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Chemical Composition of Scent-Gland Secretions in an Old World Monkey (*Mandrillus sphinx*): Influence of Sex, Male Status, and Individual Identity

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Abstract

Primates are traditionally considered to be microsmatic, with decreased reliance on olfactory senses in comparison to other sensory modalities such as vision. This is particularly the case for Old World monkeys and apes (catarrhines). However, various lines of evidence suggest that chemical communication may be important in these species, including the presence of a sternal scent-gland in the mandrill. We investigated the volatile components of mandrill odor using gas chromatography–mass spectrometry. We identified a total of 97 volatile components in 88 swabs of the sternal gland secretion and 95 samples of sternal gland hair saturated with scent-gland secretion collected from 27 males and 18 females. We compared odor profiles with features of the signaler using principle components and discriminant function analyses and found that volatile profiles convey both variable (age, dominance rank in males) and fixed (sex, possibly individual identity) information about the signaler. The combination of an odor profile that signals sex, age, and rank with increased motivation to scent-mark and increased production of secretion in high-ranking males leads to a potent signal of the presence of a dominant, adult male with high testosterone levels. This may be particularly relevant in the dense Central African rain forest which mandrills inhabit. By contrast, we were unable to differentiate between either female cycle stage or female rank based on odor profiles, which accords with behavioral studies suggesting that odor signals are not as important in female mandrills as they are in males. The similarity of our findings to those for other mammals and in primates that are more distantly related to humans suggests a broader role for odor in primate communication than is currently recognized.

Key words: communication, dominance rank, gas chromatography–mass spectrometry, microsmatic, olfaction, pheromones, signaling

Introduction

Mammalian social systems depend on signals that communicate information between individuals (Bradbury and Vehrencamp 1998). These signals often comprise complex chemosignals, which can communicate information ranging from identity (species, sex, group, and individual) to current status (social, reproductive, and health) to conspecifics (Wyatt 2003; Thom and Hurst 2004; Brennan and Kendrick 2006). Such olfactory signaling has important influences on a diversity of behaviors that are critical for reproductive success, including kin recognition (Porter and Moore 1981; Sun and Mueller-Schwarze 1997; Mateo 2006), mate choice (Penn and Potts 1998), and intrasexual competition (Gosling and Roberts 2001).

Olfactory cues mediate kin recognition in a variety of species (Wyatt 2003). The ability to recognize kin is fundamental to kin-biased social behavior (kin selection,

Hamilton 1964). It also minimizes the risks associated with mating between close relatives, which would otherwise reduce heterozygosity, and permit the expression of deleterious recessive alleles in offspring, decreasing fitness (inbreeding depression, Crnokrak and Roff 1999; Keller and Waller 2002).

In addition to conveying information concerning relatedness, odor may also inform mate choice by acting as an honest signal of condition. Scent-marking is costly both in energetic terms and in the risk of attracting predators and potential competitors (Gosling and Roberts 2001). This is consistent with the "handicap" principle of sexual selection: If traits are condition dependent, then only high quality individuals should be able to express them fully, and the opposite sex should prefer to mate with such individuals to obtain resources or genetic benefits for their offspring (Zahavi 1975; Andersson 1994). Furthermore, olfactory signals are often more labile than morphological traits, and the components of scent signals are under the control of numerous endogenous physiological and exogenous factors, including hormones. Their chemical composition may, therefore, reflect the current biological state of the marker, including social, health, and nutritional status, to potential mates more reliably than less dynamic modes of signaling (Penn and Potts 1998).

Finally, scent-glands, scent-marking behavior, and chemical signals are often more exaggerated in males than in females (Blaustein 1981), and odor signals may function in male–male competition, signaling dominance status to potential rivals. For example, the odors of male mice contain androgen-dependent volatile compounds that reflect social dominance (Gosling and Roberts 2001). The physiological consequences of encountering the scent-marks of a dominant individual include reproductive suppression in both males and females (Barrett et al. 1990; Carter and Roberts 1997). In contrast to other means of signaling dominance, for example, via visual traits, scent-marking also permits both the signaler and the receiver to avoid potential costly escalated aggression by transmitting information in the absence of the owner.

Chemical communication in primates

Olfaction is far less well understood in primates than in other mammals and our knowledge of chemical communication in primates lags behind our understanding of both visual and auditory communication (Heymann 2006). This may be because primates are traditionally regarded as microsmatic and thought to rely on other sensory modalities, such as vision, rather than olfaction (Dominy and Lucas 2001; Zhang and Webb 2003). However, various studies suggest that the role of olfaction in the regulation of primate behavior has been underestimated. For example, experiments have shown that olfactory sensitivity in squirrel monkeys is as good as, or better than, that of rats or dogs for some substances (Laska et al. 2000). Furthermore, odor signals are known to advertise reproductive state, dominance rank, and individual identity in strepsirrhines (ring-tailed lemurs, Palagi and Dapporto 2006; Scordato and Drea 2007) and callitrichids (marmosets and tamarins, Belcher et al. 1986; Epple et al. 1993; Ziegler et al. 1993; Smith et al. 1997) and sex, age, and family membership in owl monkeys (MacDonald et al. 2007). There is also evidence that odor profiles may reflect individual genotype and genetic similarity in ring-tailed lemurs (Knapp et al. 2006; Charpentier et al. 2008). Finally, olfactory cues may also mediate reproductive suppression of subordinate individuals by dominants in marmosets (Barrett et al. 1990) and mouse lemurs (Schilling et al. 1984; Izard 1990).

Although some research has been carried on olfactory communication in strephsirrhines and New World primates, very little information exists for Old World monkeys and apes (catarrhines). This is not surprising, as catarrhines are considered to be the most microsmatic primates. They have significantly higher proportion of olfactory receptor pseudogenes than other primates (Gilad et al. 2004), and the vomeronasal organ (VNO), which binds pheromones, is traditionally thought to be absent or vestigial in these species (reviews in Monti-Bloch et al. 1998; Dulac and Torello 2003). Moreover, TRPC2, a gene that is essential for VNO function in the mouse, is a pseudogene in humans (Liman and Innan 2003). However, various lines of evidence suggest that it would be premature to conclude that chemical communication is of no importance to catarrhines. First, scent-glands are known to occur in various Old World primate species, including gibbons (Geissman and Hulftegger 1994) and the genus *Mandrillus* (Hill 1970). Second, intriguing experimental evidence has shown that humans can discriminate between kin and nonkin via odor alone (Porter and Moore 1981) and are able to detect individual differences in major histocompatibility complex (MHC) genotype via olfactory cues (Wedekind et al. 1995; Wedekind and Füri 1997; Jacob et al. 2002). Third, although approximately 50% of olfactory receptor genes in hominoids (apes) are pseudogenes (vs. 0% in mice), only approximately 27% are pseudogenes in Old World monkeys (Rouquier et al. 2000). Fourth, the existence, homology and potential function of the VNO in humans, and other Old World species have been the focus of controversy (e.g., Smith, Siegel, et al. 2001 and references therein). Although it appears doubtful that Old World primates possess a VNO that is functional as a pheromone receptor (review in Dulac & Torello 2003), there is ample evidence suggesting that a functional VNO is not necessary for semiochemical communication, and that both nonvolatile and volatile chemicals received by the main olfactory epithelium function as chemical messages (e.g. Wysocki et al. 2004; Spehr et al. 2006). Taken together, this evidence suggests that odor may play a larger role in the regulation of catarrhine behavior than is currently recognized.

Chemical communication in mandrills

We report the first detailed chemical analyses of scent-gland secretions for a nonhuman catarrhine primate, the mandrill

(*Mandrillus sphinx*). Mandrills are found in the dense rain forests of Gabon, Congo, mainland Equatorial Guinea, and Cameroon to the south of the Sanaga river (Grubb 1973) and are a particularly interesting model for assessing the importance of chemical communication in Old World primates for several reasons. First, unlike most Old World monkeys, both male and female mandrills possess a sternal gland (Hill 1970), which produces a glandular secretion that they rub vigorously against tree trunks and vertical branches (Feistner 1991). These sternal glands are visible as a patch of modified hairs on the chest and are more active in males than in females, with maximum activity in alpha males, in which the hairs are dark and wet with glandular secretion (Setchell and Dixson 2001a, 2001b). Scent-glands are active throughout the year (Setchell and Dixson 2001c), males scent-mark more than females do and dominant males scent-mark more than subordinate males do (Feistner 1991).

Second, in contrast to other primate species in which chemical signaling has been studied, which live in small multimale–multifemale groups in which females are dominant over males (ring-tailed lemurs and sifaka) or are monogamous/polyandrous with high intrasexual competition between females (callitrichids), mandrills live in large multimale–multifemale groups in which males dominate females. Females form stable matrilines within these groups, whereas male group membership is more variable (Setchell and Dixson 2001a; Abernethy et al. 2002). Male–male competition is intense, with high reproductive skew in favor of the alpha male (Charpentier et al. 2005; Setchell et al. 2005). As a consequence, mandrills are extremely sexually dimorphic: Males are more than 3 times the body mass of females (Setchell et al. 2001) and possess large canine teeth (Setchell and Dixson 2002) and a suite of sexually selected traits, including bright red, blue, and violet skin coloration (Setchell and Dixson 2001a, 2001b; Setchell et al. 2001) and loud vocalizations. The evolution of such extreme, multimodal signaling may be related to the large, fluid groups in which mandrills live and their deep rain forest environment (Setchell and Kappeler 2003; Setchell et al. 2009a). It has also been suggested that odor signals may function in the suppression of secondary sexual development of subordinate males by dominants (Setchell and Dixson 2001a).

