a sample by the sum of the areas of all peaks detected in a chromatogram. To compare the similarity of chromatograms and identify compounds responsible for variance between samples, we grouped peaks which occurred repeatedly (i.e., in at least one-third of the samples of a species) at the same retention time into "RT ranges". We compared the peaks of animal and blank samples and excluded peaks which occurred at a higher intensity in the blank than in the animal samples (38 in total) from further analysis. Next, we aligned the RT ranges across species by comparing the mass spectra of the peaks manually and thus gained a total of 198 RT ranges (called compounds hereafter). Compounds can only provide meaningful and reliable information about a species if they occur in the majority of individuals of a given species. We thus further excluded compounds which did not reliably occur in samples of at least one species, that is, did not occur in at least 60% of the samples of a given species. We chose this cutoff to ensure that the respective compound occurred in the majority (i.e., more than half) of the individuals of a species while allowing for the possibility that compounds may have gone undetected in some samples due to the sampling and analytical procedure. This step was incorporated to reduce meaningless noise in the data such as information related to for example, individual identity, health state, or contaminants. With this step, we excluded another 119

compounds and thus kept 77 for statistical analyses. Notably, these 77 compounds were not necessarily specific to just one particular species but could occur in the other species as well. We additionally inspected the original 198 RT ranges but could not find any sex-specific compound within each species.

2.4 | Statistical analysis

We investigated the variance of body odor samples using different measurements of chemical complexity and different statistical approaches. The main focus of the analyses was to assess species differences, but where possible we included sex and age (as a continuous measure) as test predictors as well. All statistics were run in R (version 3.2.3; R Foundation for Statistical Computing, Vienna, Austria, 2015; http://www.R-project.org/). All tests were two-tailed and α level was set to 0.05.

2.4.1 | Body odor intensity and richness

To assess the variance in the chemical composition of body odor, we compared species, sex, and age in 195 profiles (five per individual) using two measures: richness and the intensity of the whole chromatogram. We ran two linear mixed models using richness and intensity, respectively, as the response, by applying the function lmer of the package lme4 v. 1.1.11. We log-transformed intensity and square root-transformed richness to achieve a normal distribution of the response data. Richness could not be modeled with a Poisson distribution since assumptions of dispersion were not fulfilled (overdispersed, dispersion parameter = 3.74). Species, sex, and age (*z*-transformed to a mean of 0 and standard deviation of 1) were fitted as fixed effects test predictors and a two-way interaction between species and sex was included as it is possible that differences between the sexes were not consistent across species. Furthermore, individual identity, sampling date, and the sampled body part were included as random effects control predictors in both models to control for their impact on sample variability. Sex and age were fitted as random slopes within sampling date and body part, respectively. We could not fit species as random slope within body part because of convergence issues. In the model including intensity, we further had to exclude the correlations between random slopes and the random intercept of body part to achieve convergence of the model.

In all models, we first checked model assumptions to test the validity of the models. We visually inspected q-q plots and residuals plotted against fitted values, and detected no violations of normally distributed and homogenous residuals. Further, we computed model stability and found no obvious influential cases when comparing estimates derived from the whole data set to data excluding levels one at a time. Using variance inflation factors (VIF) we checked for potential collinearity (Field, 2005; Quinn & Keough, 2002) with the function vif of the package car (Fox & Weisberg, 2011) which revealed no issues. Second, we tested the overall effect of the test predictors on the response by comparing the full model with a null model lacking the variables of interest, that is, the two-way interactions as well as the variables species, sex, and age, using a Likelihood Ratio Test (Dobson, 2002; Forstmeier & Schielzeth, 2011). Third, we checked whether the two-way interaction had a significant effect on the responses using a reduced model lacking the two-way interaction but containing all three test predictors as single variables. We removed the two-way interaction from the final models if it was not significant to facilitate interpretation of single test predictors. Finally, we determined the significance of the single test predictors by removing one predictor at a time and comparing those reduced models with the full model using Likelihood Ratio Tests (LRTs), which provides more robust *p* value estimates than those provided directly by the lmer function. Furthermore, we provide confidence intervals (derived by using the function confint.merMod from the package lme4) for the models in Table 1. Additionally, to calculate R^2-like effect sizes ("marginal" for fixed effects and "conditional" for fixed *and* random effects) for the full models, we divided the variance explained by the respective effect by the total variance.

