

2 **Sex, Age and Family differences in the chemical composition of owl monkey**
 (*Aotus nancymaae*) subcaudal scent secretions

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Short title: discrimination of owl monkey scent

20 Numerous behavioral studies have shown that animals use olfactory cues as inbreeding
avoidance or kin avoidance mechanisms, implying that scent is unique to families.

22 However, few studies have analyzed the chemical profile of a scent and ascertained the
messages that are conveyed in scent secretions. Owl monkeys (*Aotus nancymaae*) are
24 socially monogamous primates that utilize scent when interacting with foreign conspecifics.
This suggests there is a difference in the chemical composition of scent marks. We
26 chemically analyzed sub-caudal gland samples from three families of captive owl monkeys
(*Aotus nancymaae*). Samples were analyzed by capillary GC-MS and relative retention
28 time and fragment pattern was compared with known standards. Gland samples were high
in large plant-based shikimate metabolites and fatty ketones; alcohols, acids and acetates
30 were virtually absent. Gender, age, and family could be reliably classified using
discriminant analysis (92.9%, 100% and 100% respectively). Female scent profiles were
32 greater in concentration of aromatic plant metabolites, possibly the result of a different diet
or physiological differences in female metabolism as compared to male. Offspring of adult
34 age still living in their natal group showed a less complex chemical profile than their
parents. Finally, each family had its own unique and complex chemical profile. The
36 presence of family scent may play a role in mediating social interactions.

38 Key words: olfaction, scent analysis, primate, chemical communication, scent mark

INTRODUCTION

40 Olfactory communication can play an important role in the social organization of
species by conveying information about species, subspecies, individual and sexual identity,
42 as well as motivational state or environmental variables [Epple, 1976; Epple, 1978; Epple
et al., 1981; Epple et al., 1979; Halpin, 1980; Marler, 1961a]. It has been shown that
44 individuals regularly rely on olfaction to discriminate among conspecifics [Gheusi et al.,
1997], sexes [Epple, 1978; Swaisgood et al., 2000], and between cycling or non-cycling
46 females [Smith and Abbott, 1998; Ziegler et al., 1993]. Various studies have indicated that
differences in the identity and relative quantities of chemical contents in the scents have the
48 capacity to code for sex, age, individuality, and even populations [Buesching et al., 2002;
Katsir and Crewe, 1980; Lawson et al., 2000; Salamon and Davies, 1998]. For example,
50 preorbital secretions in some Eurasian deer species (*Cervidae*) have the potential to convey
information about age and sex [Lawson et al., 2000; Lawson et al., 2001]; female
52 marmosets (*Callithrix jacchus*) can be reliably differentiated based on scent mark
composition [Smith et al., 2001] and some lemur species (*Lemur catta* and *Propithecus*
54 *verreauxi coquereli*) deposit scent marks that allow them to identify species, sex, and
reproductive status [Hayes et al., 2004].

56 The ability to discriminate kin is also expected to play a prominent role in the
organization of a social species [Lena et al., 2000; Nevison et al., 2000; Tai et al., 2000].
58 Among giant pandas (*Ailuropoda melanoleuca*), there is evidence to suggest that family
members share a common chemical scent profile that can be used to identify family
60 lineages [Hagey and MacDonald, 2003]. The capacity to recognize kin may be particularly
important in socially monogamous species. Given that in most monogamous species both

62 sexes disperse, individuals will routinely encounter relatives while searching for
reproductive opportunities. It is expected that mechanisms will exist to prevent animals
64 from mating and establishing social bonds with highly related individuals. Diurnal species
can presumably benefit from a reliance on olfactory, vocal or visual cues to identify
66 conspecifics. On the other hand, the absence of visual cues in nocturnal species may
increase even further the relative importance of olfactory communication [Porter, 1998].

