Chapter 8
Olfactory Communication in the Ringtailed Lemur (*Lemur catta*): Form and Function of Multimodal Signals

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Abstract To better understand the relation between form and function in the complex olfactory communication system of the ringtailed lemur (*Lemur catta*), we integrated observational, experimental, and chemical approaches applied to a population of semi free-ranging animals at the Duke Lemur Center in Durham, North Carolina. Our aim was to examine sex-role reversal in the expression and function of scent marking and unravel the contribution of multimodal components of information transfer, with the unifying framework for all three avenues of our research being that multiplicity of form implies multiplicity of function.

8.1 Introduction

Our research program focuses on the ringtailed lemur (*Lemur catta*)—a predominantly diurnal and terrestrial Malagaszy primate that lives in socially integrated, multimale-multifemale groups. Unusually among mammals, these groups are characterized by unambiguous female dominance over males (Jolly 1966; Kappeler 1990a). Like other strepsirrhines, ringtailed lemurs are macrosmatic, arguably displaying the most complex array of scent-marking behavior within the Order Primate (Schilling 1974). Both sexes have apocrine and sebaceous gland fields in their genital regions, and males boast two additional specialized glands on their wrists and pectoral surfaces, referred to as the antebrachial and brachial organs, respectively (Montagna and Yun 1962). The secretions from these glands (see Fig. 8.1 in Scordato and Drea 2007) are used singly or in combination (e.g. when wrist marking is preceded by shoulder rubbing or when tail fur is impregnated with brachial and antebrachial secretions prior to 'stink fighting': Jolly 1966). The various odorants are deposited using unique displays that produce composite visual and olfactory cues. Wrist marking additionally produces an audible clicking sound as the antebrachial spur scars the substrate being marked. The implication of this broad scent-marking array is that, despite having complex vocal and social

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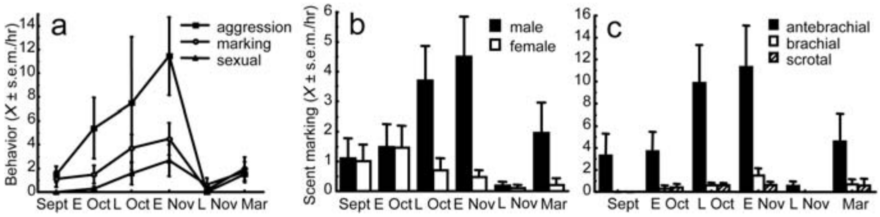

Fig. 8.1 Mean hourly rates of *L. catta* behavior during the pre-breeding (Sep, early and late Oct), breeding (early and late Nov), and post-breeding (Mar) seasons. (a) Rates of scent marking in relation to aggressive and sexual behavior, combined for both sexes. (b) Sex differences in scent marking. (c) Differential usage of male scent glands

repertoires, ringtailed lemurs rely heavily on olfactory communication. Whereas some odor signals (e.g. long-lasting cues deposited at territorial borders or as resource labels) may function equivalently in social and asocial species, others may be more tailored to group living. For instance, ephemeral signals may convey meaning only when used in specific social contexts or in conjunction with visual, behavioral, and auditory cues (Rowe 1999; Candolin 2003). Moreover, in female-dominant species, some functions may be role reversed. We examine these possibilities in three olfactory studies of *L. catta*.

8.2 Observational Study: Within-Group Variation in Scent Marking

8.2.1 Background

Based on the distribution of scent marks and on broad sex, seasonal, and rank-related differences in rates of scent marking, various researchers have proposed that *L. catta* use odor cues to demarcate territories, advertise resource ownership, signal reproductive state, and maintain intrasexual dominance (Jolly 1966; Kappeler 1990b, 1998; Mertl-Milhollen 2006). Here, we elaborate on similar findings, our primary question being whether differentiated gland usage reveals differentiated function. Thus, we additionally examined the relationship between type of scent marking and intra-group aggressive or reproductive behavior, specifically focusing on the sexual, social, and seasonal modulation of the different forms of olfactory signaling.