Third, we have shown recently that mandrills reproduce preferentially with individuals that are genetically dissimilar to themselves at the MHC (Setchell et al. 2009b). Although the striking visual secondary sexual traits possessed by male mandrills may convey information regarding mate "quality" (Zahavi 1975; Hamilton and Zuk 1982), including dominance rank (Setchell and Dixson 2001a, 2001b), they cannot signal genetic compatibility with members of the opposite sex, as this is contingent on the chooser's own genotype. However, if relatives have similar odor profiles or if genetic similarity in unrelated animals is reflected in similar odor profiles, then olfaction may play a role in the assessment of mate compatibility, as demonstrated for both rodents and humans (review in Penn 2002).

Finally, a recent study suggests that mandrills are able to discriminate paternal kin from nonkin, despite their polygynandrous mating system (Charpentier et al. 2007). The mechanism underlying this behavior is unknown, but phenotype matching based on odor is one possibility (Widdig et al. 2001). As with mate choice based on genetic dissimilarity, if odor plays a role in kin selection, then this requires that relatedness is reflected in chemical profiles.

We investigated the volatile components of mandrill sternal gland secretions using gas chromatography–mass spectrometry (GC-MS) and compared mandrill scent-gland secretions with features of the signaler. Based on current knowledge of mandrill behavior and ecology and olfactory communication in other primate species, we predicted that scent-gland secretions would encode information concerning sex and that male secretions would reflect dominance rank, and the presence of receptive females, when male–male competition is most intense. We also examined whether odor profiles signal individual identity, as reported for ring-tailed lemurs (Palagi and Dapporto 2006) and common marmosets (*Callithrix jacchus*; Smith, Tomlinson, et al. 2001).

Materials and methods

The naturalistic breeding colony at the Centre International de Recherches Médicales, in Franceville, Gabon, has provided an invaluable resource for studies of mandrill behavior and reproduction. The colony was established in 1983–1984 when 15 unrelated animals (7 males and 8 females) were released into a 6.5-ha forest enclosure (E1). A second semifree-ranging group was established in 1994 in a smaller enclosure (E2, 3.5 ha) by transferring 17 mandrills (including 6 adult females and 4 adult males) from the first enclosure. All subsequent increases in the group have been due to natural reproduction of the founder animals, countered by deaths and occasional removals. The mandrills forage freely and receive daily supplements of monkey chow, fruit, and vegetables. Water is always available from a stream, which runs through both enclosures. Group size and composition at the beginning of the study are detailed in Table 1 and correspond to smaller groups observed in the wild (Hoshino et al. 1984; Rogers et al. 1996).

Table 1 Composition of study groups in March 2004

Enclosure	Infants and juveniles		Females of breeding age	Adolescent males	Adult males	Total
	Male	Female				
1	18	27	15	7	8	75
2	12	24	15	11	6	68

Daily observations

We noted the status of females daily as cycling (females in any stage of the menstrual cycle, during which females show conspicuous perineal swellings, Dixson 1998), pregnant (assigned post hoc from the birth of an infant, beginning with the final detumescence of the perineal skin), lactating (the period following the birth of an infant to the resumption of cycling), or quiescent (not pregnant, lactating, or cycling). We calculated dominance rank separately for males and females using dyadic interaction matrices, including all interactions where one individual avoided or fled when another individual approached. Female dominance ranks were stable during the study period, male ranks changed periodically, but the identity of the top-ranking (alpha) male was always unambiguous (Setchell et al. 2008). Finally, we scored the occurrence of mate-guarding on a daily basis to determine days on which males were attracted to and actively competing for access to receptive females. Mate-guarding is an easily observed, unambiguous behavior where a male maintains close spatial proximity to a female and monitors her continuously (Setchell et al. 2005).

Odor samples

Primate center staff captured most of the mandrills in March and October 2004 and March 2005 for routine veterinary controls and as part of a larger study of sexual selection in mandrills. We collected odor samples directly from anesthetized individuals during these captures, with additional opportunistic sampling when animals were captured by primate center staff for other reasons. We obtained odor samples from males aged 6.2 to 17.3 years (n = 27, mean: 10.7 years) and females aged 6.5 to 26.4 years (n = 19, mean: 14.8 years). We term males "adolescent" until the age of 9 years, when they attain adult body mass, crown-rump length, and full expression of secondary sexual traits (Setchell et al. 2006) and "adult" thereafter. All females sampled were multiparous and adult size.

We collected odor samples in 2 ways. First, we rubbed a sterile cotton swab against the sternal gland 10 times vertically and 10 times horizontally, using steady pressure. We also exposed control swabs to the air in the primate center during sampling to identify any volatile compounds in the air that did not derive from the mandrills. Second, we collected hairs from the sternal gland area because we observed that these hairs were often wet with secretion even if the sternal gland was not active—possibly due to the effects of capture and anesthesia. We collected approximately 60 g of hair, which we cut with sterilized scissors. We transferred the swabs, hair samples, and control swabs to separate sterile vials, froze them in liquid nitrogen immediately, and stored them at –80 °C. In total, we obtained 88 swab samples and 95 samples of sternal gland hair (details in Table 2). We also collected paired samples of hairs from a non-scent gland area (the epigastric area) for 24 (25 %) of the hair samples. We were unable to collect equal numbers of replicates from all individuals because we could not guarantee to capture and sample an individual mandrill during each capture period.

Table 2 Details of samples obtained

Sample type	Sex	Number of samples					
		1	2	3	4	5	Total
Swab	Male	11	7	7	4	0	59
	Female	10	7	2	0	0	29
Hair	Male	10	6	5	4	2	63
	Female	9	8	1	1	0	32

Odor analyses

We carried out laboratory analyses of odor in the Mass Spectrometry Center, Florence University, Italy. We subjected swab samples to dynamic headspace (DHS) extraction followed by GC-MS analysis because they comprised only a very low amount of odor secretion, and DHS provides a high concentration factor for volatiles. We placed swab samples into 10-mL screw-capped vials, closed by teflon-faced rubber septa and seals (Supelco). We passed purified nitrogen (50 mL min^{-1}) through the system for 20 min at 50 °C and adsorbed the entrained volatiles on an adsorbent cartridge trap filled with XLTenax Tm (Gerstel GmbH & Co.KG), maintained at 20 °C within a Gerstel DHS device. The volatile compounds were subsequently thermally desorbed and transferred to the GC system using a thermal desorption unit (TDU; Gerstel GmbH & Co.KG). We carried out desorption at 300 °C for 10 min under a helium flow (30 mL min^{-1}) and cryofocused the analytes in a programmable temperature vaporizer injector (Gerstel CIS 4) maintained at –40 °C with liquid carbon dioxide. We injected the volatile components into the GC capillary column by heating the CIS 4 injector to 300 °C at 720 °C min^{-1}. We carried out blank analyses using an empty 10-mL vial (Supelco) to assess possible environmental contamination. We purged the adsorbent traps at 300 °C for 10 min after each analysis using the TDU apparatus to avoid any possible carryover effects.

We subjected hair samples to solid-phase microextraction (SPME) and GC-MS. We placed hair samples into 10-mL screw-capped vials and closed the vials with teflon-faced rubber septa and seals (Supelco). We introduced a 65-μm polydimethylsiloxane/divinylbenzene SPME syringe needle through the vial septum and exposed the fiber to the headspace above the sample in the vial for 20 min at 40 °C. We assessed possible environmental contamination via blank analyses using an empty 10-mL vial (Supelco) following the same procedure as for the samples and purged the fiber in the injector with the split ratio at 100:1 for 25 min after each analysis to avoid any possible carry-over effects.

We analyzed the adsorbed volatile analytes of both types of sample using a 5975C mass spectrometer (Agilent

Technologies) EI, 70 eV, coupled directly to a 7890A gas chromatograph (Agilent Technologies) equipped with a fused silica HP 5-ms capillary column (Agilent Technologies) 30 m × 0.25 mm crossbonded 5%-phenyl-95%-dimethylpolysiloxane, film thickness 0.25 μm. We maintained the injector and transfer line temperatures at 270 °C and 280 °C, respectively. We made injections in splitless mode with a constant flow of helium carrier gas of 1.5 mL min^{-1}. We started the oven temperature program at 45 °C for 2 min, then raised it by 4 °C min^{-1} to 170 °C, by 7 °C min^{-1} to 300 °C, and finally by 20 °C min^{-1} to a final temperature of 320 °C.

We standardized peak retention times using an internal standard (alpha pinene). We identified the eluted compounds by comparing the experimental spectra with those of the NIST mass spectral database, version 5.0 (Agilent Technologies). We determined the relative amounts of compounds by integrating the areas of the corresponding peaks in the total ion current profile and calculated percentages with respect to the total area. We retained peaks that comprised at least 0.05% of the total area of the chromatogram to avoid problems associated with unreliable quantification at very low relative amounts, although this may mean that we missed trace chemicals (Smith, Tomlinson, et al. 2001). This use of relative rather than total abundance of the compounds that comprise mandrill odor profiles controls for any differences in the amount of secretion produced. We analyzed all samples in a short period of time to minimize interassay variability. We used control swabs to identify compounds that did not derive from the animals and remove these from the swab results.

Data analysis

We used principal component analysis (PCA) to reduce the compounds we identified to a smaller number of uncorrelated principal components that explained most of the variance. We retained principal components with eigenvalues >1 and used these as covariates in discriminant function analysis (DFA), grouping samples using the following variables:

- Hair type: sternal gland versus epigastric (hair samples only).
- Sex of the individual sampled.
- Male age: adolescent versus adult.
- Male rank: alpha versus not alpha, and high (rank 1–3), mid (4–7), or low (8–13; we chose categories to equalize the number of samples falling into each class).
- Male competition for females: occurrence of mate-guarding on the day the sample was collected (yes/no).
- Female cycle stage: cycling (undergoing menstrual cycles), lactating, pregnant, or quiescent (none of the previous categories). Unfortunately, we obtained too few samples to include specific stage of the menstrual cycle (e.g., follicular vs. luteal).
- Female rank: high (top 25%), mid (25–75%), and low (bottom 25%).
- Identity of the individual sampled.

