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RESEARCH ARTICLE

Sex, Age, and Family Differences in the Chemical Composition of Owl Monkey (*Aotus nancymaae*) Subcaudal Scent Secretions

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Numerous behavioral studies have shown that animals use olfactory cues as inbreeding avoidance or kin avoidance mechanisms, implying that scent is unique to families. 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 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 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 time and fragment pattern was compared with known standards. Gland samples were high in large plant-based shikikate metabolites and fatty ketones; alcohols, acids, and acetates were virtually absent. Gender, age, and family could be reliably classified using discriminant analysis (92.9, 100, and 100%, respectively). Female scent profiles were 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 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 presence of family scent may play a role in mediating social interactions. Am. J. Primatol. 70:12–18, 2008.

Key words: olfaction; scent analysis; primate; chemical communication; scent mark

INTRODUCTION

Olfactory communication can play an important role in the social organization of species by conveying information about species, subspecies, individual, and sexual identity, as well as motivational state or environmental variables [Epple, 1976, 1978; Epple et al., 1979, 1981; Halpin, 1980; Marler, 1961a]. It has been shown that 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 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 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, preorbital secretions in some Eurasian deer species (*Cerividae*) have the potential to convey information about age and sex [Lawson et al., 2000, 2001]; female marmosets (*Callithrix jacchus*) can be reliably differentiated based on scent mark composition [Smith et al., 2001] and some lemur species (*Lemur catta* and *Propithecus verreauxi coquereli*) deposit scent marks that allow them to identify species, sex, and reproductive status [Hayes et al., 2004].

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]. 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 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 sexes disperse, individuals will routinely encounter relatives while searching for

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reproductive opportunities. It is expected that mechanisms will exist to prevent animals 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 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].

The owl monkeys of Central and South America are socially monogamous and nocturnal over most of their geographic range [Fernandez-Duque, 2007]. Both sexes 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; 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. 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 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].

As expected given their specialized morphology, owl monkeys (*Aotus* spp.) rely heavily on olfactory communication. They use both urine and cutaneous secretions in their 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 monkeys have also been observed self-anointing with olfactory stimulating plants and millipedes [Zito et al., 2003]. Observations of scent marking and olfactory communication in wild owl monkeys have been hard to collect systematically given their nocturnal and cathemeral habits [Fernandez-Duque, 2003; Fernandez-Duque and Erkert, 2004, 2006; Wright, 1989]. Still, ad-libitum observations indicate that animals routinely sniff each other's faces and genital areas, rub their perianal glands 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 is more frequent, the tail of some males can be saturated in urine [S. Evans, personal observation].

Given the lack of sexual dimorphism in body mass and secondary sexual 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 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 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. 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) [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 between the chemical profiles of the different families, of males and females, and of adults and juveniles.

METHODS

Subjects and sample collection

Gland secretion samples were taken from anesthetized owl monkeys (*Aotus 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 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 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 I). Two 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 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, vegetables, and monkey biscuits). They were also fed fresh

TABLE I. Sex, age group, family, and origin identity of individuals sampled

Sex	Age group	Family	Age (years)	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.

browse and were free to forage on the natural vegetation/insects/lizards and birds (occasionally) in their enclosures.

Chemical analysis

Volatile compounds were extracted for 35 min from the Q-tip using a solid phase microextractor (SPME) containing a 65 μm polydimethylsiloxane fiber. Contents were analyzed by capillary GC-MS, using a Hewlett-Packard 5890 Gas Chromatograph-5970 MSD, controlled by HP/UX Chem Station software. The column was a Supelco 60 m × 0.25 mm ID low polarity SPB-octyl, operated using a gradient of 75°C held for 9 min 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 pressure. Relative retention times and fragmentation spectra of peaks obtained by GC-MS were compared with those of known standards for identification. Blanks, collection 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 subsequent analysis.

Statistical analysis

To control for variability between samples, the data analyzed were the relative proportion of the peak size to the overall total area of the chromatogram rather than the 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 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 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 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 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 equation [McLachlan, 1992].

RESULTS

Chemical composition

Two hundred and ninety-nine volatile chemicals were identified in the samples, but 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 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 chromatogram is shown in Figure 1 for illustrative purposes.