8.2.2 Methods

Our subjects were the adult members of three mixed-sex social groups that semi free-range in large forested enclosures (3–7 ha). We present data from preliminary analyses of an on-going study, based on ∼100 hours of observation (Sep 2003-Mar 2004). During this period, the groups comprised 25 animals of all ages, but the focal subjects were five males and seven females, aged 6-18 years. We observed each subject year round (weather permitting), during two 20-min focal periods per week. We recorded their behavior in real time, using handheld computers. Our ethogram included the frequency and duration of all forms of social and scent-marking behavior.

In the Northern Hemisphere, the breeding season spans Nov-Feb. Female *L. catta* are polyestrous, cycling up to three times per year at roughly 40-day intervals (Evans and Goy 1968), and show some degree of estrus synchrony (Jolly 1966; Sauther 1991). Thus, the breeding season encompasses three peaks of sexual activity rather than representing one continuous peak; nevertheless, the majority of females conceive in the first cycle (in early-mid Nov: Drea 2007). Our observation period, therefore, encompassed the pre-breeding, peak breeding, and post-breeding seasons.

8.2.3 Results and Discussion

Male and female *L. catta* showed a dramatic increase in aggression ($F_{5,50} = 4.51$, $P < 0.005$), corresponding to seasonal patterns of sexual activity ($F_{5,50} = 2.61$, $P < 0.05$; Fig. 8.1a). Because females have infrequent cycles with narrow windows of receptivity (as little as 24 hrs), male competition for access to females is intense. Similarly, female-initiated aggression escalates concurrently. This period of heightened sexual and aggressive activity is characterized, in both sexes, by increased scent marking ($F_{5,50} = 3.38$, $P = 0.01$; Fig. 8.2a). Consistent with prior suggestions (Kappeler 1998), olfactory signaling is intricately tied to reproductive and competitive behavior.

Gross seasonal patterns in scent marking were nevertheless sexually differentiated, both in frequency, i.e., with males marking at higher rates than females ($F_{1,10} = 7.18$, $P < 0.025$), and in timing ($F_{5,50} = 2.91$, $P < 0.025$), i.e., with peak female behavior (in early Oct) preceding peak male behavior (in early Nov) by about one month (Fig. 8.1b). These different schedules could be functionally significant: Although females may scent mark to assert resource ownership at the onset of a highly competitive period (Mertl-Milhollen 2006), they also may be advertising their impending reproductive state to potential mates, including males transferring between groups. By contrast, resident males may mark during the height of the breeding season to assert their dominance status relative to other males, thereby gaining immediate female preference (through female mate choice) or priority of access to receptive females (through intraspecific competition). Although females often mate multiply (Sauther 1991), dominant males may mate first (Parga 2006). It remains unknown if mating order affects sperm competition or if cryptic mechanisms of female choice may be in operation.

We next asked if males use one type of mark over another to advertise their quality as a competitor or potential mate. Comparing rates of shoulder rubbing, wrist marking, and scrotal marking revealed strong differences ($F_{2,8} = 11.32$,