DFA generates a discriminant function (or a set of discriminant functions, where there are more than 2 groups) based on linear combinations of the predictor variables that provide the best discrimination between the groups. We tested the statistical significance of group differences using Wilks' λ and χ^2. Where results are significant, we plot functions as mean ± standard error for single functions and as scatter plots of the first 2 functions where there was more than one function. We also report classification statistics as the number of cases correctly and incorrectly assigned to each of the groups based on the discriminant analysis. Use of the same samples as for the calculation of the discriminant functions (due to low overall sample size) may lead to overestimates of accuracy, so we also report results of "leave-one-out" cross-validation analyses to address this issue.

Our data set included repeat samples for some individuals, which gives rise to problems of pseudoreplication if these nonindependent data points are treated as independent replicates and increases the risk of Type I error. To circumvent this issue, we followed up significant analyses for sex and male age using a subset of the data including one sample for each individual, selected at random. This reduced the sample size to 27 males and 18 females, as well as removing variation within individuals, which may be considerable. Other significant results (male dominance rank and the mate-guarding variable) varied within an individual, meaning that pseudoreplication would lead to less variation between states, rather than more, biasing our analyses toward a nonsignificant result.

We conducted all statistical analyses in SPSS 15.0 for Windows.

Results

Swab samples

We identified a total of 19 distinct peaks in the control swabs that were also present in all swab samples. These included siloxane derivatives and silanols, originating from the GC capillary column, phalates, alcohols, and additional peaks that could not be identified. Removing these compounds from the swab sample results yielded a total of 47 distinct peaks in 88 swab samples of mandrill sternal gland secretions that were not present in the controls. These compounds included a series of hydrocarbons and organic aliphatic acid esters, aldehydes, and ketones (tentative identifications are listed in Table 3, typical chromatograms are shown in Figure 1). Ten compounds were present in all 88 samples, the modal representation was 100%, and 53% of compounds were present in >90% of samples. When we explored the data set we found and removed 2 obvious outliers (one female and one

Table 3 Volatile compounds present in swab samples of mandrill sternal gland secretions identified tentatively using the NIST 2005 mass spectral database, listed in order of retention time

Molecular weight	Compound
116	Butanoic acid, 3-methyl-, methyl ester
88	Propanoic acid, 2-methyl-
130	Butanoic acid, 3-methyl-, ethyl ester
130	Pentanoic acid, ethyl ester
116	Hexanoic acid
114	2(3H)-Furanone, 5-ethyldihydro-
106	Pentanedinitrile, 2-methylene-
108	**Phenol, 4-methyl-**
170	*cis*-Linaloloxide
170	Linalool oxide trans
156	**Undecane**
114	2H-Pyran-2-one, tetrahydro-6-methyl-
150	Benzoic acid, ethyl ester
128	**Naphthalene**
184	Undecane, 3,6-dimethyl-
134	Benzaldehyde, 3,4-dimethyl-
184	Dodecane, 6-methyl-
164	**Benzeneacetic acid, ethyl ester**
184	Dodecane, 4-methyl-
146	Naphthalene, 1,2,3,4-tetrahydro-6-methyl-
142	**Naphthalene, 2-methyl-**
198	Dodecane, 4,6-dimethyl-
212	Pentadecane
142	Naphthalene, 2-ethyl-
282	Nonadecane, 9-methyl-
156	Naphthalene, 1,5-dimethyl-
156	Naphthalene, 1,4-dimethyl-
196	12-Methyl-oxa-cyclododec-6-en-2-one
220	**Butylated hydroxytoluene**
194	Benzoic acid, 4-ethoxy-, ethyl ester
162	1,4,8-Dodecatriene, (E,E,E)-
234	3,5-di-*tert*-Butyl-4-hydroxybenzaldehyde
254	Octadecane
252	**Oxacycloheptadec-8-en-2-one**
270	Pentadecanoic acid, 14-methyl-, methyl ester
324	1,1′-Biphenyl, 2,3′,4,4′,5-pentachloro-
296	**9-Octadecenoic acid, methyl ester, (E)-**
298	**Octadecanoic acid, methyl ester**
312	Hexadecanoic acid, butyl ester
324	1,1′-Biphenyl, 2,3,4,4′,6-pentachloro-
390	1,2-Benzenedicarboxylic acid, diisooctyl ester
—	Hydrocarbon "A"[a]
410	Squalene
—	Hydrocarbon "B"[a]
—	Hydrocarbon "C"[a]
—	Hydrocarbon "D"[a]
—	Hydrocarbon "E"[a]

Compounds in **bold font** were found in both swab and hair samples.
[a]Compounds that are hydrocarbons but we were unable to identify precisely by comparing the experimental spectra with those of the NIST mass spectral database.

male, with scores that were 9 standard deviation (SD) and 7 SD greater than the mean, respectively). This was likely due to both samples having very low total amount of secretion because the total area was very low in both samples.

PCA reduced the chemical composition of odor samples to 15 principal components, explaining a total of 79.3% of the variance. The chemical profiles of males and females were not significantly different when all males were included in the analyses, but we found a significant difference between the 2 sexes when we examined only adult individuals (Table 4, Figure 2A), with 20/28 females and 33/37 males classified correctly. This was not due to pseudoreplication: The 2 sexes were also significantly different when we used only one sample per individual, with good classification accuracy (Table 4).

Chemical profiles of adult and adolescent males were significantly different (Table 4, Figure 3A), with 92% of adult males (34/37), but only 70% of adolescent males (14/20) classified correctly. Adult and adolescent males were also significantly different when we restricted analysis to one sample per individual, and classification accuracy was high (Table 4). We found no significant difference between chemical profiles of alpha and nonalpha males, but splitting males into high, mid, and low ranking yielded 2 functions that explained 58.4% and 41.5% of the variance and significantly differentiated between male ranks, although classification was poor (Table 4). High-ranking males were classified as high or mid, mid-ranking males as mid or low, and low-ranking males were 68% correctly classified (Table 5). High-ranking males fell into 2 clusters, one clearly separated from other males and one that overlapped with mid-ranking males, whereas mid- and low-ranking males showed some overlap (Figure 4A). The separate high-ranking males were not all alpha males nor were they all samples taken during periods when mate-guarding occurred. Using adult males only, DFA also differentiated significantly between male ranks

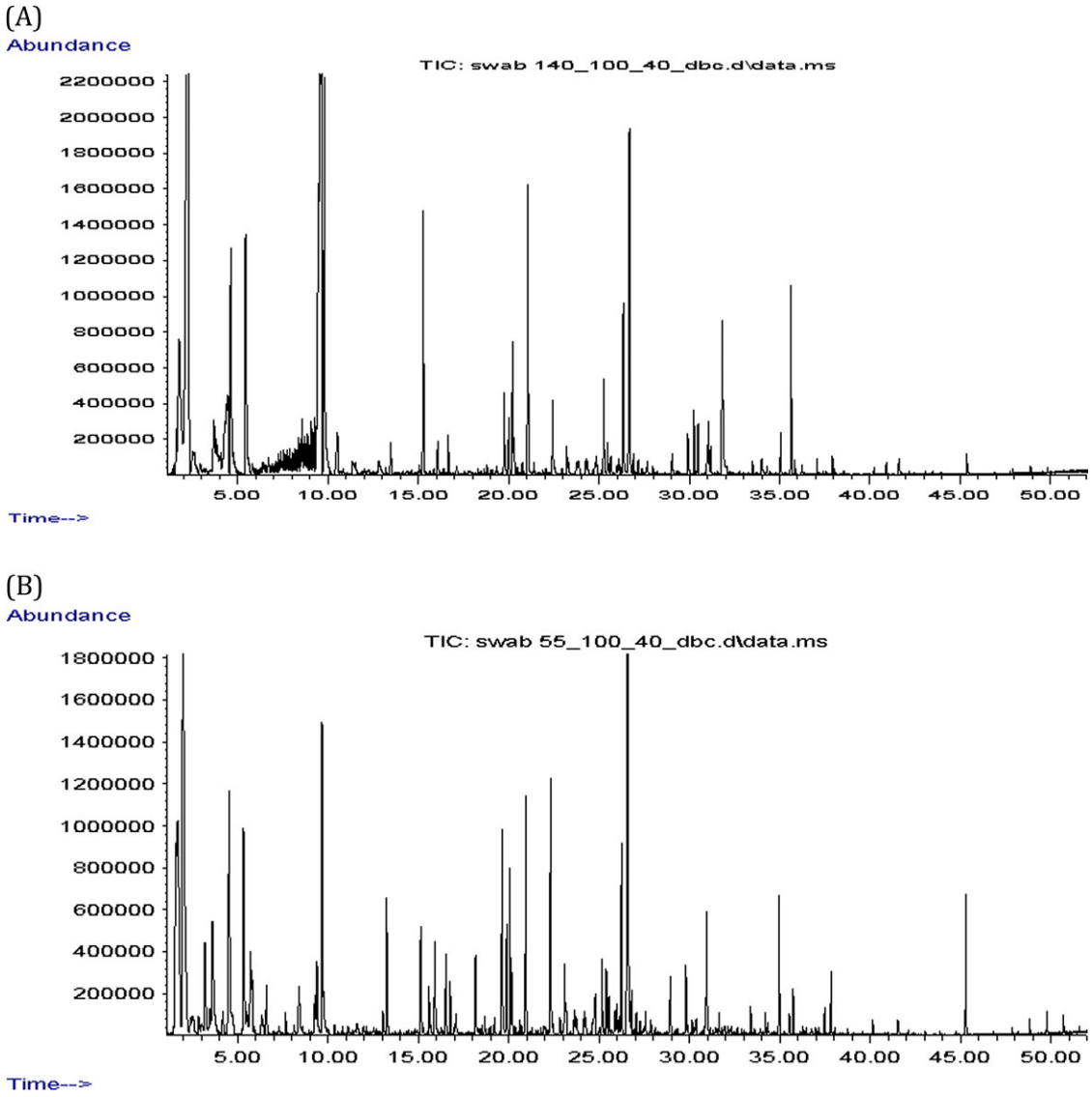

Figure 1 Example TICs of swab samples from the sternal gland of a male **(A)** and a female **(B)** mandrill.