Sex discrimination

No single compound was systematically present in one sex and absent in the other one. Still, five

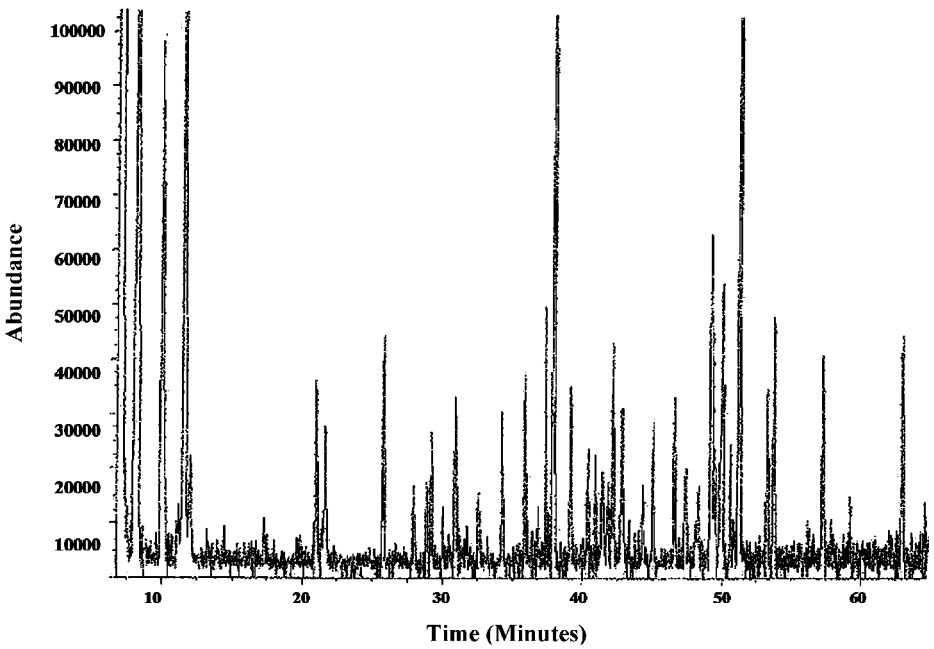

Fig. 1. Chromatogram of an owl monkey female subcaudal gland sample.

variables (Table II) were of highly discriminant value for the sexes (Fig. 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 difference in scent secretions between the two sexes may be partially composed of plant byproducts.

Age discrimination

Adults and young could be cross classified at a rate of 100% (Wilk's $\lambda = .001$) utilizing six variables (Table II). Five of the six discriminating variables (Fig. 2b) are common by products of plant metabolism. One compound (2,6-dimethyl pyridine) is an 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 intestinal system.

Kin discrimination

Finally, the three families could be correctly classified at a rate of 100% (Wilk's $\lambda = .001$) with seven discriminant variables (Fig. 2c). The range of discriminating 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 metabolite (Table II).

DISCUSSION

Chemical analyses of the owl monkey (*Aotus nancymaae*) subcaudal gland samples identified approximately 300 volatile chemicals with a smaller

TABLE II. Chemical class of discriminating compounds

Discriminating compound	Group	Chemical class
Hexanoic acid	Sex	Short-chain fatty acid
0.96O	Sex	Cyclo-alkyl compound
0.81O	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