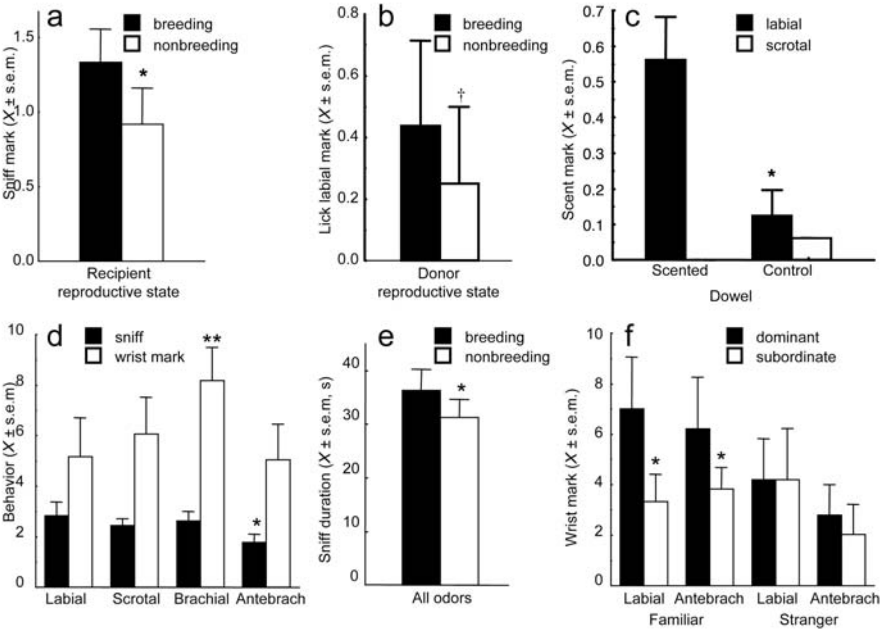

Fig. 8.2 Mean response frequency or duration by (a-c) female, F, and (d-f) male, M, *L. catta* to conspecific glandular secretions. (a) F sniffing all odorants as a function of her reproductive state (breed > non: $F_{1,3} = 28.57$, $P = 0.013^*$). (b) F licking labial odorant as a function of the donors' reproductive state (breed > non: $t_3 = 3.00$, $P = 0.58$, *n.s.*). (c) F frequency and site-specificity of scent marking as a function of odorant type: Fs counter marked the unscented dowel in response to scrotal scent, but over-marked scented dowels in response to labial scent ($t_3 = 3.87$, $P = 0.030^*$). (d) M response as a function of odorant type (antebrachial was sniffed least: $F_{3,9} = 6.75$, $P = 0.011^*$; brachial was wrist marked most: $F_{3,9} = 7.16$, $P = 0.009^{**}$). (e) M sniff duration as a function of donor reproductive state (main effect across dowels: $F_{2,6} = 57.63$, $P = 0.000$; breed > non: $P < 0.05^*$). (f) M wrist marking as a function of donor social status and familiarity: When donors were familiar (expt 1), Ms wrist marked more in response to dominant than subordinate scent ($F_{1,3} = 15.41$, $P = 0.029^*$); when donors were strangers (expt 2), Ms did not distinguish odorants by donor status ($F_{1,4} = 0.09$, $P = 0.775$)

$P = 0.005$), with the males' seasonal pattern being largely attributable to wrist marking ($F_{5,50} = 2.89$, $P < 0.01$; Fig. 8.1c). Scrotal and brachial marking occurred at low levels throughout the period of study. Lastly, although our small sample precluded statistical reliability, dominant males tended to scent mark more frequently than did subordinate males ($F_{1,3} = 6.86$, $P = 0.079$), consistent with prior reports (Jolly 1966; Kappeler 1990b). Thus, it may be that wrist marking, specifically, signals dominance in males – information that would be particularly relevant during the highly competitive breeding season. By contrast, maintaining low levels of genital or brachial marking may be effective in advertising one's continued presence throughout a territory.

8.3 Experimental Studies: Extra-Group Information Transfer

8.3.1 Background

As a complement to observing scent-marking behavior, experimentalists test animals' responses to the controlled presentation of odorants. The habituation-dishabituation paradigm has been used profitably to show that, based on scent alone, lemurs discriminate between the sexes and between unknown individuals (Mertl 1975; Harrington 1976; Dugmore, Bailey and Evans 1984; Palagi and Dapporto 2006). From our prior observations, we suspected that different kinds of scent marks might contain different messages. We also were interested in knowing if the reproductive state of the signal receiver might bear on the efficacy or value of olfactory cues. We used as our behavioral bioassay a discrimination paradigm. In a series of choice trials that modeled extra-group communication (i.e., between familiar non-group members or complete strangers), we manipulated multiple variables (e.g. sex, reproductive state, gland, age, social status, and familiarity) in both the signaler and receiver to better understand the influence of these variables on information transfer.