(Table 4), with 2 functions that explained 68.0% and 32.0% of the variance. Classification was better in this case, with 87% of high, 94% of mid, and 67% of low correct. We also found a significant influence of mate-guarding on male odor (Table 4, Figure 5), with 9/13 mate-guarding samples correctly classified and 41/44 no mate-guarding samples correctly classified.

In females, we found no significant difference in chemical profiles among cycle stages or ranks (Table 4).

Finally, DFA based on individual identity revealed 3 discriminant functions that differentiated significantly between individuals when combined (Table 4). Of these, Function 1 explained 39.4% of the variance, Function 2 explained 16.1% (0.90), and Function 3 explained 12.5% (0.88). Figure 6 illustrates the degree of separation using individuals represented by >1 sample. However, classification was relatively poor.

Hair samples

We identified a total of 59 distinct peaks in the volatile chemical composition of hair samples from mandrill sternal glands (95 samples). As for the swab samples, these compounds included a series of organic aliphatic acid esters and hydrocarbons, as well as aldehydes and ketones (tentative identifications in Table 6). Twelve compounds (20%) were present in all samples, the modal representation was 100%, and 33 (56%) were present in >90% of samples. Nine of the compounds identified in hair were also found in the swab samples, and all but 5 of the 59 compounds were also found in epigastric hair samples.

PCA of the identified compounds yielded 18 principal components, explaining a total of 76.8% of the variance. The chemical profiles of sternal gland hairs were significantly

Table 4 Results of DFA comparing odor profiles of different groups of mandrill sternal gland samples

Sample	Test	Data set	λ	χ^2	df	*P*	% Correct	% Cross-validation
Swab	Males versus females	All data	0.82	15	15.41	0.422		
	Adult males versus females	All data	0.63	15	25.76	0.041	81.5	69.2
		One sample per ID	0.26	15	32.64	0.005	97.1	84.1
	Adult versus adolescent males	All data	0.55	15	27.99	0.022	84.2	63.2
		One sample per ID	0.17	15	29	0.016	100.0	84.6
	Alpha versus nonalpha males	All data	0.8	15	10.16	0.810		
	Male rank class	All data	0.33	30	49.72	0.013	61.8	41.8
		Adults only	0.11	30	56.74	0.002	88.9	72.2
	Mate-guarding in males	All data	0.55	15	28.61	0.018	87.7	73.7
	Female cycle stage	All data	0.06	30	38.71	0.132		
	Female rank	All data	0.14	30	35.18	0.236		
	Individual identity	All data	0.00	660	896.14	<0.001	68.4	
Hair	Males versus females	All data	0.45	18	85.20	<0.001	87.4	82.4
		One sample per ID	0.47	18	26.66	0.086		
	Adult males versus females	All data	0.38	18	58.76	<0.001	89.5	89.3
		One sample per ID	0.29	18	27.21	0.075		
	Adult versus adolescent males	All data	0.56	18	30.25	0.035	80.5	64.9
		One sample per ID	0.17	18	26.87	0.082		
	Alpha versus nonalpha males	All data	0.52	18	32.17	0.021	93.2	84.9
	Male rank class	All data	0.36	36	49.73	0.064		
		Adults only		18	21.07	0.276		
	Mate-guarding in males	All data	0.46	18	20.06	0.329		
	Female cycle stage	All data	0.09	54	47.62	0.717		
	Female rank	All data	0.2	36	33.37	0.599		
	Individual identity	All data	0	810	0.00	<0.001	62.0	

We report classification results only for significant analyses. Cross-validation could not be performed for individual identity because some individuals contributed only one sample to the data set. df, degrees of freedom.

different from those of epigastric hair (DFA: $\lambda = 0.60$, $\chi^2_{18} = 55.12$, $P < 0.001$; note that this analysis does not account for the paired nature of the samples); all further analyses concern only sternal gland hairs.

Chemical profiles of males and females were significantly different, with good classification (Table 4, Figure 2B). However, this may have been due to pseudoreplication because when we restricted analysis to one sample per individual, differentiation based on sex was no longer significant (Table 4). Chemical profiles of adult males were significantly different from those of females, with good classification, but again, differentiation was no longer significant when we restricted the data set to one sample per individual (Table 4).

Chemical profiles of adolescent and adult males were significantly different (Figure 3B), with 33/39 adults and 19/24 adolescents correctly classified. However, when we restricted analysis to one sample per individual, the differentiation was no longer significant (Table 4), although only one sample was incorrectly classified for each group (11/12 adolescents, 13/14 adults). Chemical profiles of alpha and nonalpha males were significantly different (Table 4, Figure 4B), with perfect classification accuracy for alpha males (8/8 samples) and 95% for nonalpha males (49/52 correct). However, chemical profiles for different male rank classes were not significantly different, either for all males or for adult males only, and chemical profiles did not differ between days when mate-guarding did and did not occur (Table 4).

We found no significant difference between chemical profiles with female cycle stage or rank (Table 4).

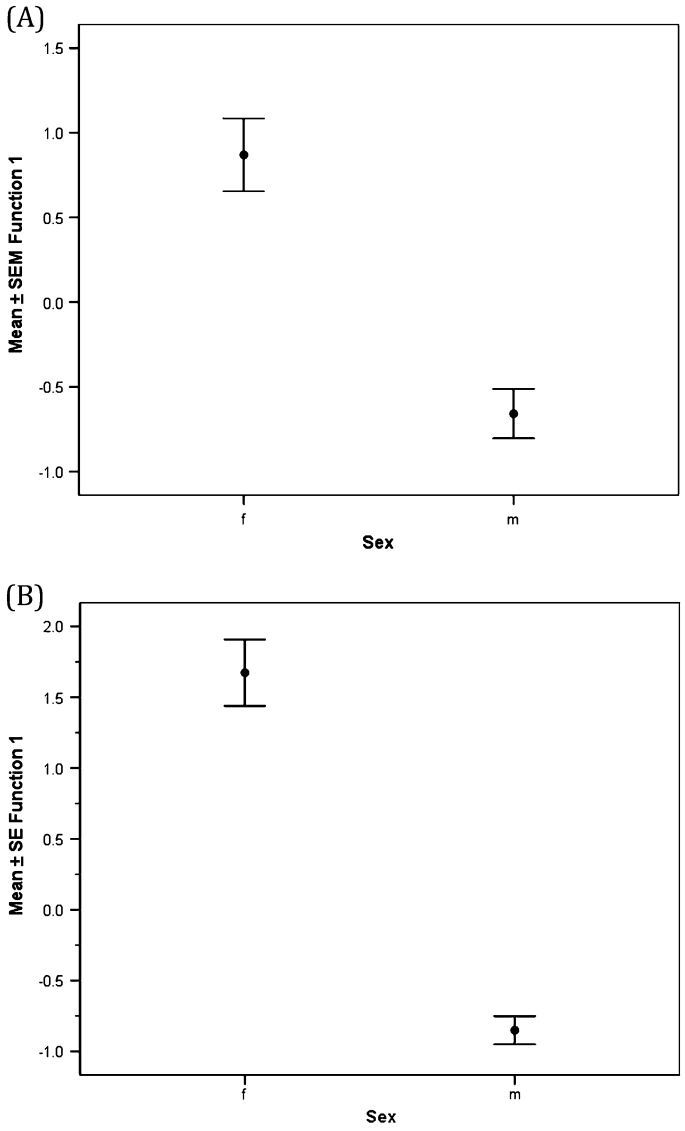

Figure 2 Discriminant function differentiating volatile profiles of male and female mandrills, based on **(A)** swab samples, **(B)** hair samples.