68 The owl monkeys of Central and South America are socially monogamous and
nocturnal over most of their geographic range [Fernandez-Duque, 2007]. Both sexes
70 disperse from their natal groups and wander solitarily until they find a reproductive
opportunity in a social group [Fernandez-Duque, 2007; Fernandez-Duque et al., 2006;
72 Fernandez-Duque and Huntington, 2002]. Sexual dimorphism in body mass is negligible
and there are no conspicuous sex differences in the appearance of the external genitalia.
74 Owl monkeys have morphological adaptations that indicate some substantial reliance on
smell. They have apocrine glands on the lips, nose, brow and perianal areas [Hanson and
76 Montagna, 1962, Hill et al., 1959], a functional vomeronasal organ [Hunter et al., 1984b],
and olfactory bulbs that are the largest among the platyrrhines [Wright, 1989].

78 As expected given their specialized morphology, owl monkeys (*Aotus spp.*) rely
heavily on olfactory communication. They use both urine and cutaneous secretions in their
80 scent-marking behaviors and olfaction plays a prominent role in sexual recognition and
aggression [Dixson, 1994; Hunter and Dixson, 1983a; Hunter et al., 1984b]. Captive owl
82 monkeys have also been observed self-anointing with olfactory stimulating plants and
millipedes [Zito et al., 2003]. Observations of scent marking and olfactory communication
84 in wild owl monkeys have been hard to collect systematically given their nocturnal and

cathemeral habits [Fernandez-Duque, 2003; Fernandez-Duque and Erkert, 2004;
86 Fernandez-Duque and Erkert, 2006; Wright, 1989]. Still, *ad-libitum* observations indicate
that animals routinely sniff each other's faces and genital areas, rub their perianal glands
88 against branches or conspecifics, and wet their hands and feet with urine [Moynihan, 1964].
In captivity, males also drink urine of the females and during the time of year when mating
90 is more frequent, the tail of some males can be saturated in urine [Evans, pers. obs.].

Given the lack of sexual dimorphism in body mass and secondary sexual
92 characteristics, the minimal differences in the appearance of the external genitalia, and their
nocturnal habits, it is predicted that owl monkeys regularly use olfactory cues to identify
94 members of the opposite sex and relatives. If owl monkeys are relying on olfactory
communication to identify kin and individuals of the opposite sex, one possible mechanism
96 is a family and sex difference in the chemical composition of the scent. There have been no
studies examining if members of an owl monkey family share a unique smell (i.e.
98 phenotype matching), or whether they learn via conditioning the scents of individual family
members and respond aggressively to individuals with a novel scent (i.e. direct familiarity)
100 [Hepper, 1991]. In this study we present chemical analyses of perianal gland scent samples
obtained from individuals in three owl monkey families to evaluate if there are differences
102 between the chemical profiles of the different families, of males and females, and of adults
and juveniles.

104

METHODS

106 *Subjects and Sample Collection*

Gland secretion samples were taken from anesthetized owl monkeys (*Aotus*

108 *nancymaae*) during a regularly scheduled physical examination conducted at the DuMond
conservancy in Florida in January 2001. Samples were collected by rubbing the gland with
110 a sterile Q-tip a few times and applying as much pressure as one would apply when
cleaning an area of skin with alcohol. Each sample was stored in a glass vial with a Teflon
112 lined cap (Scientific Specialties Inc, Randallstown, MD) at -20°C until analysis. A single
sample was taken from 14 individuals living in three family groups (Table 1). Two
114 families consisted of a pair of reproducing adults with three offspring, whereas the third
family had only two offspring. The sample from the adult female in one of the families
116 with three offspring could not be included in the analyses because it was not readable on
the gas chromatograph. The monkeys were fed a wide variety of food items (fresh fruit,
118 vegetables and monkey biscuits). They were also fed fresh browse and were free to forage
on the natural vegetation/insects/lizards and birds (occasionally) in their enclosures.

