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ORIGINAL ARTICLE

Evidence for scent marking in vervet monkeys?

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Abstract We used data from two troops of free-ranging vervet monkeys (*Chlorocebus aethiops*) to assess the proposition that the conspicuous chest rubbing observed in this species constitutes scent-marking behavior. Our data indicate that chest-rubbing behavior is associated with higher-ranking males who are more likely to do so during the breeding season in areas where territorial encounters occur. We found no indication that chest rubbing was triggered directly by encounters between troops. We conclude that these data, in conjunction with reports of chest rubbing from other Old World monkeys, are sufficiently suggestive of scent marking to warrant further, directed research and support the suspicion that olfactory cues remain important to catarrhines in a number of domains.

Keywords Vervet monkey · Olfaction · Dominance · Territoriality

Introduction

A wide range of mammalian species use glandular chemical secretions to flag individual identity, status, reproductive condition, and spatial occupancy (Thiessen and Rice 1976; Gosling and Roberts 2001). In primates, such scent-marking behavior is widespread among prosimians and New World monkeys (e.g., Gould and Overdorff 2002; Pochron et al. 2005; Heyman 2006) but relatively uncommon in both Old World monkeys and apes. Sternal scent glands have been discovered in both gibbons and mandrills (Geissman 1987; Setchell et al. 2010a), and there have been observations of scent-marking behavior in a number of cercopithecine species (Geissman 1987). These findings, combined with evidence demonstrating that at least one species of Old World monkey, *Macaca nemestrina*, displays olfactory discriminatory abilities on a par with those of squirrel monkeys (Hübener and Laska 1998), along with field data suggesting strongly that olfactory cues are used in mate assessment (Clarke et al. 2009; Setchell et al. 2010b), indicates that olfaction may continue to serve a communicatory function among the catarrhines despite the increasing importance of the visual modality over the course of their evolution (Barton 1998). Gartlan and Brain (1968) and Basckin and Krige (1973) reported that male vervet monkeys (*Chlorocebus aethiops pygerythrus*) perform conspicuous chest-rubbing behavior in social contexts. These studies do not provide quantitative support for this interpretation, which they derived from the behavior's sex specificity and its stereotypy. We have been working on the same subspecies of vervet in South Africa, and our objective here is to confirm that similar conspicuous chest rubbing is also performed in our population of vervets and to present data that bear on its interpretation.

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Methods

Data collection

Data presented here were collected from two habituated vervet monkey troops—RBM ($N = \sim 48$) and RST

($N = \sim 72$)—in Samara Private Game Reserve, Graaff Reinet, Eastern Cape, South Africa (32°22′S, 24°52′E. McDougall et al. 2010; Pasternak et al. personal observation). All adults of both sexes ($N_{\text{RBM males}} = 10$, $N_{\text{RBM females}} = 15$; $N_{\text{RST males}} = 10$, $N_{\text{RST females}} = 23$) were individually recognizable. One or more observers conducted full-day follows over a 10-month period (February 2010 to November 2010), and monthly observation effort is expressed as the number of person-days ($N = 586$ days. $N_{\text{RBM}} = 252$ days; $N_{\text{RST}} = 334$ days). As chest-rubbing behavior was infrequent, we report all observed instances. These were recorded by all observers as ad libitum data onto electronic data loggers using a standardized form that included a GPS record of spatial location. Whereas it is clear that we will have missed many instances of chest rubbing, there is no indication that, with observation effort accounted for, there is any systematic bias in the data set (see below). Consequently, for general analyses, we pooled data from the two troops in order to conserve sample size. Ongoing data on aggressive interactions were used to generate dominance hierarchies.

Data analysis

The nature of the data and the small sample sizes necessitated the use of nonparametric tests (binomial, Spearman's rho, Kolmogorov's D, Mann–Whitney U tests), with probabilities of occurrence adjusted appropriately to account for differences in the representation of the two sexes and monthly differences in observation effort. Spatial location data were extracted using proprietary GIS software. As the same data were used for multiple comparisons, we applied the Bonferroni correction and set $P < 0.0083$ (0.05/6). Analyses were conducted in JMP 9 (SAS Institute 2007) and all tests are two tailed.