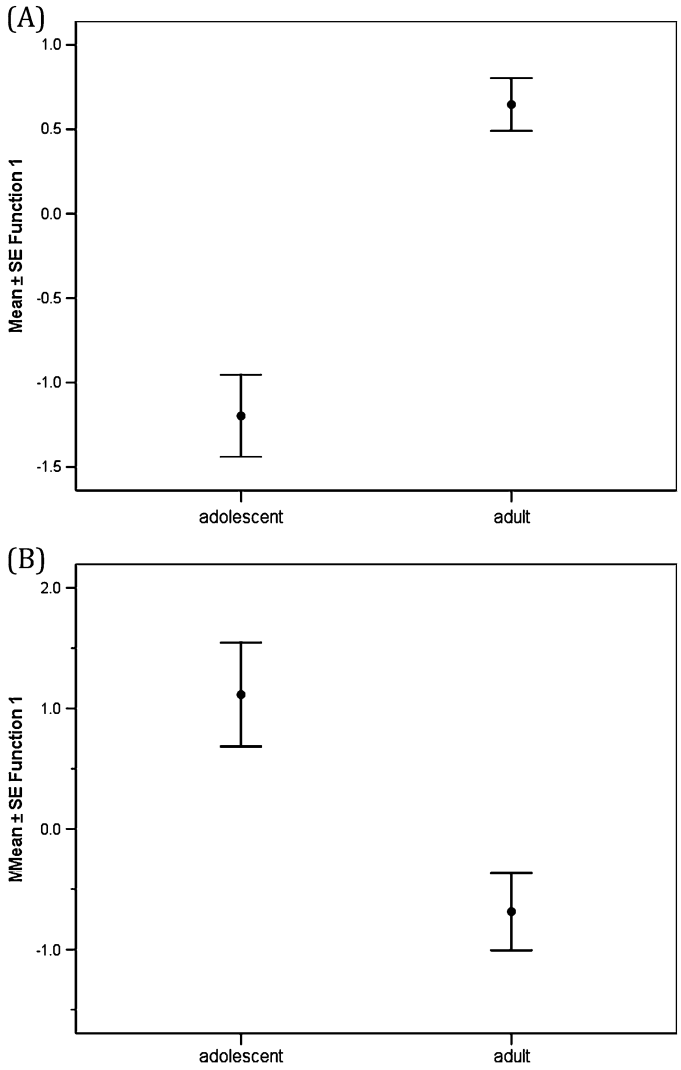

Figure 3 Discriminant function differentiating volatile profiles of adolescent and adult males, based on **(A)** swab samples, **(B)** hair samples.

Finally, DFA of volatile profiles from hair samples based on individual identity revealed 11 functions, explaining a total of 97.2% of the variance. Together these functions differentiated significantly between individuals, although classification was poor (Table 4).

Table 5 Count (%) of correct assignments of swab volatile profiles by male rank

		Predicted group			Total
		High	Mid	Low	
Actual group	High	7 (46.7)	8 (53.3)	0 (0.0)	15
	Mid	0 (0.0)	14 (66.7)	7 (33.3)	21
	Low	2 (10.5)	4 (21.1)	13 (68.4)	19

Discussion

We identified a total of 97 volatile components in the chemical profile of swabs of the sternal gland secretion, sternal gland hair, and epigastric hair from mandrills. Many of the compounds identified were volatile hydrocarbons that have also been identified in GC-MS odor profiles for other mammals, including primates. For example, 4-methyl phenol and generic lactones have been identified in odor secretions of *C. jacchus* (Smith, Tomlinson, et al. 2001), generic hydrocarbons and pentadecane have been found in *Lemur catta* (Hayes et al. 2004; Knapp et al. 2006), and hexanoic acid has also been identified in *L. catta* (Knapp et al. 2006) and *Aotus nancymaae* (MacDonald et al. 2007). As in lemurs (Scordato et al. 2007), some compounds were

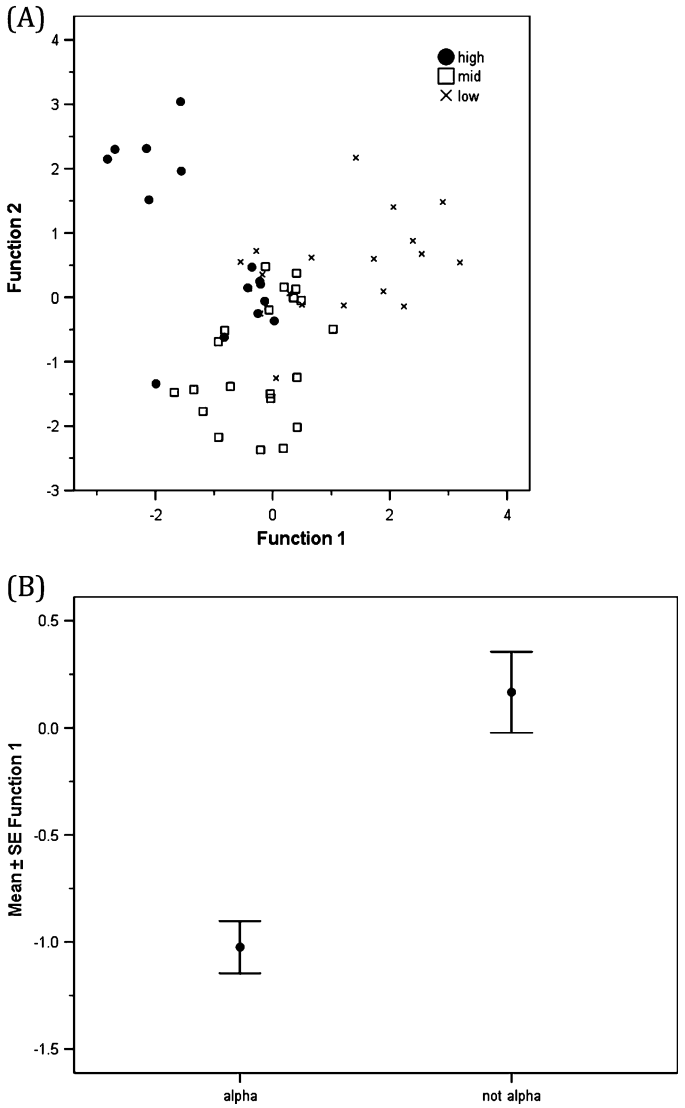

Figure 4 Discriminant function differentiating volatile profiles of males based on rank: **(A)** rank class, based on swab samples, **(B)** alpha versus not alpha, based on hair samples.

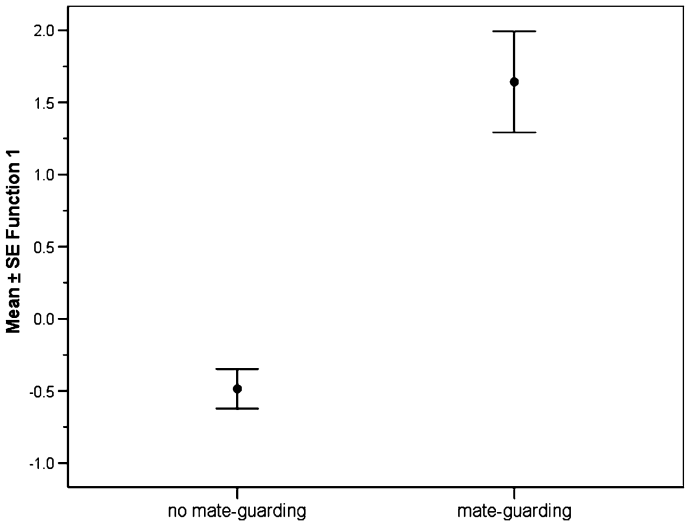

Figure 5 Discriminant function differentiating volatile profiles of males on days when mate-guarding occurred and days when no mate-guarding occurred, based on swab samples.

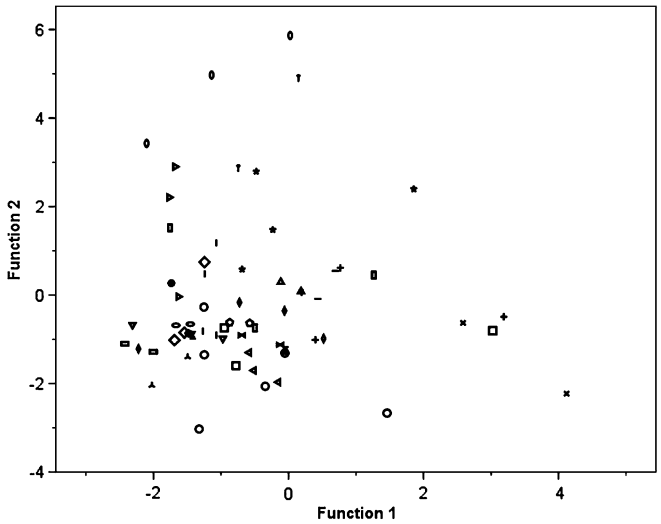

Figure 6 Discriminant function differentiating volatile profiles from different individual mandrills, based on swab samples. Each symbol represents a different individual. Plot shows only individuals contributing >1 sample, for simplicity.

relatively high–molecular weight hydrocarbons, including squalene, which may act as a fixative that slows the release of more volatile compounds, as suggested for 2-phenoxyethanol in rabbits (Hayes et al. 2003) and major urinary proteins in mice (Hurst et al. 1998).

Only 9 compounds were present in both swab and hair samples from the sternal gland. This relatively low degree of overlap may be due to the different chemical methods that we used for the 2 samples, which reduces our ability to compare the results directly. However, the 2 types of sample may also differ in composition because both include different substances that do not derive directly from the scent-gland. Swab samples may include epidermal compounds, whereas the chemical components of sternal hair samples overlapped to a large extent with those for hair from elsewhere on the body (epigastric hair), although odor profiles for hair from the 2 sites were significantly different. Sternal gland hair may also accumulate scent-gland secretion over time, whereas the swab samples measure recent scent-gland activity. Nevertheless, both swabs and hair samples measure potential odor signals that are transferred to the substrate during scent-marking because both skin and hair are rubbed against the tree when mandrills scent-mark. Furthermore, both may contribute to an individual's body odor, transmitting information to conspecifics during social interactions.