120 *Chemical Analysis*

Volatile compounds were extracted for 35 minutes from the Q-tip using a solid
122 phase microextractor (SPME) containing a 65 μ polydimethylsiloxane fiber. Contents were
analyzed by capillary GC-MS, using a Hewlett-Packard 5890 Gas Chromatograph-5970
124 MSD, controlled by HP/UX Chem Station software. The column was a Supelco 60 m x
0.25 mm ID low polarity SPB-octyl, operated using a gradient of 75°C held for 9 min
126 followed by a 1.6°/min ramp up to 210°C. A splitless injection was used with an injection
temperature of 250°C. Helium was used as the carrier gas with a 7 psi column head
128 pressure. Relative retention times and fragmentation spectra of peaks obtained by GC-MS
were compared with those of known standards for identification. Blanks, collection

130 materials, cleaning fluid, and other environmental items were also analyzed by GC-MS.
These compounds were noted on any subject's chromatogram and removed from
132 subsequent analysis

Statistical Analysis

134 To control for variability between samples the data analyzed was the relative
proportion of the peak size to the overall total area of the chromatogram rather than the
136 absolute concentration of the peak. Fisher's stepwise discriminant analysis (DA) was used
to assess which chemical compounds, if any, could be used to define the groups and to
138 predict group membership (SPSS 10.0, Chicago, NY). DA, generally recommended when
there are numerous dependent variables, consists of a set of procedures that creates new
140 variables as combinations of the original variables so that group differences are maximized.
Additionally, DA identifies those dependent variables that are the most parsimonious in
142 distinguishing among the groups. The final step consists in generating a classification table
(prediction matrix) to assess the performance of the DA. This is done using the predictive
144 equation generated by the DA to back predict samples and to identify correct
classifications, false positives, and false negatives to assess the robustness of the DA
146 equation [McLachlan, 1992].

RESULTS

Chemical Composition

Two hundred and ninety-nine volatile chemicals were identified in the samples, but
150 only those chemicals found in at least 10% of them (n = 113 chemicals) were used for
statistical analysis. All chemicals were identified by their common name or given a number
152 based on the combination of mass spectral fragmentation patterns and relative retention

times (e.g. alcohol, lipid, ketone, etc.) [McLafferty and Turecek, 1993]. A female

154 chromatogram is shown in Figure 1 for illustrative purposes.

Sex Discrimination

156 No single compound was systematically present in one sex and absent in the other
one. Still, five variables (Table 2) were of highly discriminant value for the sexes (Figure
158 2a), accurately classifying samples according to sex with a cross-validation rate of 92.9%
(Wilk's $\lambda=.001$). Two of the four compounds are aromatic plant metabolites suggesting the
160 difference in scent secretions between the two sexes may be partially comprised of plant
byproducts.

162 *Age Discrimination*

Adults and young could be cross classified at a rate of 100% (Wilk's $\lambda=.001$)
164 utilizing six variables (Table 2). Five of the six discriminating variables (Figure 2b) are
common by products of plant metabolism. One compound (2,6-dimethyl pyridine) is an
166 important plant metabolite used to maintain homeostasis in intestinal bacteria [Kaiser et al.,
1996]. Swabs from adults were higher in this compound, suggesting a more developed
168 intestinal system.

Kin Discrimination

170 Finally, the three families could be correctly classified at a rate of 100% (Wilk's
 $\lambda=.001$) with seven discriminant variables (Figure 2c). The range of discriminating
172 compounds among the three families was more diverse including a furan and lactone
commonly found in urine, one terpene, two small alcohols, a branched alkane, and a plant
174 metabolite (Table 2).

176 **DISCUSSION**

178 Chemical analyses of the owl monkey (*Aotus nancymaae*) subcaudal gland samples
180 identified approximately 300 volatile chemicals with a smaller subset having discriminatory
182 capacity. The results suggested that there was information contained in the chemical
184 content of the samples that could be used for reliable identification of sex, age and family
identity, consisting primarily of plant metabolites and short chain fatty acids. In the
following paragraphs we discuss each of these main results as they relate to the
monogamous social organization of owl monkeys and their nocturnal and cathemeral
activity patterns.