Results

Description

We recorded 34 instances of stereotyped chest rubbing ($N_{\text{RBM}} = 10$; $N_{\text{RST}} = 23$). Troop differences in frequency were accounted for by observation effort ($\chi^2 = 0.11$; 1 *df*, $P = 0.74$). In all instances, the behavior took this general form (Fig. 1):

The animal stood bipedally by, or climbed a short distance (<1 m) up, a slanted tree trunk, grabbed it with both arms, and then rubbed its chest ($N = 29$) or throat and cheek ($N = 5$) on the trunk repeatedly. After several repetitions, the performer stopped and made nasal contact with the trunk (assumed to be sniffing), after which it resumed chest rubbing. This sequence was repeated one or more times before the animal dismounted and left the area. In only one instance was chest rubbing preceded by any apparent olfactory investigation of the substrate by the performer. Although another animal immediately came up and placed its nose onto the substrate on five of the 34 occasions, this was obviously not the predominant response to chest rubbing.

Sex differences

A total of 14 animals of both sexes (13 adults and one juvenile) were seen to rub their chests; however, more adult males (10/20) than females (3/38) did so ($\chi^2 = 13.4$, 1 *df*, $P < 0.01$), and more occurrences overall ($N = 28$) were associated with males.

Male rank differences

The median rank of males who chest rubbed was 3.5 (highest rank 1) and that of males who were not observed

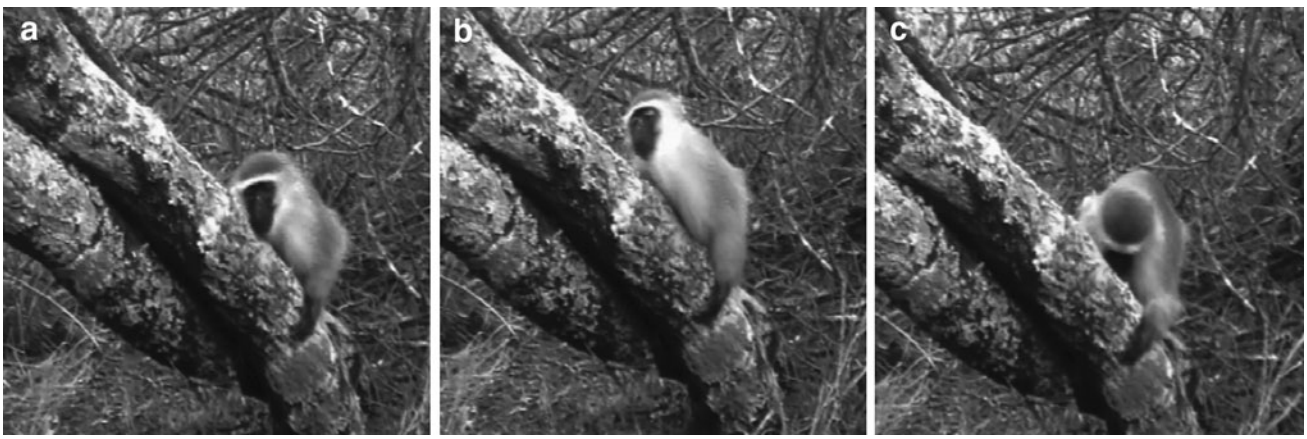

Fig. 1 An adult male rubs his chest on an inclined branch (stills extracted from videotape). He begins by rubbing his cheek (**a**) and then moves his body forward so that the chest is drawn over the surface (**b**). He then places his nose onto the surface at the point where he had made contact (**c**)

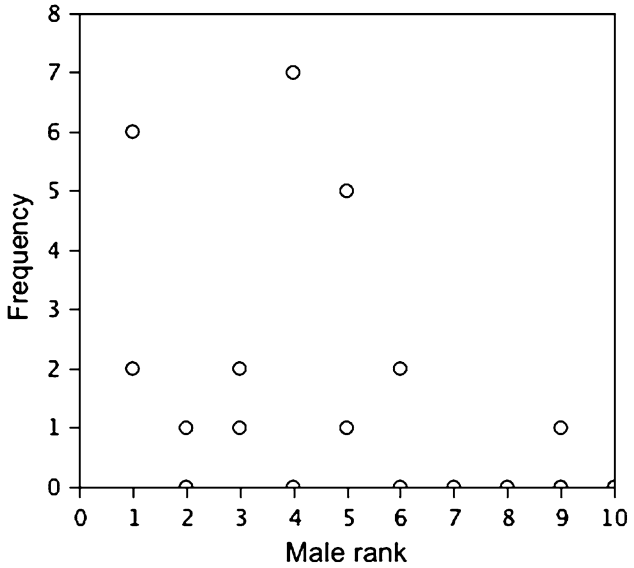

Fig. 2 Relationship between male rank (highest rank 1) and observed frequency of chest rubbing. Data from the two troops are combined