8.3.2 Methods

In experiment 1, four male and four female *L. catta* (two dominant and subordinate members per sex) served as adult 'recipients' during 'choice' trials in which we presented secretions derived from the various glands (labial, scrotal, brachial, and antebrachial) of 18 adult conspecific 'donors.' Most of these animals were from the same three social groups as before; however, in all cases, we presented the recipients with the odorants of non-group donors. Although housed in separate forested pens, the lemurs were nonetheless familiar with one another. Our design thus modeled the encounters that might occur between animals occupying adjacent territories. By contrast, we ran experiment 2 using five adult males that were unfamiliar with any of the donors. Using cotton swabs (precleaned with methanol and pentane), we collected monthly odorant samples from manually restrained donors. We stored the samples in similarly precleaned vials at $-80\,^{\circ}\mathrm{C}$, and parsed them between these experiments and our subsequent GC-MS study (see section 8.4). Using the GS-MS procedures described later, we verified that storage did not affect sample integrity.

In experiment 1, we tested recipients during their breeding and nonbreeding seasons. In each period, we presented them with two series of four trials, one series each for odorants derived from dominant versus subordinate donors, and one trial each per type of glandular secretion. Within trials, we presented the recipients with a choice between two odorants, both obtained from the same type of gland, from animals of equivalent social status, but from donors in breeding versus nonbreeding seasons. In experiment 2, we tested the recipients only during their nonbreeding season and presented them with two series of four trials, one series each for the donors' breeding versus nonbreeding season, and each of the four trials again representing each of the four glands. Within each trial, the two odorants presented had been obtained from the same type of gland, but from animals that differed in social status. In both experi-ments, we videotaped the 10-min trials, which were later scored by two observers blind to the goals of the study. The behavior of interest included approach frequency, time in proximity, sniff frequency and duration (which we interpreted as investigation of the volatile fraction of odorants), lick frequency (which we interpreted as investigation of the nonvolatile fraction of odorants), and counter- or over-marking (which we interpreted as competitive; for more details, see Scordato et al. (in press).

8.3.3 Results and Discussion

The presentation of different odorants produced varying levels of investigation or responsiveness in female and male recipients. The interest of female recipients was directed primarily to the scent of other females, and varied with their own reproductive state (Fig. 8.2a) and that of the female donors (Fig. 8.2b). Thus, mainly during the breeding season, females sniffed (Fig. 8.2a), licked (Fig. 8.2b), and countermarked (Fig. 8.2c) odorants derived from other reproductive females. From these findings, we conclude that female scent marking functions primarily in reproductive advertisement and intra-sexual competition, and that male scent marks are minimally functional in female assessment of mates. By contrast, male recipients were interested in all secretions, although their responses varied by odorant type (Fig. 8.2d). Males appeared to use odorants to monitor the reproductive state of both sexes (Fig. 8.2e). Thus, as is the case for females, male scent marking appears to function in intrasexual competition, but unlike the case for females, males may derive olfactory information relevant to mate assessment. Lastly, we found that males discriminated between the odorants of dominant versus subordinate donors if the donors were familiar (expt 1), but not if they were strangers (expt 2; Fig. 8.2f). Thus, we suspect that individual identity, but not dominance status, may be encoded within the chemical matrix of scent secretions and that the pairing of social and olfactory signals requires associative learning.

8.4 Chemical Study: Information Content in Glandular Secretions

8.4.1 Background

Behavioral bioassays are inextricably linked with chemical studies to decipher the information content of olfactory signals (Albone 1984). As a complement to the experimental approach described above, several research groups have applied chemical approaches, particularly gas chromatography and mass spectrometry (GC-MS), to the analysis of strepsirrhine glandular secretions. These researchers have reported differences in the semiochemistry of various glandular secretions (Hayes, Morelli and Wright 2004, 2005), as well as seasonal (Hayes et al. 2006) and individual differences (Palagi and Dapporto 2006). Likewise, we have used GC-MS analysis of scent composition to test for chemical differences between all types of glandular secretions in *L. catta*. We asked if the chemical composition of these secretions varied by gland, season (i.e., reproductive state), individual, and/or the dominance status of the signaler. From the responses we had observed in our behavioral bioassays, we predicted that differentiated chemical patterns would emerge for each gland, as well as across seasons and between individuals; however, we did not expect that social status would be encoded within the chemical matrix of scent secretions.