2.4.2 | Similarity between chemical profiles

To test if odor samples originating from the same species were more similar than samples taken from different species, we conducted an "analysis of similarity" (ANOSIM). We based the ANOSIM on Bray-Curtis indices for all combinations of sample dyads, within and across species (Weiß, Marcillo et al., 2018). The basis of these calculations are the standardized (peak area/ sum of peak areas of the 77 peaks per sample × 100) and log-transformed intensities of the 77 compounds per sample. We used a customized ANOSIM script written by Lars Kulik that allowed controlling for repeated samples per individual by permuting within individuals only. To further assess which species combinations were more similar, we ran post hoc pairwise ANOSIM including data of only two species at a time. To visualize similarities between samples in a two-dimensional non-metric multidimensional scaling plot we used the functions vegdist of the package MASS (Venables & Ripley, 2002) and ordiplot of the package vegan.

2.4.3 | Relative abundance of compounds

Finally, to investigate if specific compounds are associated with species, sex or age, we used the composition (relative intensities) of the 77 compounds. Therefore, we calculated a generalized linear mixed model using the package lme4. The relative peak areas of the 77 compounds per sample were fitted as the response. We transformed the standardized peak areas; arcsine and log(x + 0.01); to achieve a normal distribution and vectorized the multivariate data matrix of sample ($N = 195$) and compound ($N = 77$; Jamil, Ozinga, Kleyer, & ter Braak, 2013). Species and sex (dummy-coded and centered), and age (*z*-transformed) were fitted as fixed effects test predictors. We included sample number, compound ID, and individual identity as random effects to prevent heteroscedastic variance resulting from the vectorized data matrix (Jamil et al., 2013) as well

TABLE 1 Results of the linear mixed models estimating the impact of species, sex, and age on the richness and intensity of body odor samples of four great ape species

Term	Estimate	*SE*	CI_{lower}	CI_{upper}	χ^2	*df*	*p* value
Richness							
Intercept	11.37	0.29	10.80	12.28	[a]	[a]	[a]
Species	[a]	[a]	[a]	[a]	28.62	3	<0.001
Chimpanzee[b]	0.60	0.32	−0.46	1.26	[a]	[a]	[a]
Gorilla[b]	2.72	0.42	1.88	3.82	[a]	[a]	[a]
Orangutan[b]	0.39	0.34	−0.56	1.30	[a]	[a]	[a]
Age[c]	0.63	0.21	0.36	0.82	6.13	1	0.01
Sex, male[d]	0.54	0.37	0.01	0.89	1.87	1	0.17
Species × sex	[a]	[a]	[a]	[a]	1.90	3	0.59
Intensity							
Intercept	17.35	0.17	17.07	17.73	[a]	[a]	[a]
Species	[a]	[a]	[a]	[a]	28.36	3	<0.001
Chimpanzee[b]	0.29	0.16	−0.19	0.54	[a]	[a]	[a]
Gorilla[b]	1.16	0.19	0.78	1.57	[a]	[a]	[a]
Orangutan[b]	0.24	0.19	−0.26	0.55	[a]	[a]	[a]
Age[c]	0.20	0.06	0.12	0.30	5.81	1	0.02
Sex, male[d]	0.10	0.12	−0.07	0.27	0.56	1	0.46
Species × sex	[a]	[a]	[a]	[a]	3.51	3	0.32

Note. Nonsignificant interactions were removed from the final models. Remaining results were derived from full models excluding the nonsignificant interaction. Given are model estimates and *SE* for all test predictors, as well as a result of the likelihood ratio tests (full vs. reduced models) where applicable.