The chemical analyses of the samples generated both expected and unexpected
186 results. The ubiquitous presence of short chain fatty acids was expected since these
compounds function as efficient messengers of scent due to their ability to form salts and to
188 their slow evaporation rate [Albone and Shirley, 1983]. On the other hand, the absence of
large chain fatty acids was somewhat unexpected, since they are regularly found in the
190 chemical pattern of other animal gland samples [Albone and Shirley, 1983]. For example,
carnivore gland secretions are rich in acids that result from bacterial metabolism of amino-
192 acids and a symbiotic production of scent between the host and bacteria. The absence of
large acids in the owl monkey samples may indicate that the external glandular region of
194 owl monkeys is relatively devoid of bacteria, in contrast to what has been found, for
example, in the giant panda and Indian mongoose (*Herpestes auropunctatus*) [Hagey and
196 MacDonald, 2003; Gorman, 1976]. The detection of small alcohols suggests that some
byproducts of intestinal bacteria's metabolism may be contributing to the scent profile. It is

198 reasonable that the small alcohols in the gland secretions originated from bacterial by-
products from feces, given that the caudal scent gland is adjacent to the anus. Compounds
200 normally detected in urine were also found in the samples, providing additional evidence of
contamination from the anus and urinary tract.

202 Individuals could be reliably classified by sex using a combination of five chemical
compounds. This result indicates that the chemical composition of the scent could
204 effectively be used to communicate gender between conspecifics. The main sex difference
in the chemical profile was a greater concentration of aromatic plant metabolites in female
206 samples than male ones. Aromatic metabolites are six-carbon cyclic compounds difficult to
break down by mammals and, with the exception of estrogen, cannot be manufactured by
208 them [Schmid and Amrhein, 1995]. The presence of aromatics in female samples could
indicate a sex difference in the plants being eaten or in the manner plant material is being
210 digested. Alternatively, the findings could reflect sex differences in digestion as opposed to
differences in food intake.

212 The importance of a sex-specific scent mark cannot be overemphasized in a
sexually monomorphic species. In captivity, aggression appears to be higher between
214 same-sex individuals [Dixon, 1983]. Same-sex pairs of owl monkeys were more
aggressive than opposite-sexed pairs; aggression was preceded by olfactory inspection, and
216 olfactory cues may have assisted members of the same sex to recognize others as potential
aggressors [Hunter and Dixon, 1983a]. An ability to identify the opposite sex can
218 undoubtedly play a significant role during the intergroup encounters that regularly take
place in free-ranging owl monkeys.

220 Not surprisingly, there were pronounced differences between the chemical profile of

the samples of the adult and young. All young shared a unique scent chemical profile that
222 was aromatically less complex than the one of adults. It is possible that some of the
components of the scent gland secretion are the byproducts of the developing digestive
224 system. Juvenile intestines move from a sterile environment at birth to the introduction of a
microbial flora in a maternal milk diet, and then readjust to a different flora based on a solid
226 diet. Based on alterations to their bile salts, the entire process can take several years [Hagey
et al., 1997] modifying the chemical content of gland secretions. The difference in the
228 profiles between the age classes (and also sex and family) could also be due to a difference
in consumption of food. The older class may dominate the young and consume more
230 higher-quality food [Ferkin et al., 1997], or a difference in diet may be due to other factors
but data were not collected to evaluate those possibilities.