to do so was 7.5. This difference was significant (Mann–Whitney test: $z = -2.38$, $N_1 = 13$; $N_2 = 7$, $P = 0.0083$). Higher-ranking males chest rubbed significantly more than lower-ranking males (Spearman's $\rho = -0.57$, $N = 20$, $P < 0.01$; Fig. 2).

Seasonal differences

To determine whether male chest rubbing was disproportionately associated with the months over which mating was observed (April–July), we used observation effort to estimate expected frequencies during and outside the breeding season (Fig. 3). We found that chest rubbing was significantly more frequent during the mating season ($\chi^2 = 8.67$, 1 *df*, $P < 0.01$).

Spatial location

To investigate whether chest rubbing was influenced by spatial location, we identified the location of chest rubbing in relation to, and distance from, territorial boundaries (determined from localities of observed conflict between the study and neighboring troops) (Fig. 4). The mean distance from a boundary was 40.2 [standard deviation (SD) 34.3]. An exponential distribution provided the best fit to the data (Fig. 5), indicating a rapid decay in the likelihood of recording chest rubbing with increasing distance from the boundary (Kolmogorov $D = 0.165$, $N = 28$, $P = 0.15$). Nevertheless, given a total of 525 intertroop encounters over the same period ($N_{RBM} = 178$; $N_{RST} = 349$), there is little evidence that chest rubbing was triggered by boundary disputes; we recorded only three instances that followed immediately from an intertroop conflict.

Discussion

Our results indicate that vervets rubbed their chests in a relatively stereotyped way and that performance was likely to have been regulated by olfactory feedback. In the absence of a full histological analysis of skin from the sternal region and analysis of any substance transferred onto tree trunks via chest rubbing, it would be premature to state with certainty that this represents scent-marking behavior, although it is strongly suggestive. Montagna (1972) notes that sebaceous glands in nonhuman primates are generally confined to the face and anogenital region, whereas apocrine glands, which are often associated with distinctive odors, occur throughout the hairy skin. Indeed, reports of scent-marking behavior among several other guenon species (cited in Geissman 1987), along with the

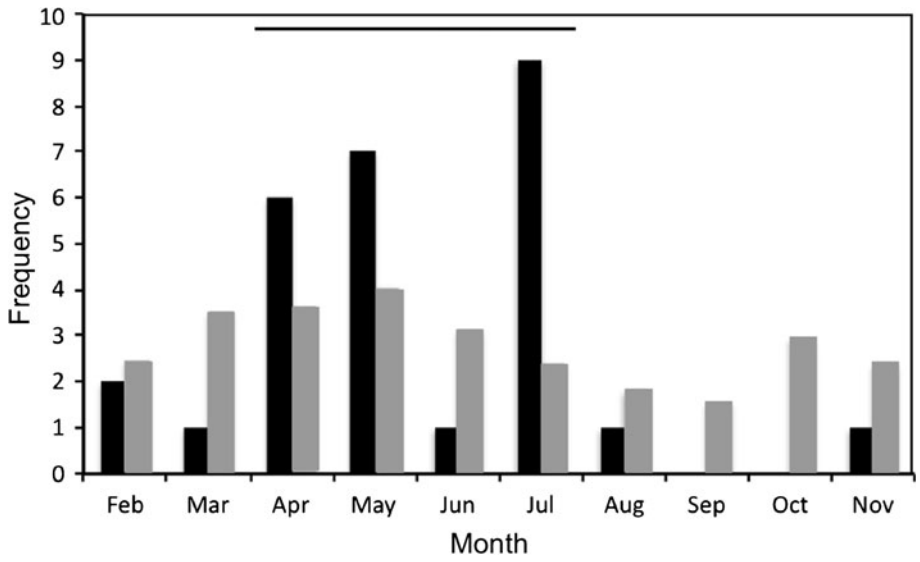

Fig. 3 Distribution of chest rubbing across the study period. *Black bars* are observed frequencies; *grey bars* are the expected values. The *black line* identifies the period over which mating took place