8.4.2 Methods

We obtained secretions ($\sim$ 25 samples per gland type) from 14 adult *L. catta* (seven per sex) during the prebreeding, breeding, and nonbreeding seasons. We adapted the solvent extraction technique (using methyl-*tert*-butyl ether) described by Safi and Kerth (2003) and ran our samples using an HP 5890 series II GC, fitted with a double-focusing JEOL JMS-SX 102A high-resolution MS and an HP-5MS fused silica (5% phenyl)-methylpolysiloxane column ($30\,\text{m} \times 0.25\,\text{mm} \times 0.25\,\mu\text{m}$, Agilent). The injector temperature was set at 280 °C, the ion source at 190 °C, and helium was the carrier gas. We used the following temperature protocol (after 3-min solvent delay): 80–180 °C at a rate of 20 °C/min (held 2 min at 80 °C); 180–320 °C at 7 °C/min (held 5 min at 320 °C). The entire run lasted 32 min; no compounds eluted after 27 min. Our standards included 15µl each of squalene, farnesol, farnesal, and seven alkenes (C12-C18) in 50 ml of solvent. Using both retention time and mass spectra, we used the NIST 2002 Mass Spectral Library to tentatively identify peaks. We used integration software to calcualate the relative area of each component and principal component (PC) analysis to reduce the dimensionality of the data. We then performed linear discriminate analysis (LDA) on PCs with eigenvalues > 1, using gland, season, animal identity or social status as the independent variable. We performed these analyses in JEOL MS analysis software and JMP 6, and report Wilkes' lamda as our test of group differences. We present the preliminary results from these analyses. For methodological details and results on a larger data set, see Scordato et al. (in press).

8.4.3 Results and Discussion

Antebrachial secretions were comprised primarily of low-molecular weight compounds. Because of the high volatility of these secretions, we could not produce reliable chromatograms using our routine extraction procedure. We are currently analyzing these secretions using solid phase dynamic extraction techniques (in col-

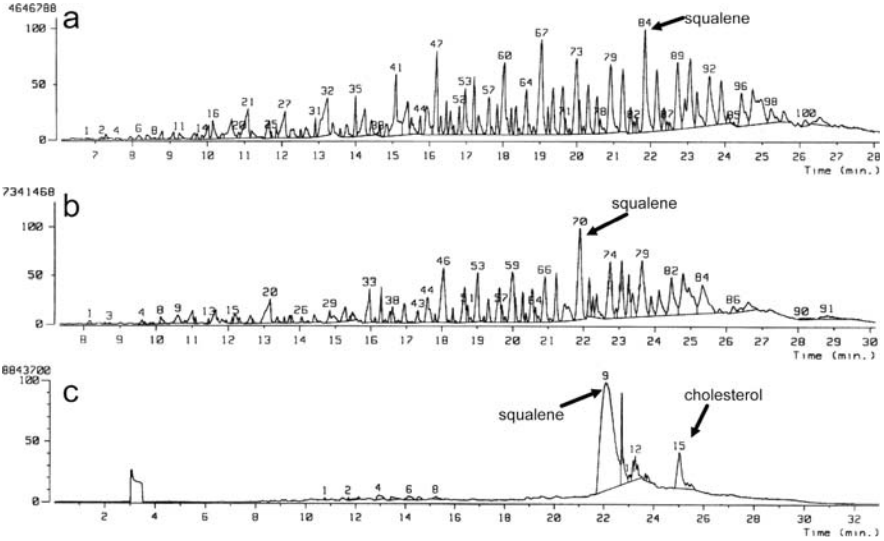

Fig. 8.3 Gas chromatograms of *L. catta* (a) labial, (b) scrotal, and (c) brachial secretions

laboration with Thomas Goodwin, Hendrix College). The remaining three types of odorant for which we obtained reliable results had 102 compounds: 57 for labial, 52 for scrotal, and 39 for brachial secretions. From the mass spectra, it can be seen that labial (Fig. 8.3a) and scrotal (Fig. 8.3b) secretions are composed primarily of organic acid esters, whereas brachial secretions (Fig. 8.3c) are composed predominantly of squalene ($C_{30}H_{50}$, MW = 410.7) and cholesterol ($C_{27}H_{46}O$, MW = 386.7).

