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Scents and sensibility: information content of olfactory signals in the ringtailed lemur, *Lemur catta*

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The function of olfactory signalling in social species is less well understood than in asocial species. Consequently, we examined olfactory communication in the ringtailed lemur, a socially complex primate that retains a functional vomeronasal organ, has well-developed scent glands and shows a suite of scent-marking behaviour. To assess the information content of different types of scent gland secretions, we decoupled olfactory cues from the visual and behavioural modalities with which scent marking is normally associated. We presented male and female subjects (signal receivers) with a series of choice tests between odours derived from conspecific donors (signal senders) varying by sex, age, social status and reproductive condition. We additionally examined the influence of the receivers' reproductive state and familiarity with the signaller. The reproductive condition, social status and familiarity of senders and receivers affected signal transmission; specifically, male receivers attended most to the odours of conspecifics in breeding condition and to the odours of familiar, dominant animals. By contrast, females varied their responses according to both their own reproductive state and that of the sender. Based on male and female patterns of countermarking, we suggest that scent marking serves a function in intergroup spacing and intrasexual competition for both sexes, as might be expected in a female-dominant species. By contrast, minimal female interest in male odours counters a female mate choice function for scent marking in this species. Nevertheless, scent marks are critical to male–male competition and, therefore, may be subject to sexual selection.

Keywords: chemical communication; female dominance; individual recognition; intrasexual competition; *Lemur catta*; mate choice; reproductive signalling; ringtailed lemur; scent marking; seasonality

The study of mammalian olfactory communication focuses on relatively asocial species (Ralls 1971; Brown & Macdonald 1985; Johnston 2003) that can benefit from the dispersed 'bulletin board' effect inherent to olfactory signals (Alberts 1992). In contrast, because social taxa rely on both visual and auditory means of communication, researchers often treat visual and acoustic systems as the primary sensory modalities and substrates of sexual selection (Trivers 1972; Ryan et al. 1990; Andersson 1994). Although the function of olfactory communication in socially complex species remains poorly studied, odour cues are critical to mediating intragroup interaction, especially for those species that have specialized scent glands and display complex scent-marking repertoires. To better understand the function of chemical signals in such a species, we examined the responses of ringtailed lemurs to conspecific scent presented during a series of choice tests.

Chemically complex mixtures of volatile and nonvolatile compounds (Belcher et al. 1990; Hurst et al. 1998), deposited as glandular secretions, urine, faeces or saliva, broadcast information in the absence of the signal sender (Mykytowycz 1970; Thiessen & Rice 1976). In relatively asocial species, this chemical matrix may contain information about sex, physiological and reproductive state (Swaisgood et al. 2000; Ferkin et al. 2004), territorial ownership (Hurst 1989; Brashares & Arcese 1999; Roberts & Dunbar 2000), and family membership (Buesching et al. 2002) or individual identity (Johnston & Jernigan

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1994; Hurst et al. 2001). Scent marks also encode information about individual quality, such as dominance (Thomas 2002), parasite load (Kavaliers et al. 2004; Zala et al. 2004) or MHC type (Penn 2002; Leinders-Zufall et al. 2004). As scent marking is costly (Gosling et al. 2000; Roberts et al. 2001), both the qualitative and quantitative properties of olfactory cues can provide honest information about the signaller's competence (Rich & Hurst 1998, 1999; Gosling & Roberts 2001). Thus, scent signals may function as sexually selected characteristics (Blaustein 1981; Penn & Potts 1998) that potentially influence mate choice (Roberts & Gosling 2003; Brennan 2004; Neff & Pitcher 2005).

Scent marks also may encode similar information in social species. For instance, ground squirrels use odour cues for kin recognition, suggesting a mechanism for nepotistic behaviour and inbreeding avoidance (Mateo 2002, 2006). Hyaenas scent-mark to advertise occupancy of a territory (Mills & Gorman 1987) and convey information about sex, individual identity, and possibly reproductive state (Drea et al. 2002a, b). Likewise, various primates rely on scent to assess a signaller's reproductive state, dominance status, or individual identity (strepsirrhines: Mertl 1975; Harrington 1976, 1977; callitrichids: Belcher et al. 1986; Epple et al. 1993; Ziegler et al. 1993, 2005; Smith et al. 1997; Ferris et al. 2004) and modulate the reproductive competence of conspecifics (strepsirrhines: Schilling et al. 1984; Perret 1992; callitrichids: Abbott 1984).