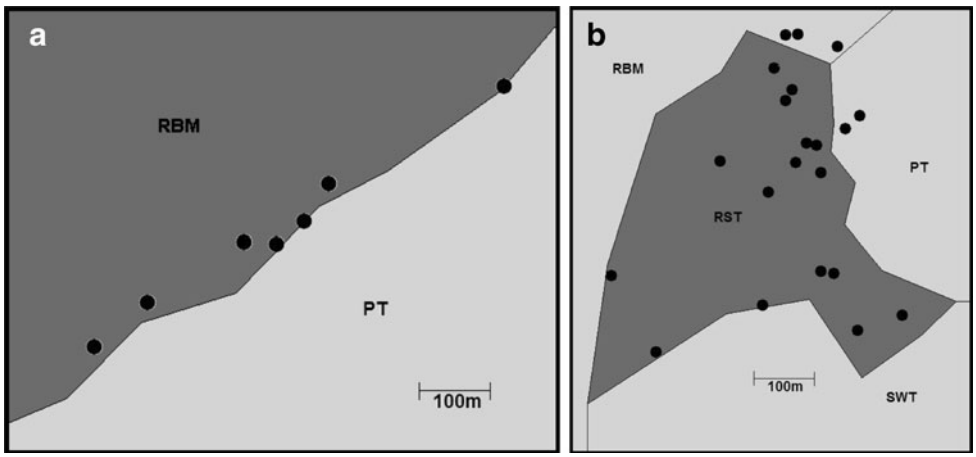

Fig. 4 Spatial location of chest rubbing by males in two habituated vervet monkey troops—RBM (**a**) and RST (**b**). The boundaries between the study troops and their neighbors were drawn by connecting the locations at which aggressive intertroop encounters were recorded

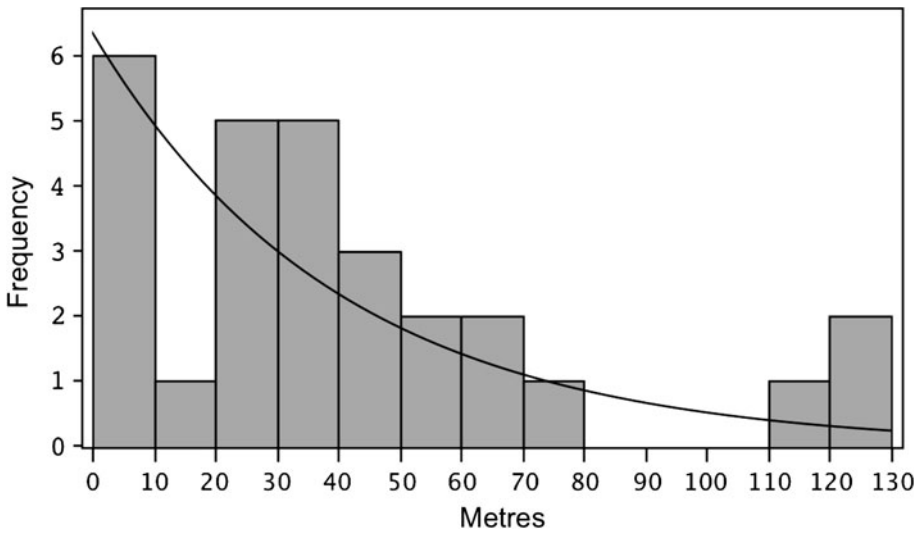

Fig. 5 Frequency with which chest-rubbing behavior was recorded at different distances from territorial boundaries. *Black line* indicates the fitted exponential distribution

demonstration of a sternal gland in mandrills (Setchell et al. 2010a), suggests that further investigation along these lines among vervet monkeys would be profitable.