CI: confidence interval; *df*: degree of freedom; *SD*: standard deviation; *SE*: standard error.

[a]Not shown because of having only limited interpretation.

[b]Bonobo as reference category.

[c]z-Transformed, mean ± *SD* of the original values = 14.795 ± 10.047.

[d]Female as reference category.

as pseudoreplication. Body part and sampling day were fitted as additional random effects. As test predictors, we included the random slopes of the fixed effects species, sex, and age within the compound (Weiß, Marcillo et al., 2018). Furthermore, to achieve more reliable *p* values, random slopes of age and sex within observation day as well as species, sex, and age within body part were added to the model. We inspected a q-q plot to check for normal distribution and homogeneity of the residuals, which revealed no violation of assumptions. Although a slight bottom effect was detected when plotting residuals against fitted values, no issues were revealed when checking model stability and VIFs (derived as described above). As in the other models, we determined significance of the full model including all test predictors as well as significance of the individual test predictors (here, the random slopes) with LRTs.

2.5 | Substance identification

Finally, we wanted to identify the substances which appeared to affect the variance between samples. We focused on compounds showing the steepest slopes within predictors (i.e., larger than the average slope ± 1 *SD*) in the model described above. Using the NIST Mass Spectral Library (NIST08; National Institute of Standards and Technologies, Gaithersburg, MD), we compared the obtained mass spectra of substances to those of the best matches of the library. With the substance identification, we were able to further discriminate between contaminants and substances likely originating from the apes.

3 | RESULTS

In all 195 great ape samples analyzed, we detected 29,650 peaks in total. On average, a great ape chromatogram contained 152.1 ± 47.8 peaks (min: 36, max: 393; see also Table S3). Of the 77 compounds reliably found in at least one species, on average 37.6 ± 14.3 were found per sample (min: 3 and max: 68). An exemplary representation of chemical profiles of the four species can be found in Figure S1.

3.1 | Body odor intensity and richness

Results of the full models (compared to the null models) showed that the three test predictors species, sex, and age had a significant effect on richness (LRT: $\chi^2 = 40.95$, degrees of freedom (*df*) = 8, $p < 0.001$,

R^2m = 0.24, R^2c = 0.65; Table 1). In detail, the richness of chromatograms was affected by single test predictors after removing the two-way interaction of species and sex which had no significant effect on the response (LRT: χ^2 = 1.896, *df* = 3, *p* = 0.594). Specifically, richness differed between species (LRT: χ^2 = 28.62, *df* = 3, *p* < 0.001; see Figure 1a), with most peaks detected in gorillas and fewest in bonobos. Chimpanzees and orangutans showed intermediate richness. Across species, age had a significant impact on the richness (LRT: χ^2 = 6.13, *df* = 1, *p* = 0.01; see Figure 1b), with samples of older individuals being richer than younger individuals. Finally, the richness did not differ significantly between sexes (LRT: χ^2 = 1.87, *df* = 1, *p* = 0.17).

The overall intensity of odor samples was significantly influenced by the test predictors species, sex, and age (full vs. null model; LRT: χ^2 = 37.65, *df* = 8, *p* < 0.001, R^2m = 0.31, R^2c = 0.48; Table 1). Again, this was due to effects of single test predictors,