232 Alternatively, the differences in the scent patterns of the breeding adults and their
offspring could be the result of arrested development or physiological suppression.
234 Reproductive suppression of daughters has been very well documented in callitrichids
[Snowdon et al., 2005], titi monkeys (*Callicebus moloch*) [Valeggia et al., 1995],
236 orangutans (*Pongo pygmaeus*) [Maggioncalda et al., 1999] and sugar gliders (*Petaurus
breviceps*) [Stoddart et al., 1994]. Captive male owl monkeys (*A. lemurinus*) show the
238 same pattern of physical and hormonal development when housed with their parents or
alone [Dixson et al., 1980], but do not reproduce while with their parents. Approximately
240 half of the young in the study had reached the age when they normally reproduce in
captivity, between three and four years old [Gozalo and Montoya, 1990]. The different
242 scent profiles of young and adults may serve to defray any potential conflict between
sexually mature offspring and their parents, transmitting a non-threatening message and

244 avoiding misdirected aggressiveness by the parents. Adult owl monkeys can be very
aggressive toward strange conspecifics, but levels of aggression do not regularly increase
246 between parent and offspring during maturity [Dixson, 1983]. However, the potential that
reproductive suppression, if any, was mediated through social or physiological mechanisms
248 was not investigated in this study.

Finally, individuals could also be reliably assigned to their corresponding families
250 based on the chemical profile of their scent gland secretions. But a correct family identity
classification required that a more diverse number of chemical compounds be used than
252 when classifying individuals by sex or age. Family classification relied less on plant
metabolites and more on waxy lipids. One family had more than twelve times the amount
254 of styrene than the other two families. Lipids last longer than plant aromatics and can
therefore be used to form a long-term scent that will be robust and stable over time. A
256 long-lasting message could be particularly useful for signaling the boundaries of a territory
if constant marking is impractical.

258 The distinct family chemical profiles provide evidence that owl monkey scent
secretions may be family specific (i.e. phenotype matching). The presence of a family
260 scent could play a role in other social interactions, such as in emigration from their natal
group and the posterior process of mate choice and pair formation. Individuals may search
262 for a new group that has a substantially different scent versus one with a high degree of
similarity which they would avoid to reduce inbreeding. Naturally, our preliminary
264 findings of family matching need to be examined further. The proximate mechanisms
underlying the possible functioning of a specific family scent are unknown. In Bechstein's
266 bat (*Myotis bechsteinii*), chemical profiles of scent secretions differed between colonies.

The bats engaged in face rubbing which could have resulted in a homogenized colony scent
268 used for recognition. This was supported behaviorally as encounters between individuals
from different colonies with very distinct chemical profiles were agonistic towards each
270 other [Safi and Kerth, 2003].

It seems reasonable to expect most scents to be the result of an interaction between
272 genetic and environmental factors [Porter 1998]. If the production of family-specific scent
secretions were entirely genetic, one would expect them to remain constant over time.
274 Although longitudinal samples were not taken in this study, scent composition cannot be
entirely under genetic control. The unrelated breeding adults within the same family have a
276 similar scent, suggesting that scent is at least partially, if not entirely, a result of
environmental factors. Common environmental contributors to scent include both diet and
278 related gut flora. Owl monkeys do not utilize dermal bacteria for their scent secretions (as
shown by the absence of dermal bacterial byproducts in the scent), but this does not exclude
280 bacteria contribution from other roles producing a family scent. Each family could possess
a unique combination of gastrointestinal flora. The presence of certain compounds, such as
282 the aromatic rings, suggests that bacteria are metabolizing plant materials and indirectly
contributing to the scent profile.

284 These findings should be considered preliminary and further investigation with
larger samples sizes and behavioral manipulation is suggested. For example, while we
286 have identified that sex, age and family can be discriminated by the chemical composition
of scent secretions, it is yet unknown if and how the animals are actually using this
288 information during social interactions. Additionally, the role of non-volatile compounds
such as proteins should also be investigated as this study was limited to volatile compounds

290 of low molecular weight.