The chemical composition of the various secretions provides further clues as to their differentiated functions: Genital and brachial secretions contain greasy, high-molecular weight compounds, such as squalene, which is a recognized fixative that may increase signal longevity (Alberts 1992). By contrast, antebrachial secretions are low molecular weight compounds, deposited primarily during social displays. Such ephemeral signals may be deployed primarily for within-group communication because they require integration of multiple sensory modalities for full efficacy of signal transmission. If, however, the volatile antebrachial secretions are combined with the squalene-based brachial secretions, as is the case for a percentage of wrist marking and during tail marking, they may produce a more durable signal that could function long after the signal sender is gone.

Despite similarity between the secretions of the two genital glands, differences between the chemical profiles of all three types of secretions emerged in the LDA (Fig. 8.4a). Likewise, reliable seasonal variation appeared in the chemical profiles derived from all three sources (labial: Fig. 8.4b; scrotal: Wilks' lambda = 0.018, $P < 0.01$; brachial: Wilks' lambda = 0.136, $P < 0.05$). We also found the anticipated individual-specific signatures in scent secretions derived from the genital glands (labial: Wilks' lambda = 0.000, $P < 0.01$; scrotal: Fig. 8.4c), but not from

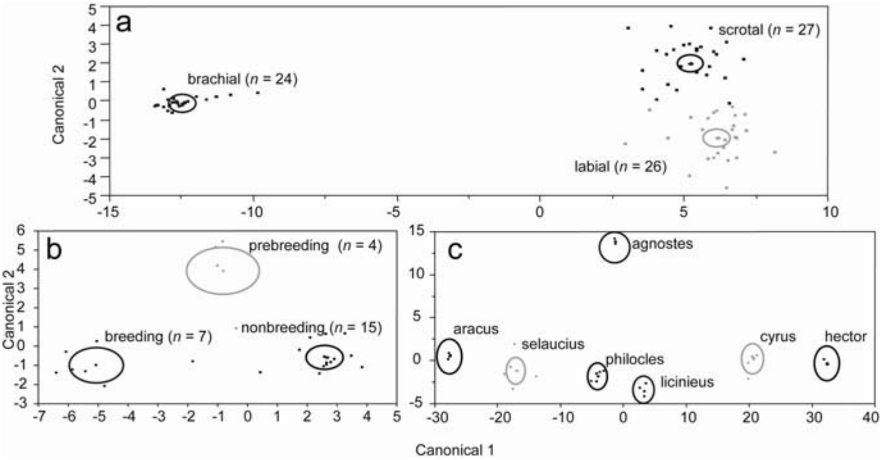

Fig. 8.4 Discriminant analyses of the principal chemical components in *L. catta* scent secretions by (a) gland, (b) season, and (c) individual. (a) Accurate classification of 97.5% of labial, scrotal, and brachial samples ($n = 77$) by gland of origin (Wilks' lambda = 0.003; $P < 0.001$). (b) Reliable differentiation of 100% of labial samples ($n = 26$) into prebreeding, breeding, and nonbreeding seasons (Wilks' lambda = 0.018, $P < 0.01$). (c) Individual 'scent signatures' in the scrotal secretions from seven males. LDA performed on 17 principal components correctly classified 100% of these samples to the individuals from which they were collected (Wilks' lambda = 0.000, $P < 0.002$)

the brachial gland (Wilks' lamba = 0.013, $P > 0.10$). The latter finding contrasts with a prior report (Palagi and Dapporto 2006) and may reflect differences between the sampling regimens or analytical procedures used in the two studies (Scordato et al. 2007). Lastly, we found no evidence that social status reliably predicted the chemical profiles of any of the glandular secretions (data not shown). Coupling these findings, with our previous bioassay results, we have shown that lemurs can use olfactory cues to recognize individual conspecifics and modulate their response to a signal based on a combination of factors, including their own physiological state, the physiological state of the signal sender, and their prior experience with that animal.