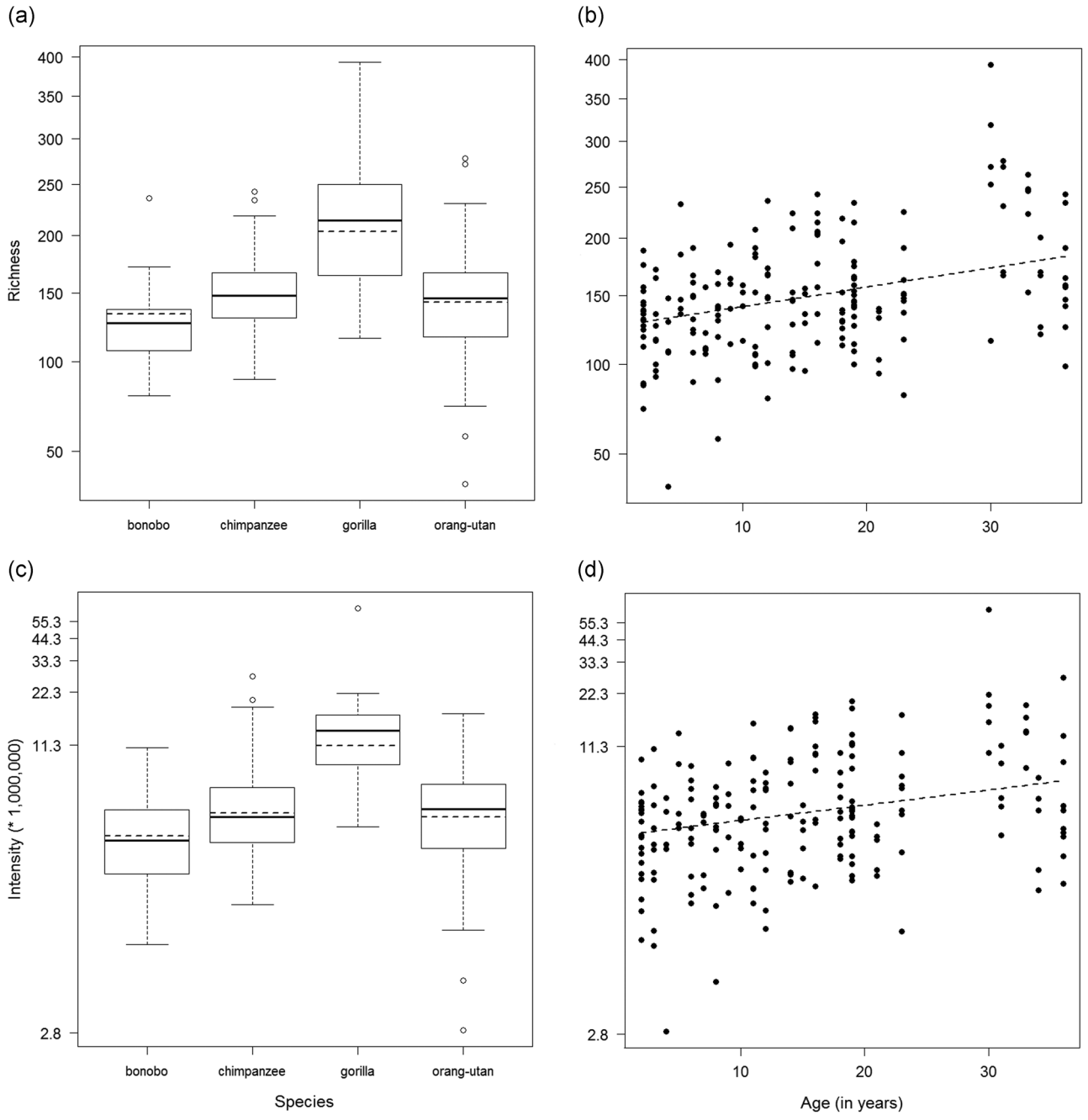

FIGURE 1 Variance in the richness (a, b) and intensity (c, d) of chemical profiles between species (a, c) and across age (b, d). (a, c) Boxes represent medians and first and third quartiles, whiskers represent 2.5% and 97.5%, and ○ outliers of the data. Dashed lines represent model estimates corrected for repeated measures per individual (five samples per individual, total *N* = 195) and other control predictors

after dropping the nonsignificant two-way interaction of species and sex from the final model (LRT: $\chi^2 = 3.507$, $df = 3$, $p = 0.320$; Table 1). In detail, intensity differed between species (LRT: $\chi^2 = 28.36$, $df = 3$, $p < 0.001$; see Figure 1c) with gorillas showing the most intense samples, whereas bonobos had samples of the lowest and chimpanzees and orangutans samples of intermediate intensity. Intensity also varied across age and increased in older individuals (LRT: $\chi^2 = 5.81$, $df = 1$, $p = 0.02$; see Figure 1d). No significant difference in intensity could be detected between sexes (LRT: $\chi^2 = 0.56$, $df = 1$, $p = 0.46$).