Table 6 Volatile compounds present in hair samples from mandrill sternal gland secretions identified tentatively using the NIST 2005 mass spectral database, listed in order of retention time

Molecular weight	Compound
76	Carbon disulfide
102	Propanoic acid, 2-methyl-, methyl ester
102	Butanoic acid, methyl ester
116	Propanoic acid, 2-methyl-, ethyl ester
116	Butanoic acid, 3-methyl-, methyl ester
116	Pentanoic acid, methyl ester
130	Butanoic acid, 3-methyl-, ethyl ester
102	Butanoic acid, 3-methyl-
114	Heptanal
151	Oxime-, methoxy-phenyl-
130	Hexanoic acid, methyl ester
144	Hexanoic acid, ethyl ester
128	Octanal
198	2,3,4,5,6-Pentafluorobenzylalcohol
144	Heptanoic acid, methyl ester
136	D-Limonene
130	1-Hexanol, 2-ethyl-
142	Cyclohexanecarboxylic acid, methyl ester
108	**Phenol, 4-methyl**
136	Benzoic acid, methyl ester
156	**Undecane**
142	Nonanal
158	Octanoic acid, methyl ester
342	Fluoren-9-ol, 3,6-dimethoxy-9-(2-phenylethynyl)-
150	Benzeneacetic acid, methyl ester
128	**Naphthalene**
172	Octanoic acid, ethyl ester
170	Dodecane
170	3-Nonenoic acid, methyl ester[a]
172	Nonanoic acid, methyl ester
164	**Benzeneacetic acid, ethyl ester**
164	Benzenepropanoic acid, methyl ester
142	**Naphthalene, 2-methyl-**
186	Decanoic acid, methyl ester
200	Decanoic acid, ethyl ester
200	Undecanoic acid, methyl ester
202	Octanedioic acid, dimethyl ester
220	**Butylated hydroxytoluene**[a]
220	1,9-Cyclohexadecadiene
218	1s,4R,7R,11R-1,3,4,7-Tetramethyltricyclo[5.3.1.0(4,11)] undec-2-en-8-one
220	**Butylated hydroxytoluene**[a]
214	Dodecanoic acid, methyl ester
216	Nonanedioic acid, dimethyl ester
226	Hexadecane
216	Sebacic acid monomethyl ester
242	Methyl tetradecanoate
256	Methyl 9-methyl tetradecanoate
256	Tetradecanoic acid, 12-methyl-, methyl ester
256	Pentadecanoic acid, methyl ester
252	**Oxacycloheptadec-8-en-2-one**
268	9-Hexadecenoic acid, methyl ester (Z)
270	Hexadecanoic acid, methyl ester
294	9,12-Octadecadienoic acid (Z, Z), methyl ester
296	9-Octadecenoic acid, methyl ester
296	13-Octadecenoic acid, methyl ester
296	9-Octadecenoic acid (Z), methyl ester
296	11-Octadecenoic acid, methyl ester, (Z)
298	**Octadecanoic acid, methyl ester**
228	Phenol, 4,4′-(1-methylethylidene)bis-

Compounds in **bold font** were found in both swab and hair samples.
[a]Compounds that refer to 2 isomers of the same compound (butylated hydroxytoluene).

Hair odor (and possibly sternal gland odor) may include bacterial breakdown products in addition to compounds produced by the host organism. Indeed, many of the volatile fatty acids that we identified are produced by bacteria, over which the host may have little control, other than providing a substrate and warm incubation conditions. However, selective bacterial colonization, dependent on genotype, has been proposed as an underling mechanism for individual odor types (Schellinck and Brown 1992). This suggests that such compounds may vary systematically among individuals, and contribute to differences in odor profiles, rather than obscuring them.

As in other primate species (lemurs, Hayes et al. 2006; Palagi and Dapporto 2006; marmosets, Smith, Tomlinson, et al. 2001), a high percentage of chemicals were shared among profiles. In combination with the significant differences we found between odor profiles, this suggests that variation in mandrill chemical signals may depend more on the relative concentration of compounds (quantitative

variation), and on complex interactions between components, than on the simple presence or absence of specific chemicals (qualitative variation). This accords with "chemical signature" theories of odor signaling, in which the overall properties of a complex mixture of chemicals are greater than the sum of the effects of its constituent parts (Singer et al. 1997; Schaefer et al. 2001). Such a view is supported by behavioral bioassays. For example, behavioral responses to chemically complex, natural odorants in beavers (*Castor canadensis*) are stronger than to any single individual component of the signal or even than to synthetic mixtures of components (e.g., Mueller-Schwarze 1992; Schulte et al. 1994). Electrophysiological studies potentially explain this phenomenon by showing that the response of individual olfactory neurons to chemical mixtures cannot be predicted by simply summing the effects of the individual compounds (Duchamp-Viret et al. 2003) and that mixtures stimulate neurons in the olfactory cortex that are not stimulated by their individual component odorants (Zou and Buck 2006).

We were able to differentiate between males and females based on the volatile profiles of swab profiles when we considered only adult individuals but not when we included adolescent males. Volatile profiles of hair samples allowed us to differentiate the sexes, but when we restricted the data set to one sample per individual, the differentiation was no longer significant, although classification remained good. These results suggest that volatile profiles contained some information concerning sex in mandrills, as in other mammals (Wyatt 2003), including ring-tailed lemurs (Hayes et al. 2004; Scordato et al. 2007) and owl monkeys (MacDonald et al. 2007) but not sifakas (Hayes et al. 2004, 2006). The lack of a consistent pattern of differentiation between the sexes may be explained by the odor profiles of young and low-ranking males resembling those of females. This is supported by the differences in odor profiles that we found with male age and status.

In males, swab samples differentiated between adolescents and adults. The same was true for hair samples, although the differentiation was nonsignificant when we used only one sample per individual. The difference between adolescent and adult males may be relevant to other mandrills because a fully adult male presents more of threat to other males than a male that is still maturing, whereas a female may prefer to associate with, and reproduce with, a fully adult male, who has demonstrated his ability to survive to adulthood. Similarly, young male elephants produce a very different odor profile in their temporal gland secretion during musth than that produced by mature males (Rasmussen et al. 2002), and males appear to base their interactions on this odor difference, with younger males avoiding the scent of mature males, whereas mature males ignore that of young males (Rasmussen et al. 2002). The lack of a perfect discrimination between adolescent and adult male mandrills is likely to be due to the artificial nature of this distinction—males vary in the pace of their development, so some males will be fully developed at 9 years but others may still be maturing (Setchell et al. 2006).

Our results concerning male rank differed slightly between the 2 types of sample, but our overall finding was that volatile profiles do contain information concerning male rank. Swab profiles differentiated between rank classes, and some high-ranking males clearly fell into a class of their own. Hair samples differentiated between alpha and nonalpha males, with perfect classification for alpha males and 95% for nonalpha males. These results are similar to those for other mammals, in which odor profiles of dominant and subordinate males also differ, including European rabbits (Hayes et al. 2003) and mice (review in Gosling and Roberts 2001). However, they differ from those for other primates: the odor profiles of ring-tailed lemurs do not differ with rank (Scordato et al. 2007), and although saddleback tamarins are able to discriminate between scent-marks by unfamiliar dominant and subordinate males (Belcher et al. 1986), it is not clear whether this is due to the chemical profile of the scent-mark or to differences in the amount of scent applied by the male (Scordato et al. 2007). In mandrills, information concerning dominance rank is highly relevant to conspecifics because a high-ranking male represents a dangerous rival to other males and an attractive mate to females. In the deep forest environment, where males are not necessarily permanently associated with the social group of females (Setchell and Dixson 2001a; Abernethy et al. 2002), odor may provide an important, long-lasting signal of the presence and status of a male.

We also detected an influence of male–male competition and the presence of receptive females on male odor profiles, with swab profiles showing a significant influence of mate-guarding, although hair samples did not. This may relate to the fact that swab samples represent the most recent sternal gland activity—that is, when mate-guarding is actually occurring—whereas hairs may represent a longer time period of secretion, possibly including secretion that predated the mate-guarding. Similar influences of the breeding season on odor profiles have been reported for ring-tailed lemurs (Scordato et al. 2007) and sifaka (Hayes et al. 2006).

Together, our results for male age, status, and mate-guarding suggest that volatile profiles are influenced by endocrine status in male mandrills. Testosterone in mandrills is higher in adult than adolescent males (Setchell and Dixson 2002), higher in dominant males (Setchell and Dixson 2001a), and increases in the presence of receptive females (Setchell et al. 2008). However, testosterone is not perfectly related to male rank and also increases in periods of rank instability (Setchell et al. 2008). If odor profiles accurately reflect testosterone levels, as in male mice (Gosling and Roberts 2001), rather than rank itself, which seems likely, then the imperfect relationship between rank and testosterone may explain why we did not find a difference between alpha and nonalpha male swab profiles or a relationship between hair profiles and rank class in males.

Our use of relative rather than total abundance of the compounds that comprise mandrill odor profiles controls for any differences in the amount of secretion produced. However,

differences in odor profiles according to sex, age, and male status in mandrills are also accentuated by behavior and the quantity of secretion produced. Male mandrills scent-mark more than females, adult males mark more than younger males, and dominant males mark the most (Feistner 1991). Males also have far more active scent-glands than females, adult males have more active glands than younger males, and dominant males are the most active of all (Setchell and Dixson 2001a, 2001b). The combination of an odor profile that signals sex, age, and rank, increased motivation to mark in high-ranking males (so much so that high-ranking males often have grazed chests which occasionally get infected), and increased production of secretion, leads to a potent signal of the presence of a dominant, adult male with high testosterone levels in the forest. Such signals may help to mediate male interactions, and avoid confrontation and physical aggression between rival males, in addition to potentially attracting females. Thus, odor may act in a similar fashion to the bright red coloration that male mandrills also display, which signals dominance (Setchell and Dixson 2002), mediates male interactions (Setchell and Wickings 2005), and is attractive to females (Setchell 2005). Unlike visual signals, odor has the additional advantage of continuing to inform conspecifics in the absence of the signaler (Gosling and Roberts 2001), whereas signal degradation provides information about the timing of scent-mark deposition. Finally, scent-marking also permits both the signaler and the receiver to avoid potential costly escalated aggression by transmitting information in the absence of the owner.