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REFERENCES

- 302 Albone E, Shirley S. 1983. Mammalian Semiochemistry. New York: John Wiley & Sons
Limited. 349 p.
- 304 Buesching CD, Newman C, Macdonald DW. 2002. Variations in colour and volume of the
subcaudal gland secretion of badgers (*Meles meles*) in relation to sex, season and
306 individual-specific parameters. *Z Saeugetierkd* 67:147-156.
- Dixon A. 1983. The owl monkey (*Aotus trivirgatus*). In: Hearn J, editor. Reproduction in
308 New World primates New models in medical sciences. Lancaster, England:
International Medical Publishers. p 69-113.
- 310 Dixon A. 1994. Reproductive biology of the owl monkey. In: Baer J, Weller R, Kakoma I,
editors. *Aotus: the owl monkey*. San Diego: Academic Press. p 113-132.
- 312 Dixon AF, Gardner JS, Bonney RC. 1980. Puberty in the male owl monkeys (*Aotus*
trivirgatus griseimembra): a study of physical and hormonal development. *Int J*
314 *Primatol* 1:129-139.
- Epple G. 1976. Chemical Communication and Reproductive Processes in Nonhuman
316 Primates. In: Doty RL, editor. *Mammalian Olfaction, Reproductive Processes, and*
Behavior. New York: Academic Press. p 257-282.
- 318 Epple G. 1978. Studies on the nature of chemical signals in scent marks and urine of
Saguinus fuscicollis (Callitrichidae, Primates). *J Chem Ecol* 4:383-394.
- 320 Epple G, Golob NF, Cebul M-S, Smith ABI. 1981. Communication by scent in some
Callitrichidae (Primates) - An interdisciplinary approach. *Chem Senses* 6:377-390.
- 322 Epple G, Golob NF, Smith AB. 1979. Odor Communication in the Tamarin *Saguinus*
fuscicollis (Callitrichidae): Behavioral and Chemical Studies. In: Ritter FJ, editor.

- 324 Chemical Ecology: Odour Communication in Animals: Elsevier, North-Holland
Biomedical Press. p 117-130.
- 326 Ferkin M, Sorokin E, Johnston R, Lee C. 1997. Attractiveness of scents varies with protein
content of the diet in meadow voles. *Anim Behav* 57:133-141.
- 328 Fernandez-Duque E. 2003. Influences of moonlight, ambient temperature and food
availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*).
330 *Behav Ecol Sociobiol* 54:431-440.
- Fernandez-Duque E. 2007. The Aotinae: Social Monogamy in the Only Nocturnal
332 Haplorhines. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK,
editors. *Primates in Perspective*. Oxford: Oxford University Press. p 139-154.
- 334 Fernandez-Duque E, Di Fiore A, Juárez C. 2006. Demographics and ranging of floaters in
socially monogamous owl monkeys (*Aotus azarai*). *Am J Primatol*.
- 336 Fernandez-Duque E, Erkert HG. 2004. Cathemerality and lunarphilia in owl monkeys of
the Argentinean Chaco. *Folia Primatol* 75 S1:67.
- 338 Fernandez-Duque E, Erkert HG. 2006. Cathemerality and lunar periodicity of activity
rhythms in owl monkeys of the Argentinian Chaco. *Folia Primatol* 77:123-138.
- 340 Fernandez-Duque E, Huntington C. 2002. Disappearances of individuals from social groups
have implications for understanding natal dispersal in monogamous owl monkeys
342 (*Aotus azarai*). *Am J Primatol* 57:219-225.
- Gheusi G, Goodall G, Dantzer R. 1997. Individually distinctive odours represent individual
344 conspecifics in rats. *Anim Behav* 53:935-944.
- Gorman M. 1976. A mechanism for individual recognition by odour *Herpestes*
346 *auropunctatus*. *Anim Behav* 24:141-145.