3.2 | Similarity between chemical profiles

We compared all chemical profiles on the basis of the 77 compounds consistently found and established that samples from the same species were more similar to each other than samples from different species (ANOSIM: $R = 0.40$, $p = 0.001$). Using nonmetric multidimensional scaling, species clearly separate from each other, with bonobos and chimpanzees, as well as chimpanzees and orangutans being closest together (Figure 2).

Pairwise ANOSIM tests further revealed that all pairs of species differ significantly from each other, that is, samples of the same species are always more similar to each other than samples of different species. Samples of chimpanzees and gorillas as well as gorillas and orangutans were distinguished best (with a higher R) and samples of chimpanzees and orangutans least (with a lower R, see Table 2).

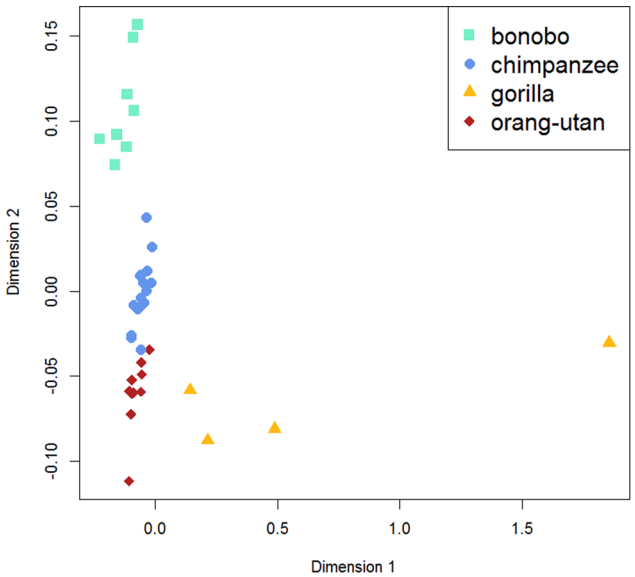

FIGURE 2 Two-dimensional nonmetric multidimensional scaling plot showing the impact of species on similarity between odor samples. Axes have arbitrary scales. The distance between two data points reveals how similar those profiles are, with more similar profiles being closer together. One data point resembles one individual ($N = 39$), but each point results from the mean of five samples per individual

TABLE 2 Results of post hoc pairwise analysis of similarity (ANOSIM) tests comparing the similarity of chemical profiles within and between two species on the basis of 77 compounds

Species 1	Species 2	R	P
Bonobo	Chimpanzee	0.42	0.001
Bonobo	Gorilla	0.33	0.001
Bonobo	Orangutan	0.43	0.001
Chimpanzee	Gorilla	0.60	0.001
Chimpanzee	Orangutan	0.18	0.001
Gorilla	Orangutan	0.73	0.001

Note. High R values indicate higher similarity within than between species and thus a good distinction between the respective species.

3.3 | Relative abundance

Investigating whether the three test predictors species, sex, and age had an impact on the relative composition of the 77 compounds, we found a significant effect (full vs. null model comparison; LRT: $\chi^2 = 3,975.00$, $df = 20$, $p < 0.001$). Specifically, the relative composition of the 77 compounds varied across species (LRT: $\chi^2 = 3,888.20$, $df = 15$, $p < 0.001$) and age (LRT: $\chi^2 = 67.04$, $df = 6$, $p < 0.001$). The effect of sex was only marginally significant (LRT: $\chi^2 = 12.47$, $df = 6$, $p = 0.05$).