8.5 Conclusion

Through the information revealed in a series of integrated observational, experimental, and chemical studies of olfactory communication, we suggest that scent marking in the ringtailed lemur produces composite olfactory, visual, and sometimes auditory signals that contain a complex combination of ephemeral and long-lasting cues and serve differentiated functions. Consistent with prior suggestions (Kappeler 1998; Mertl-Milhollen 2006), one primary function of scent marking, in *both* sexes, involves intrasexual competition – to advertise resource ownership, assert status, and maintain intrasexual dominance hierarchies; another involves mediating reproductive behavior. Whereas female interest in, and countermarking of, scent marks is most prominently directed toward labial marks, particularly during the breeding season, male scent generates little female interest or competitive response. Thus, within this female-dominated society, males appear to pose minimal threat to females, whereas females closely monitor one another. Unlike for other female mammals, female mate choice in lemurs may not be heavily influenced by male olfactory cues.

Males, on the other hand, show great interest in the odorants of both sexes, even though they respond differently by odorant type, e.g. predominantly licking labial secretions, but primarily wrist marking in response to male scent. The style of response may reflect the information conveyed in the scent mark: males may lick a female's mark to assess her reproductive state, whereas countermarking a male's mark may reflect intrasexual competition. Based on differential response, we suggest that the various male glands serve specialized functions, some of which may require social experience for effective transmission. We propose that the stable content of scrotal marks lay claim to resources, the act of antebrachial marking displays dominance to onlookers, and brachial compounds function as fixatives of highly volatile chemicals, prolonging the otherwise ephemeral signals in antebrachial marks.

As we suspected, multiplicity of form reflects multiplicity of function; however, the diversity of form also encompasses diverse mechanisms of transmission. For instance, some information, such as dominance status, is conveyed solely by the observable (and sometimes audible) behavioral component of wrist marking and, therefore, may function primarily for instantaneous intra-group communication. Because dominance hierarchies are relational, the communication of rank is most relevant to other group members. Moreover, because the hierarchies of male *L. catta* can be transient, long-lasting signals of dominance could become irrelevant over time. Both of these features are reflected in the rank-differentiated usage and ephemeral chemistry of wrist marks. Nevertheless, if a longer-lasting signal of male competence is required, antebrachial secretions might gain longevity by being mixed with the fixative components of brachial secretions. Such is the case during a subset of wrist marking, but also during tail marking and stink fighting, which occur most commonly during aggressive, inter-group encounters.

Some information (e.g. reproductive state) appears to be contained solely within the chemical matrix of certain marks, particularly within the stable genital secretions. Thus, longer-lasting signals may be broadcast to any animal that comes in contact with labial or scrotal marks. Such a scenario seems particularly applicable to females that scent mark most frequently prior to the onset of estrus cycles, but nonetheless when their sex steroids are on the rise (Drea 2007). Such advertisement may encourage male immigration at a time that would maximize the opportunity of female mate choice, even if the mechanism of, or criteria for, selection remain obscure.

Lastly, some information (e.g. gland of origin and individual identity) is duplicated in the behavior and chemistry of scent marking, suggesting that transmission of certain information targets both group and non-group members. Communicating individual identity would facilitate claiming ownership of resources, and it would benefit the signaler to broadcast such information in a long-lasting cue. It should come as no surprise, especially with respect to a socially complex primate, that effective transmission of information, particularly when conveyed through multiple channels, requires some degree of associative learning. The integration of multimodal information is evidenced, for instance, by the pairing of unique and presumably permanent ‘scent signatures’ with more transient observable qualities, such as behavioral displays of dominance status. Further studies promise to shed additional light on the differentiated functions and multimodal mechanisms of lemur scent marking.