In females, we were unable to differentiate between either cycle stage or female rank based on either swab or sternal gland hair samples. However, our results for cycle stage should be regarded as preliminary, as we were unable to address changes across the menstrual cycle. Odor profiles vary with season in female ring-tailed lemurs (Scordato et al. 2007) and sifaka (lumping the 2 sexes, Hayes et al. 2006), and it remains possible that female mandrill odor also advertises receptivity. The lack of a relationship between odor profile and rank in mandrills is not surprising, however, because although dominant females may mark more often, female mandrills rarely scent-mark (Feistner 1991 and Setchell JM, personal observation), suggesting that odor is not as important in female signaling as it is in males. This is not surprising because rank is stable in female mandrills, unlike in males, meaning that an up-to-date signal of status is unnecessary.

Finally, we found a significant signal of individual identity in the volatile profiles of both swab and hair samples, based on group differences, although classification was rather poor in both cases. These results should be regarded as preliminary because they are based on few replicates for each individual. Nevertheless, they suggest that odor may encode information about signaler identity in mandrills, as demonstrated for other mammals (Wyatt 2003; Thom and Hurst 2004), including lemurs (Palagi and Dapporto 2006; Scordato et al. 2007) and marmosets (Smith, Tomlinson, et al. 2001; Smith 2006). Experiments have also demonstrated that lemurs (Palagi and Dapporto 2006), various species of New World monkeys (Epple et al. 1979, 1988; Laska and Hudson 1995; Smith 2006), and humans (Porter and Moore 1981) are able to distinguish between the scents of individual conspecifics. Our results for mandrills fill a phylogenetic gap between humans and more distantly related primate species and suggest that Old World primates are not as microsmatic as previously assumed. The possibility that stable individual volatile profiles may occur in mandrills also suggest that, like lemurs (Charpentier et al. 2008), they may be able to advertise information about their genotype, facilitating mate choice for genetically dissimilar individuals (Setchell et al. 2009b), inbreeding avoidance (Charpentier et al. 2005), and behavioral bias toward paternal as well as maternal kin (Charpentier et al. 2007). We are currently investigating relationships between odor profiles and MHC genotype and between genetic relatedness and odor similarity in mandrills.

In conclusion, our findings suggest that mandrill volatile profiles convey both variable (age, dominance status in males) and fixed (sex, possibly individual identity) information about the signaler. The similarity of our findings to those for primates that are more distantly related to humans suggests a broader role for odor in primate communication than is currently recognized, in line with other evidence reviewed in the introduction. Future studies should address the question of whether odor signals individual identity using more replicates for each individual and whether odor profiles communicate health status, as in mice, where females are able to discriminate between the odors of infected versus noninfected males (Kavaliers and Colwell 1992; Zala et al. 2004) or quality, as in humans, where women prefer the scent of symmetrical men (Thornhill et al. 2003). Future work should also examine information perceived by the recipient, for example, via habituation/dishabituation tests (e.g., Mateo 2006; Palagi and Dapporto 2006) or paired-choice experiments (Smith 2006; Scordato and Drea 2007). Finally, we focused on the volatile components of mandrill odor. However, chemical signals are mixtures of both volatile and nonvolatile compounds, and high–molecular weight (nonvolatile) compounds may also be required for perception of the full biological information contained in a scent signal (Alborne 1984; Belcher et al. 1990; Hurst et al. 1998). For example, volatiles are thought to be the long-distance, airborne, ''broadcast'' component of a scent signal in mice, important for drawing receivers' attention to the location of scent-marks, and to any changes in the odor sphere, such as scent from a new individual or a change in the status of a familiar individual. By contrast, once a scent-mark has been located and investigated, highly polymorphic involatile components (''major urinary proteins'') provide a reliable short-range signal of ownership (Hurst et al. 2001; Nevison et al. 2003).

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References

Abernethy KA, White LJT, Wickings EJ. 2002. Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. J Zool. 258:131–137.

Alborne ES. 1984. Mammalian semiochemistry. New York: J Wiley.

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Barrett J, Abbott DH, George LM. 1990. Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. J Reprod Fertil. 90:411–418.

Belcher A, Epple G, Greenfield KL, Richards LE, Kuderling I, Smith AB. 1990. Proteins—biologically relevant components of the scent marks of a primate (*Saguinus fuscicollis*). Chem Senses. 15:431–446.

Belcher AM, Smith AB, Jurs PC, Lavine B, Epple G. 1986. Analysis of chemical signals in a primate species (*Saguinus fuscicollis*): use of behavioral, chemical, and pattern recognition methods. J Chem Ecol. 12:513–531.

Blaustein AR. 1981. Sexual selection and mammalian olfaction. Am Nat. 117:1006–1010.

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland (MA): Sinauer Associates.

Brennan PA, Kendrick KM. 2006. Mammalian social odours: attraction and individual recognition. Philos Trans R Soc Lond B Biol Sci. 361: 2061–2078.

Carter CS, Roberts RL. 1997. The physiological basis of cooperative breeding in rodents. In: Solomon MG, French JA, editors. Cooperative breeding in mammals. Cambridge (UK): Cambridge University Press. p. 231–266.

Charpentier M, Boulet M, Drea CM. 2008. Smelling right: the scent of male lemurs advertises genetic quality and relatedness. Mol Ecol. 17: 3225–3233.

Charpentier M, Peignot P, Hossaert-McKey M, Gimenez O, Setchell JM, Wickings EJ. 2005. Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). Behav Ecol. 16:614–623.

Charpentier MJE, Peignot P, Hossaert-McKey M, Wickings EJ. 2007. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. Anim Behav. 73:37–45.

Crnokrak P, Roff DA. 1999. Inbreeding depression in the wild. Heredity. 83:260–270.

Dixson AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings. Oxford: Oxford University Press.

Dominy NJ, Lucas PW. 2001. Ecological importance of trichromatic vision to primates. Nature. 410:363–366.

Duchamp-Viret P, Duchamp A, Chaput M. 2003. Single olfactory sensory neurons simultaneously integrate the components of an odor mixture. Eur J Neurosci. 18:2690–2696.

Dulac C, Torello AT. 2003. Molecular detection of pheromone signals in mammals: from genes to behaviour. Nat Rev Neurosci. 4:551–562.

Epple G, Belcher AM, Kuderling I, Zeller U, Scolnick L, Greenfield KL, Smith ABI. 1993. Making sense out of scents: species differences in scent glands, scent-marking behaviour, and scent-mark composition in the Callitrichidae. In: Rylands AB, editor. Marmosets and tamarins: systematics, behaviour, and ecology. Oxford: Oxford University Press. p. 123–151.

Epple G, Golob NF, Smith AB III. 1979. Odor communication in the tamarin *Saguinus fuscicollis* (Callitrichidae). Behavioral and chemical studies. In: Ritter FJ, editor. Chemical ecology: odor communication in animals. Amsterdam (The Netherlands): Elsevier North-Holland Biomedical Press. p. 117–130.

Epple G, Kuderling I, Belcher AM. 1988. Some communicatory functions of scent marking in the cotton-top tamarin *Saguinus oedipus oedipus*. J Chem Ecol. 14:503–515.

Feistner ATC. 1991. Scent marking in mandrills, *Mandrillus sphinx*. Folia Primatol. 57:42–47.

Geissman T, Hulftegger AM. 1994. Olfactory communication in gibbons? In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N, editors. Current primatology, vol. 2: social development, learning and behaviour. Strasbourg (France): Université Louis Pasteur. p. 199–206.

Gilad Y, Wiebe V, Prezeworski M, Lancet D, Pääbo S. 2004. Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates. PLoS Biol. 2(1):e5.

Gosling LM, Roberts SC. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. Adv Stud Behav. 30: 169–217.

Grubb P. 1973. Distribution, divergence and speciation of the drill and mandrill. Folia Primatol. 20:161–177.

Hamilton WD. 1964. The genetical evolution of social behavior: I. J Theor Biol. 7:1–16.

Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites. Science. 218:384–387.

Hayes R, Morelli T, Wright P. 2004. Anogenital gland secretions of *Lemur catta* and *Propithecus verreauxi coquereli*: a preliminary chemical examination. Am J Primatol. 63:49–62.

Hayes RA, Morelli TL, Wright PC. 2006. Volatile components of lemur scent secretions vary throughout the year. Am J Primatol. 68:1202–1207.

Hayes RA, Richardson BJ, Wyllie SG. 2003. To fix or not to fix: the role of 2-phenoxyethanol in rabbit, *Oryctolagus cuniculus*, chin gland secretion. J Chem Ecol. 29:1051–1060.

Heymann EW. 2006. The neglected sense-olfaction in primate behavior, ecology, and evolution. Am J Primatol. 68:519–524.

Hill WCO. 1970. Primates, comparative anatomy and taxonomy, vol. 8, Cynopithecinae, Papio, Mandrillus, Theropithecus. Edinburgh (UK): Edinburgh University Press.

Hoshino J, Mori A, Kudo H, Kawai M. 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. Primates. 25: 295–307.

Hurst JL, Payne CE, Nevison CM, Marie AD, Humphries RE, Robertson DHL, Cavaggioni A, Beynon RJ. 2001. Individual recognition in mice mediated by major urinary proteins. Nature. 414:631–634.

Hurst JL, Robertson DHL, Tolladay U, Beynon RJ. 1998. Proteins in urine scent marks of male house mice extend the longevity of olfactory signals. Anim Behav. 55:1289–1297.

Izard MK. 1990. Social influences on the reproductive success and reproductive endocrinology of prosimian primates. In: Ziegler TE, Bercovitch FB, editors. Socioendocrinology of primate reproduction. New York: Wiley-Liss. p. 159–186.