We identified 40 compounds for which the variance was larger than one standard deviation from the average when inspecting the random slopes estimates, suggesting that those compounds are responsible for the variance related to one or several test predictors. In detail, 37 of these compounds were associated with the variance between species (see Figure S2). One of these compounds was specific to orangutans (unknown substance identity) and 11 were detected only in gorillas (tentatively identified as acetate, acid ester, and terpenes). Eleven compounds were found in all species but in varying concentrations (alkanes, alkanals, triterpene, alkanols, acid esters, steroids, potential contaminants, and unknown identity), whereas 14 compounds were found in only two or three of the four species (Table S4).

Six compounds were related to variance between sexes (identified as terpene derivative, steroids, terpenoids, and potential contaminants), of which five compounds had higher concentrations in male samples and one in female samples. Finally, seven compounds were associated with variance across age (identified as alkane, terpene derivative, steroids, terpenoids, and potential contaminants), five of which were more pronounced in younger individuals than in older ones and two compounds more in older than in younger ones. Several compounds could not be reliably identified and thus remain as "unknowns," whereas several others were identified as contaminants originating, for example, from the GC-MS column or sampling material. A detailed list of all 40 compounds including information on the substance identity and random slope estimates is provided in Table S4.

4 | DISCUSSION

In the present study, we were able to show that the body odor of great apes differs across species and age, while effects of sex were

not conclusive. Species differed in measures describing odor profiles as a whole (i.e., richness, intensity, and similarity to other profiles) as well as more detailed measures (i.e., the relative abundance of specific compounds). Furthermore, age influenced richness and intensity of samples as well as the relative abundance of specific compounds. Regarding sexes, we found variance only on the level of specific compounds.

We had hypothesized that richness and intensity of samples would vary between species and that the patterns of variation would reflect the complexity of their social systems. Although richness and intensity indeed varied between species, the specific patterns did not support our first hypothesis that species living in larger and more complex groups (bonobos and chimpanzees) would have richer and more intense body odor profiles (Freeberg et al., 2012). Instead, intensity and richness of chemical profiles were highest in gorillas, intermediate in chimpanzees and orangutans, and lowest in bonobos. Gorillas further had the largest number of compounds that were unique to the species. One alternative explanation could be the strength of mating competition, which is lowest in bonobos (Surbeck & Hohmann, 2013), intermediate in gorillas and orangutans (Fox, 2002; Robbins et al., 2004) and highest in chimpanzees (Nishida, 1968, 1983). However, though chimpanzee groups comprise multiple males which together protect their group against rivaling groups (Goodall, 1986), in gorillas usually only one male leads a group (Robbins et al., 2004) and protects his females and offspring against competitors. Thus, the need to signal body strength, condition or health might be larger in male gorillas. Accordingly, a richer and more intense body odor could make it possible for rivals to assess a male's quality from a larger distance, which can minimize the frequency of contact aggression. Along this line, it would have been helpful to incorporate rank data into this study to examine the influence of competition more closely; however, male dominance data were unfortunately not completely available for all species. Future studies should, therefore, evaluate the effect of dominance on body odor variance in great apes, as demonstrated in mandrills where male but not female ranks could be differentiated comparing chemical profiles of scent-gland secretions (Setchell et al., 2010). Overall, when comparing these results to our previous study investigating the sniffing frequency of mostly the same great ape individuals in the same setup as here (Jänig et al., 2018), both chemical complexity and sniffing frequency were highest in gorillas, lowest in bonobos and intermediate in chimpanzees and orangutans. Thus, both sniffing frequency and body odor complexity might resemble the general importance of olfaction for the respective species.

The chemical composition of odor samples on the basis of 77 compounds was more similar in samples of the same species than in samples of different species, and individuals clearly group together by species when visualizing the similarity. In line with our second hypothesis regarding the phylogenetic distances between species, we would have expected chimpanzees and bonobos to have the most similar profiles and orangutans to have odor profiles that are the most distant to the other species. In contrast, however, samples of chimpanzees and orangutans grouped together closest, whereas samples of chimpanzees and bonobos were only of intermediate similarity. Conspicuously, the odors of gorillas appeared to vary more between individuals than in the other species, which was mainly driven by one individual, an adult female. The sample size of gorillas, however, was small ($N = 4$), which warrants further investigations if and why gorilla odors vary more than in other great apes. Some possible explanations, however, might be reproductive status (which we could not control in this study) or undetected health issues.