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References

Alberts, A.C. (1992) Constraints on the design of chemical communication systems in terrestrial vertebrates. Am. Nat. 139 supp, s62–s89.

Albone, E.S. (1984) *Mammalian Semiochemistry*. Wiley and Sons, New York.

Candolin, U. (2003) The use of multiple cues in mate choice. Biol. Rev. 78, 575–595.

Drea, C.M. (2007) Sex differences and seasonal patterns in steroid secretion in *Lemur catta*: Are socially dominant females hormonally ‘masculinized’? Horm. Behav. In press.

Dugmore, S.J., Bailey, K. and Evans, C.S. (1984) Discrimination by male ring-tailed lemurs (*Lemur catta*) between the scent marks of male and those of female conspecificis. Int. J. Primatol. 5, 235–245.

Evans, C.S. and Goy, R.W. (1968) Social behaviour and reproductive cycles in captive ringtailed lemurs (*Lemur catta*). J. Zool, Lond. 156, 181–197.

Harrington, J.E. (1976) Discrimination between individuals by scent in *Lemur fulvus*. Anim. Behav. 24, 207–212.

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

Hayes, R.A., Morelli, T.L. and Wright, P.C. (2005) The chemistry of scent marking in two lemurs: *Lemur catta* and *Propithecus verreauxi coquereli*. In: R.T. Mason, M.P. LeMaster and D. Müller-Schwarze, (Eds.), *Chemical Signals in Vertebrates, X*. Springer Press, New York, pp. 159–167.

Hayes, R.A., Morelli, T.L. and Wright, P.C. (2006) Volatile components of lemur scent secretions vary throughout the year. Am. J. Primatol. 68, 1–6.

Jolly, A. (1966) *Lemur Behavior: A Madagascar Field Study*. University of Chicago Press, Chicago.

Kappeler, P.M. (1990a) Female dominance in *Lemur catta*: more than just female feeding priority?

Folia Primatol. 55, 92–95.

Kappeler, P.M. (1990b) Social status and scent-marking behaviour in *Lemur catta.* Anim. Behav. 40, 774–776.

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

Mertl, A.S. (1975) Discrimination of individuals by scent in a primate. Behav. Biol. 14, 505–509.

Mertl-Milhollen, A.S. (2006) Scent marking as resource defense by female *Lemur catta*. Am. J. Primatol., 68, 605–621.

Montagna, W. and Yun, J.S. (1962) The skin of primates. X. The skin of the ringtailed lemur (*Lemur catta*). Am. J. Phys. Anthropol. 20, 95–117.

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

Parga, J.A. (2006) Mulitiple mating and female mate choice in *Lemur catta*: does it pay to be a dominant male? Am. J. Phys. Anthropol. 42 supp, 144–144.

Rowe, C. (1999) Receiver psychology and the evolution of multicomponent signals. Anim. Behav. 58, 921–931.

Safi, K. and Kerth, G. (2003) Secretions of the interaural gland contain information about individuality and colony membership in the Bechstein's bat. Anim. Behav. 65, 363–369.

Sauther, M. (1991) Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly special reserve, Madagascar. Am. J. Phys. Anthropol. 84, 463–477.

Schilling, A. (1974) A study of marking behaviour in *Lemur catta*. In: R.D. Martin, G.A. Doyle and A.C. Walker (Eds.), *Prosimian Biology.* University of Pittsburgh Press, Pittsburgh, pp. 347–362.

Scordato, E.S. and Drea, C.M. (2007) Scents and sensibility: information content of olfactory signals in the ringtailed lemur (*Lemur catta*). Anim. Behav. 73, 301–314.

Scordato, E.S., Dubay, G. and Drea, C.M. (2007) Chemical composition of scent marks in the ringtailed lemur, *Lemur catta*: glandular differences, individual signatures, and seasonal variation. Chem. Senses. In press.