Jacob S, McClintock MK, Zelano B, Ober C. 2002. Paternally inherited HLA alleles are associated with women's choice of male odor. Nat Genet. 30:175–179.

Kavaliers M, Colwell DD. 1992. Aversive responses of female house mice to the odors of parasitized males: neuromodulatory mechanisms and implications for mate choice. Ethology. 95:202–212.

Keller L, Waller DM. 2002. Inbreeding effects in wild populations. Trends Ecol Evol. 17:230–241.

Knapp LA, Robson J, Waterhouse JS. 2006. Olfactory signals and the MHC: a review and a case study in *Lemur catta*. Am J Primatol. 68: 568–584.

Laska M, Hudson R. 1995. Ability of female squirrel monkeys (*Saimiri sciureus*) to discriminate between conspecific urine odors. Ethology. 99: 39–52.

Laska M, Seibt A, Weber A. 2000. 'Microsmatic' primates revisited: olfactory sensitivity in the squirrel monkey. Chem Senses. 25:47–53.

Liman ER, Innan H. 2003. Relaxed selective pressure on an essential component of pheromone transduction in primate evolution. Proc Natl Acad Sci U S A. 100:3328–3332.

MacDonald EA, Fernandez-duque E, Evans S, Hagey LR. 2007. Sex, age, and family differences in the chemical composition of owl monkey (*Aotus nancymaae*) subcaudal scent secretions. Am J Primatol. 70:12–18.

Mateo JM. 2006. The nature and representation of individual recognition odours in Belding's ground squirrels. Anim Behav. 71:141–154.

Monti-Bloch L, Jennings-White C, Berliner DL. 1998. The human vomeronasal system. Ann N Y Acad Sci. 855:373–389.

Mueller-Schwarze D. 1992. Castoreum of beaver (*Castor canadenis*): function, chemistry and biological activity of its components. In: Doty RL, Mueller-Schwarze D, editors. Chemical signals in vertebrates VI. New York: Plenum. p. 457–464.

Nevison CM, Armstrong S, Beynon RJ, Humphries RE, Hurst JL. 2003. The ownership signature in mouse scent marks is involatile. Proc Biol Sci. 270:1957–1963.

Palagi E, Dapporto L. 2006. Beyond odor discrimination: demonstrating individual recognition by scent in *Lemur catta*. Chem Senses. 31: 437–443.

Penn D, Potts WK. 1998. Chemical signals and parasite-mediated sexual selection. Trends Ecol Evol. 13:391–396.

Penn D. 2002. The scent of genetic compatibility: sexual selection and the Major Histocompatibility Complex. Ethology. 108:1–21.

Porter RH, Moore JD. 1981. Human kin recognition by olfactory cues. Physiol Behav. 27:493–495.

Rasmussen LEL, Riddle HS, Krishnamurthy V. 2002. Mellifluous matures to malodorous in musth. Nature. 415:975–976.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG. 1996. Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. Am J Primatol. 40:297–313.

Rouquier S, Blancher A, Giorgi D. 2000. The olfactory receptor gene repertoire in primates and mouse: evidence for reduction of the functional fraction in primates. Proc Natl Acad Sci U S A. 97: 2870–2874.

Schaefer ML, Young DA, Restrepo D. 2001. Olfactory fingerprints for major histocompatibility complex-determined body odors. J Neurosci. 21: 2481–2487.

Schellinck HM, Brown RE. 1992. Why does germfree rearing eliminate the odors of individuality in rats but not in mice? In: Doty RL, Mueller-Schwarze D, editors. Chemical signals in vertebrates VI. New York: Plenum Press. p. 237–241.

Schilling A, Perret M, Predine J. 1984. Sexual inhibition in a prosimian primate: a pheromone-like effect. J Endocrinol. 102:143–151.

Schulte B, Müller-Schwarze D, Tang R, Webster F. 1994. Beaver (*Castor canadensis*) responses to major phenolic and neutral compounds in castoreum. J Chem Ecol. 20:3063–3081.

Scordato ES, Drea CM. 2007. Scents and sensibility: information content of olfactory signals in the ringtailed lemur, *Lemur catta*. Anim Behav. 73:301–314.

Scordato ES, Dubay G, Drea CM. 2007. Chemical composition of scent marks in the ringtailed lemur (*Lemur catta*): glandular differences, seasonal variation, and individual signatures. Chem Senses. 32:493–504.

Setchell JM. 2005. Do female mandrills (*Mandrillus sphinx*) prefer brightly coloured males? Int J Primatol. 26:713–732.

Setchell JM, Charpentier M, Abbott KA, Wickings EJ, Knapp LA. Forthcoming. 2009a. Is brightest best? Testing the Hamilton-Zuk hypothesis in mandrills. Int J Primatol. 30:825–844.

Setchell JM, Charpentier M, Wickings EJ. 2005. Mate-guarding and paternity in mandrills (*Mandrillus sphinx*): factors influencing monopolisation of females by the alpha male. Anim Behav. 70:1105–1120.

Setchell JM, Charpentier MJE, Abbott KA, Wickings EJ, Knapp LA. Forthcoming. 2009b. Opposites attract: MHC-associated mate choice in an anthropoid primate. J Evol Biol. 23:136–148.

Setchell JM, Dixson AF. 2001a. Arrested development of secondary sexual adornments in subordinate adult male mandrills (*Mandrillus sphinx*). Am J Phys Anthropol. 115:245–252.

Setchell JM, Dixson AF. 2001b. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. Horm Behav. 39:177–184.

Setchell JM, Dixson AF. 2001c. Circannual changes in the secondary sexual adornments of semifree-ranging male and female mandrills (*Mandrillus sphinx*). Am J Primatol. 53:109–121.

Setchell JM, Dixson AF. 2002. Developmental variables and dominance rank in male mandrills (*Mandrillus sphinx*). Am J Primatol. 56:9–25.

Setchell JM, Kappeler PM. 2003. Selection in relation to sex in primates. Adv Stud Behav. 33:87–173.

Setchell JM, Lee PC, Wickings EJ, Dixson AF. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). Am J Phys Anthropol. 115:349–360.

Setchell JM, Smith T, Wickings EJ, Knapp LA. 2008. Social correlates of testosterone and ornamentation in male mandrills. Horm Behav. 54: 365–372.

Setchell JM, Wickings EJ. 2005. Dominance, status signals and coloration in mandrills (*Mandrillus sphinx*). Ethology. 111:25–50.

Setchell JM, Wickings EJ, Knapp LA. 2006. Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank and group association. Am J Phys Anthropol. 131:498–510.

Singer AG, Beauchamp GK, Yamazaki K. 1997. Volatile signals of the major histocompatibility complex in male mouse urine. Proc Natl Acad Sci U S A. 94:2210–2214.

Smith T. 2006. Individual olfactory signatures in common marmosets (Callithrix jacchus). Am J Primatol. 68:585–604.

Smith TD, Siegel MI, Bonar CJ, Bhatnagar KP, Mooney MP, Burrows AM, Smith MA, Maico LM. 2001. The existence of the vomeronasal organ in postnatal chimpanzees and evidence for its homology to that of humans. J Anat. 198:77–82.

Smith TE, Abott DH, Tomlinson AJ, Mlotkiewicz JA. 1997. Differential display of investigative behavior permits discrimination of scent signatures from familiar and unfamiliar socially dominant female marmoset monkeys (*Callithrix jacchus*). J Chem Ecol. 23:2523–2546.

Smith TE, Tomlinson AJ, Mlotkiewicz JA, Abbott DH. 2001. Female marmoset monkeys (*Callithrix jacchus*) can be identified from the chemical composition of their scent marks. Chem Senses. 26: 449–458.

Spehr M, Kelliher KR, Li X-H, Boehm T, Leinders-Zufall T, Zufall F. 2006. Essential role of the main olfactory system in social recognition of major histocompatibility complex peptide ligands. J Neurosci. 26: 1961–1970.

Sun LX, Mueller-Schwarze D. 1997. Sibling recognition in the beaver: a field test for phenotype matching. Anim Behav. 54:493–502.

Thom MD, Hurst JL. 2004. Individual recognition by scent. Ann Zool Fenn. 41:765–787.

Thornhill R, Gangestad SW, Miller R, Scheyd G, McCollough JK, Franklin M. 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behav Ecol. 14:668–678.

Wedekind C, Füri S. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? Proc R Soc Lond B Biol Sci. 264:1471–1479.

Wedekind C, Seebeck T, Bettens F, Paepke AJ. 1995. MHC-dependent mate preferences in humans. Proc Biol Sci. 260:245–249.

Widdig A, Nurnberg P, Krawczak M, Streich WJ, Bercovitch FB. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proc Natl Acad Sci U S A. 98:13769–13773.

Wyatt T. 2003. Pheromones and animal behaviour: communication by smell and taste. Cambridge (UK): Cambridge University Press.

Wysocki C, Yamazaki K, Curran M, Wysocki L, Beauchamp G. 2004. Mice (*Mus musculus*) lacking a vomeronasal organ can discriminate MHC-determined odortypes. Horm Behav. 46:241–246.

Zahavi A. 1975. Mate selection—a selection for handicap. J Theor Biol. 53:205–214.

Zala SM, Potts WK, Penn DJ. 2004. Scent-marking displays provide honest signals of health and infection. Behav Ecol. 15:338–344.

Zhang J, Webb DM. 2003. Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. Proc Natl Acad Sci U S A. 100:8337–8341.

Ziegler TE, Epple G, Snowdon CT, Porter TA, Belcher AM, Kuderling I. 1993. Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. Anim Behav. 45:313–322.

Zou Z, Buck LB. 2006. Combinatorial effects of odorant mixes in olfactory cortex. Science. 311:1477–1481.