Regarding sexes, we hypothesized that males have richer and more intense samples than females. This hypothesis found no robust support in our data, as neither richness nor intensity of chemical profiles varied significantly between sexes. In addition, the effect of sex on the relative composition of certain compounds was only marginally significant. Similarly, no significant difference in the number of compounds could be found between male and female spotted hyenas, although at the behavioral level, females reacted faster to scent marks of other females compared to those of males (Burgener, Dehnhard, Hofer, & East, 2009). In several species of Strepsirrhines, the richness in compounds did not vary between sexes either, but specific compounds were produced by only one sex, consistent with a sex-specific chemical signature (delBarco-Trillo et al., 2011, 2012). Although we could not detect compounds uniquely present in one sex, we found six compounds which varied between sexes in their relative abundance. Five of these were more intense in males, one in females. This is similar to findings in humans showing that certain compounds vary between sexes in abundance, but none are unique to one sex suggesting a multivariate cue for sex (Penn et al., 2007). Whether the subtle differences detected in the relative abundance of some compounds translate into perceivable differences between sexes needs to be tested in the future. It should be mentioned, that we sampled females across all reproductive states as it was logistically not possible to control for cycle states in all species. This probably increased the variance among female odor profiles and made the statistical analyses of sex differences more conservative. Along with a sample size of only one male in orangutans and gorillas, this might be a reason why sex differences were small in our study. In sum, our results regarding variance between the sexes were rather inconclusive, calling for further investigations.

Richness and intensity, that is, the chemical complexity, of odor profiles increased with age, supporting our fourth hypothesis. This could be associated with a higher importance of social (particular olfactory) communication with increasing age, but could also represent maturational changes in physiology which might be reflected in body odor (e.g., sebaceous and apocrine glands becoming active with puberty (Montagna & Parakkal, 1974). Notably, however, five of the seven compounds that were associated strongest with age were more pronounced in younger individuals than in older ones. Though this pattern contradicts part of our hypothesis, it resembles findings in humans, where odor of older people was rated as less intense (Mitro et al., 2012).

Regarding substance identity, species differences were, amongst others, due to several steroids. Steroids occur in sebaceous and apocrine glands of mammals, they are an important component in secretions and also appear to affect the incidence of bacterial

occurrence (Theis et al., 2013). Furthermore, other substances such as aldehydes, alcohols, alkanals, alkanols, and acid esters have been found in mammals before (Charpentier et al., 2012; Costello et al., 2014; Drea, 2015; Setchell et al., 2010), yet they have not been assigned to a specific context.

With the present study, we were able to show that body odor varies across species and age in hominids, whereas our results afford no strong conclusions about sex differences. A study involving more animals could substantiate our findings. Future investigations should also focus on the information content of the species' body odor in more detail and test the functionality of whole body odor as well as specific substances in behavioral experiments. Furthermore, our study showed that even when using blank samples to remove contaminants, the compounds used for statistical analysis may still comprise compounds not originating from the sampled animals such as dirt or remains of the environment on the skin. Without prior identification of compounds, relying only on summary measures such as the richness or intensity of a sample to describe animal scents, therefore, exhibits just the starting point to understand olfactory communication of hominids.

In conclusion, with our study, we contributed to a fundamental understanding of the importance and purpose of chemical communication in great apes. We showed that the body odor of hominid species varies and contains various kinds of information potentially relevant for social communication. Indications that chemical complexity may reflect social characteristics such as strength of male–male competition warrant further investigations. Future studies should comprise populations both in captivity and in the wild. The opinion of microsmatic hominids should finally be revised.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

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

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