- 348 Gozalo A, Montoya E. 1990. Reproduction in the owl monkey (*Aotus nancymai*)
(Primates:Cebidae) in captivity. Am J Primatol 21:61-68.
- 350 Hagey L, Gavrilkina M, Hofmann AF. 1997. Age-related changes in the biliary bile acid
composition of bovids. Can J Zool 75:1193-1201.
- 352 Hagey L, MacDonald E. 2003. Chemical cues identify gender and individuality in giant
pandas (*Ailuropoda melanoleuca*). J Chem Ecol 29:1479-1488.
- 354 Halpin Z. 1980. Individual odors and individual recognition: review and commentary. Biol
Behav 5:233-248.
- 356 Hanson G, Montagna W. 1962. The skin of primates. XII The skin of the owl monkeys
(*Aötus trivirgatus*). Am J Phys Anthropol 20:421-429.
- 358 Hayes RA, Morelli TL, Wright PC. 2004. Anogenital gland secretions of *Lemur catta* and
Propithecus verreauxi coquereli: A preliminary chemical examination. Am J
Primatol 63:49-62.
- 360 Hepper P. 1991. Kin Recognition. Cambridge, UK: Cambridge University Press. 457 p.
- 362 Hill, WCO, Appleby, HM, Auber, L. 1959. The specialised area of skin glands in *Aotes*
Humboldt (*Simiae platyrrhini*). Trans R Soc Edinb 63:535-551.
- 364 Hunter A, Dixson A. 1983a. Anosmia and aggression in male owl monkeys (*Aotus*
trivirgatus). Physiol Behav 30:875-879.
- 366 Hunter A, Fleming D, Dixson A. 1984b. The structure of the vomeronasal organ and
nasopalatine ducts in *Aotus trivirgatus* and some other primate species. J Anat
138:217-225.
- 368 Kaiser J, Feng, Y, Bollaq, J. 1996. Microbial metabolism of pyridine, quinoline, acridine
and their derivatives under aerobic and anaerobic condiotns. Microbiol Rev 60:483-

370 498

Katsir Z, Crewe R. 1980. Chemical communication in *Galago crassicaudatus*:

372 investigation of the chest gland secretion. S Afr J Zool 15:249-254.

Lawson RE, Putman RJ, Fielding AH. 2000. Individual signatures in scent gland secretions

374 of Eurasian deer. J Zool 251:399-410.

Lawson RE, Putman RJ, Fielding AH. 2001. Chemical communication in Eurasian deer

376 (*Cervidae*): do individual odours also code for attributes? J Zool 253:91-99.

Lena JP, De Fraipont M, Clobert J. 2000. Affinity towards maternal odour and offspring

378 dispersal in the common lizard. Ecol Lett 3:300-308.

Maggioncalda A, Sapolsky R, Czekala N. 1999. Reproductive hormone profiles in captive

380 male orangutans: implications for understanding developmental arrest. Am J Physiol

Anthropol 109:19-32.

382 Marler P. 1961a. The logical analysis of animal communication. J Theor Biol 1:295-317.

McLachlan G. 1992. Discriminant Analysis and Statistical Pattern Recognition. New

384 York: John Wiley & Sons, INC.

McLafferty F, Turecek F. 1993. Interpretation of Mass Spectra. Sausalito, CA: University

386 Science Books.

Moynihan M. 1964. Some behavior patterns of playtyrrhine monkeys. I. The night monkey

388 (*Aotus trivirgatus*). Smithsonian Miscellaneous Collections 146:1-84.

Nevison CM, Barnard CJ, Beynon RJ, Hurst JL. 2000. The consequences of inbreeding for

390 recognizing competitors. Pro R Soc Lond B Biol Sci 267:687-694.

Porter RH. 1998. Olfaction and human kin recognition. Genetica 104:259-263.