The finding that chest rubbing was, on the whole, a behavior performed during the breeding season by high-ranking males near their territory boundaries, suggests that, if chest rubbing serves to scent-mark the territory, it may be involved in intrasexual competition and serve as a marker to other, potentially immigrant, males (Gosling and Roberts 2001). Although the observation of marking by females also requires further consideration, the proposal here would be that immigrant males can use the information contained in scent marks to assess the resource-holding potential of the territory occupants and make decisions about whether to attempt immigration accordingly. As Gosling and Roberts (2001) have shown, males may either detect intrinsic properties of scent marks (e.g., androgen-dependent volatiles), remember past contests and odor of their opponents, and associate these with scent marks or remember the smell of recently encountered scent marks and match this smell with any potential opponents that they meet subsequently. Many species switch between all these mechanisms, and Gosling and Roberts (2001) suggest they are used conditionally, depending on the information available and cost–benefit ratio for the receivers. Given the greater propensity of higher-ranking males to mark, signaling of intrinsic quality would seem a plausible mechanism to test among vervets, although it is clear that scent matching would also allow potential immigrants to assess opponents and decide whether to attempt immigration into the troop (see also Kappeler 1990, 1998; Gould and Overdorff (2002).

It is also possible that scent marking may have an influence on female behavior. Among prong-horn antelope, for example, it has been suggested that scent marks hold females to familiar smelling territories and increase their sexual receptivity (Thiessen and Rice 1976). Female philopatry would suggest that the former explanation is unlikely in vervets, and the lack of olfactory investigation suggests that marking may not serve to increase female

receptivity (it is also unclear whether male marking is of the magnitude and frequency needed to influence female receptivity significantly). It would, however, be interesting to relate the incidence of male scent-marking behavior to the number of sexually receptive females present in the group at the time, but unfortunately, we do not have the sample size that would enable us to perform such an analysis.

In conclusion, our results suggest strongly that vervet male chest rubbing may serve a scent-marking function, based on its spatial patterning and differential performance by males of different rank, as well as being consistent with data from other Old World monkey species. More detailed histological and behavioral studies are needed to confirm this, but our data add to a growing body of evidence suggesting that olfactory cues continue to play a role in the social behavior of Old World monkeys and that their characterization as microsmatic may have been premature.

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References

Barton RA (1998) Visual specialization and brain evolution in primates. Proc R Soc Ser B Lond 265:1933–1937

Basckin DR, Krige PD (1973) Some preliminary observations on the behaviour of an urban troop of vervet monkeys (*Cercopithecus aethiops*) during the birth season. J Behav Sci 1:287–296

Clarke PMR, Barrett L, Henzi SP (2009) What role do olfactory cues play in chacma baboon mating? Am J Primatol 71:1–10

Gartlan JS, Brain CK (1968) Ecology and social variability in *Cercopithecus aethiops* and *Cercopithecus mitis*. In: Jay P (ed) Primates: studies in adaptation and variability. Holt, Rinehart and Wilson, New York, pp 253–292

Geissman T (1987) A sternal gland in the siamang gibbon (*Hylobates syndactylus*). Int J Primatol 8:1–15

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

Gould L, Overdorff DJ (2002) Adult male scent-marking in *Lemur catta*. Int J Primatol 23:575–586

Heyman EW (2006) Scent marking strategies of new world primates. Am J Primatol 68:650–661

Hübener F, Laska M (1998) Assessing olfactory performance in an old world primate, *Macaca nemestrina*. Physiol Behav 64:521–527

Kappeler PM (1990) Social status and scent-marking behaviour in *Lemur catta*. Anim Behav 40:774–778

Kappeler PM (1998) To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. Behav Ecol Sociobiol 42:411–421

McDougall P, Forshaw N, Barrett L, Henzi SP (2010) Leaving home: responses to water depletion by vervet monkeys. J Arid Env 74: 924–927

Montagna W (1972) The skin of nonhuman primates. Am Zool 12:109–124

Pochron ST, Morelli TL, Scirbona J, Wright PC (2005) Sex differences in scent-marking in *Propithecus edwardsi* of Ranomafana N.P., Madagascar. Am J Prim 66:97–110

SAS Institute (2007) JMP start statistics. Duxbury Press, Pacific Grove

Setchell JM, Vaglio S, Moggi-Cecchi J, Boscaro F, Calamai L, Knapp LA (2010a) Chemical composition of scent-gland secretions in an old world monkey (*Mandrillus sphinx*): influence of sex, male status and individual identity. Chem Senses 35:205–220

Setchell JM, Charpentier MJE, Abbott KM, Wickings EJ, Knapp LA (2010b) Opposites attract: MHC-associated mate choice in a polygynous primate. J Evol Biol 23:136–148

Thiessen D, Rice M (1976) Mammalian scent-gland marking and social behaviour. Psychol Bull 83:505–539