In both social and asocial species, the efficacy of a chemical cue depends on several factors, including its information content, the latency between signal deposition and detection, signal 'purity', and the physiological state of both the signal sender and receiver. Incorporating visible signs of scent marking (e.g. scrapings: Allen et al. 1999; tree gouging: Miller et al. 2003) may draw additional attention to a mark in the absence of the signaller. In social species, however, marking often occurs in view and earshot of conspecifics (Lazaro-Perea et al. 1999), permitting the integration of distinct behavioural, visual, or acoustic cues with olfactory deposition. Thus, information transmission in social taxa may rely on multicomponent, context-dependent signals (see reviews in: Rowe 1999; Candolin 2003).

Ringtailed lemurs represent an especially appropriate system for the study of chemical signalling. They show the most complex social organization among strepsirrhine primates, living in multimale-multifemale groups (Jolly 1966) characterized by unambiguous female social dominance over males (Kappeler 1990a). They cannot produce the complex facial expressions that characterize most anthropoids, but retain a functional vomeronasal organ, have a highly developed suite of sexually dimorphic scent glands, and rely on olfactory communication as a primary sensory modality (Schilling 1979; Martin 1990). Females retain the typical mammalian reproductive pattern, showing a brief, seasonal oestrus, with few visual signs of ovulation (Evans & Goy 1968). Mating and sociosexual behaviour do not occur outside of oestrus; nevertheless, females may mate multiply during this period (Koyama 1988; Sauther 1991; Parga 2006b). Thus, ringtailed lemurs represent an evolutionary intermediary between 'ancestral' rodent-like mammals that communicate primarily via chemical signals and in which female receptivity is strictly mediated by hormones, and the more 'derived' simian primates that communicate primarily via visual signals and in which females display situation-dependent receptivity (Hrdy & Whitten 1987).

Ringtailed lemurs display an unusually complex scent-marking repertoire (Jolly 1966; Schilling 1974); males have three species-specific scent glands (Fig. 1), each of which is used in a distinct manner. During 'wrist marking', males draw their antebrachial organ across a substrate, gouging the substrate as the secretion is deposited and producing an audible clicking sound from the spur. 'Shoulder rubbing' involves mixing the secretions of the male antebrachial and brachial organs by pressing each

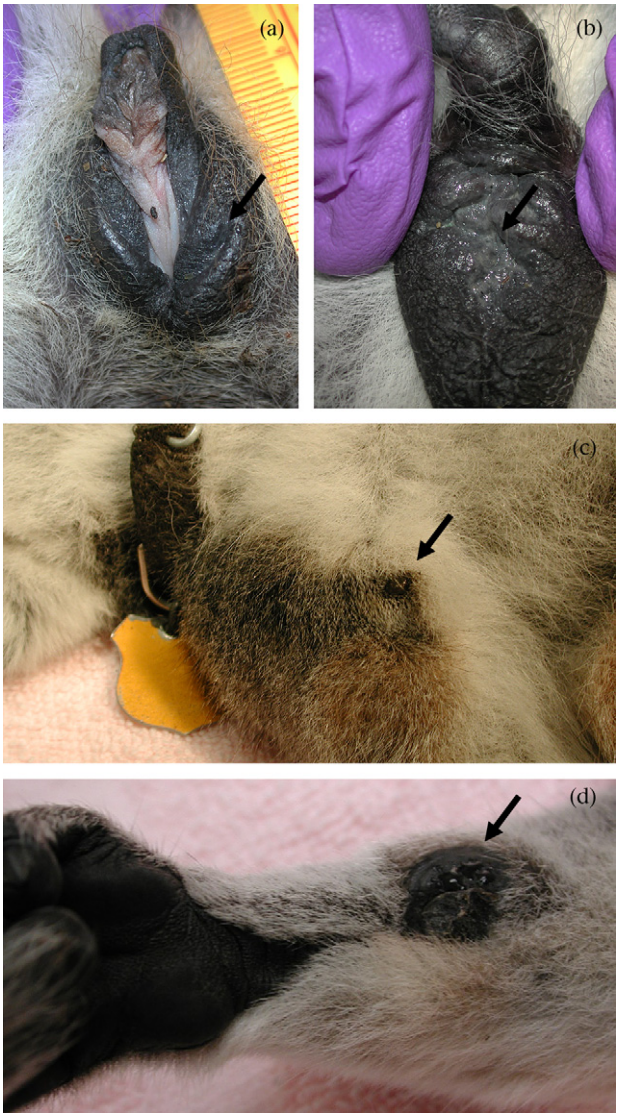

Figure 1. Photographs of the scent glands and glandular secretions of adult ringtailed lemurs. (a) Female ringtailed lemurs have a glandular field in the folds of their labia majora. Male ringtailed lemurs have species-specific (b) scrotal, (c) brachial and (d) antebrachial glands, each of which produces a unique scent. Note the greasy brown secretion from the brachial gland and the clear droplets from the antebrachial gland (adjacent to the antebrachial spur).