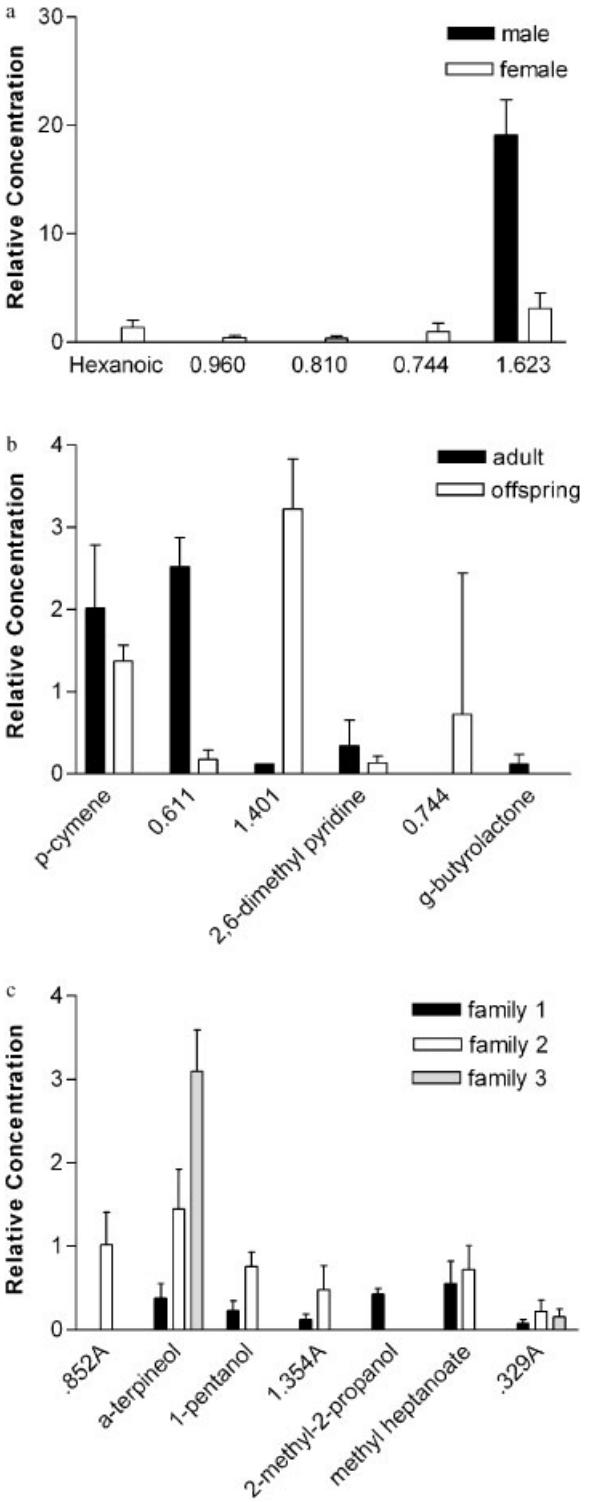

Fig. 2. Mean relative concentration of discriminating chemical compounds to classify groups by (a) sex (b) age, and (c) family. Bars represent standard error of the means.

subset having discriminatory capacity. The results suggested that there was information contained in the chemical 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 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 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 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-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 owl monkeys is relatively devoid of bacteria, in contrast to what has been found, for example, in the giant panda (*Ailuropoda melanoleuca*) and Indian mongoose (*Herpestes auropunctatus*) [Gorman, 1976; Hagey and MacDonald, 2003]. The detection of small alcohols suggests that some byproducts of intestinal bacteria's metabolism may be contributing to the scent profile. It is 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 normally detected in urine were also found in the samples, providing additional evidence of contamination from the anus and urinary tract.

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 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 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 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 digested. Alternatively, the findings could reflect sex differences in digestion as opposed to differences in food intake.

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

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 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 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 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 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 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.

Alternatively, the differences in the scent patterns of the breeding adults and their offspring could be the result of arrested development or physiological suppression. Reproductive suppression of daughters has been very well documented in callitrichids [Snowdon et al., 2005], titi monkeys (*Callicebus moloch*) [Valeggia et al., 1995], orangutans (*Pongo pygmaeus*) [Maggioncalda et al., 1999] and sugar gliders (*Petaurus breviceps*) [Stoddart et al., 1994]. Captive male owl monkeys (*A. lemurinus*) show the 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 half of the young in the study had reached the age when they normally reproduce in captivity, between 3 and 4 years old [Gozalo and Montoya, 1990]. The different 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 avoiding misdirected aggressiveness by the parents. Adult owl monkeys can be very aggressive toward strange conspecifics, but levels of aggression do not regularly increase between parent and offspring during maturity [Dixson, 1983]. However, the potential that reproductive suppression, if any, was mediated through social or physiological mechanisms was not investigated in this study.

Finally, individuals could also be reliably assigned to their corresponding families 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 when classifying individuals by sex or age. Family classification relied less on plant metabolites and more on waxy lipids. One family had more than 12 times the amount 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 long-lasting message could be particularly useful for signaling the boundaries of a territory if constant marking is impractical.

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 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 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 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 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 used for recognition. This was supported behaviorally as encounters between individuals from different colonies with very distinct chemical profiles were agonistic toward each other [Safi and Kerth, 2003].

It seems reasonable to expect most scents to be the result of an interaction between 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. 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 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 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 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 the aromatic rings, suggests that bacteria are metabolizing plant materials and indirectly contributing to the scent profile.

These findings should be considered preliminary and further investigation with larger samples sizes and behavioral manipulation is suggested. For example, while we 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 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 of low molecular weight.

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