392 Safi K, Kerth G. 2003. Secretions of the interaural gland contain information about

- individuality and colony membership in the Bechstein's bat. *Anim Behav* 63:363-
 394 369.
- Salamon M, Davies NW. 1998. Identification and variation of volatile compounds in
 396 sternal gland secretions of male koalas (*Phascolarctos cinereus*). *J Chem Ecol*
 24:1659-1676.
- 398 Schmid J, Amrhein N. 1995. Molecular organization of the shikimate pathway in higher
 plants. *Phytochemistry* 39:737-749.
- 400 Smith TE, Abbott DH. 1998. Behavioral discrimination between circumgenital odor from
 peri-ovulatory dominant and anovulatory female common marmosets (*Callithrix*
 402 *jacchus*). *Am J Primatol* 46:265-284.
- Smith TE, Tomlinson AJ, Mlotkiewicz JA, Abbott DH. 2001. Female marmoset monkeys
 404 (*Callithrix jacchus*) can be identified from the chemical composition of their scent
 marks. *Chem Senses* 26:449-458.
- 406 Snowdon C, Ziegler T, Widowski T. 2005. Further hormonal suppression of eldest
 daughter cotton-top tamarins following birth of infants. *Am J Primatol* 31:11-21.
- 408 Stoddart DM, Bradley AJ, Mallick J. 1994. Plasma testosterone concentration, body-
 weight, social-dominance and scent-marking in male marsupial sugar gliders
 410 (*Petaurus Breviceps* Marsupialia, Petauridae). *J Zool* 232:595-601.
- Swaigood RR, Lindburg DG, Zhou XP, Owen MA. 2000. The effects of sex, reproductive
 412 condition and context on discrimination of conspecific odours by giant pandas.
Anim Behav 60:227-237.
- 414 Tai FD, Wang TZ, Zhao YJ. 2000. Inbreeding avoidance and mate choice in the mandarin
 vole (*Microtus mandarinus*). *Can J Zool* 78:2119-2125.

416 Vallengia CR, Mendoza SP, Mason WA. 1995. Reproduction in titi monkey (*Callicebus*
418 *moloch*) female offspring: social suppression vs autoregulation. *Am J Primatol*
36:160.

Wright PC. 1989. The nocturnal primate niche in the New World. *J Hum Evol* 18:635-658.

420 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*.
422 *Anim Behav* 45:313-322.

Zito M, Evans S, Weldon P. 2003. Owl monkeys (*Aotus* spp.) self-anoint with plants and
424 millipedes. *Folia Primatol* 74:159-161.

426

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Table 1: Sex, age group, family and origin identity of individuals sampled.

Sex	Age Group	Family	Age (yrs)	Origin
F	Adult	1	10	Captive born
M	Adult	1	10	Captive born
M	Offspring	1	4	Captive born
M	Offspring	1	3	Captive born
F	Adult	2	Unknown	Wild caught
M	Adult	2	Unknown	Wild caught
F	Offspring	2	1	Captive born
F	Offspring	2	3	Captive born
M	Offspring	2	3	Captive born
M	Adult	3	Unknown	Unknown
M	Offspring	3	2	Captive born
F	Offspring	3	4	Captive born
F	Offspring	3	3	Captive born

unknown: animals imported from the wild as adults, age could not be determined

Table 2: Chemical class of discriminating compounds.

Discriminating Compound	Group	Chemical Class
hexanoic acid	sex	short-chain fatty acid
0.960	sex	cyclo-alkyl compound
0.810	sex	acyl thiophene
0.744	sex	undetermined
1.623	sex	plant metabolite
p-cymene	age	plant metabolite
0.611	age	plant metabolite
1.401	age	metabolite of primate urines
2,6-dimethyl pyridine	age	plant metabolite
0.744	age	undetermined
γ -butyrolactone	age	short-chain fatty acid
.852A	kin	furan
α -terpineol	kin	plant metabolite
1-pentanol	kin	short-chain fatty acid
1.354a	kin	lactone
2-methyl-2-propanol	kin	metabolic alcohol
methyl heptanoate	kin	short-chain fatty ester
.329a	kin	branched alkane

FIGURE LEGENDS

Figure 1 Chromatogram of an owl monkey female subcaudal gland sample.

Figure 2 Mean relative concentration of discriminating chemical compounds to classify groups by a) sex b) age and c) family. Bars represent standard error of the means.