



Latrine behaviour as a multimodal communicatory signal station in wild lemurs: the case of *Hapalemur meridionalis*



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Latrine behaviour is the repeated use of specific sites for defecation/urination, and is common among most mammals, including carnivores, herbivores, marsupials and rodents. While rare among primates, latrine use has been observed among some lemurs. It has been hypothesized that group-living primates may use latrines to maintain intergroup spacing (i.e. territorial defence) and for female advertisement of sexual condition. To test these, we conducted focal follows of three neighbouring southern bamboo lemur, *Hapalemur meridionalis*, groups in Mandena littoral forest of southeast Madagascar. From January to December 2013, we recorded all occurrences of latrine behaviour and characterized latrine sites to determine what factors influenced returning to specific latrines. Additionally, we attempted to elucidate the functional role of scent marking at latrines. We assessed the degree of home range overlap between neighbouring groups, and recorded intergroup aggression. Overall, latrines were almost exclusively visually conspicuous sites and located in the core areas of group home ranges. Best-fit models indicated that multiply visited latrines occurred more often in core areas, and were influenced by both sexes. Glandular scent marking at latrine sites was driven by males, and occurred more during the nonmating season. Males overmarked female scent-marks less often during the mating season and more often when younger males were likely to disperse. Thus, overmarking at latrine sites may function as a mate-guarding strategy to deter new males. Latrine use supports the energy frugality hypothesis, which proposes that lemur social systems, known for female social dominance and low rates of agonism, evolved as responses to the low productivity of Malagasy forests. The deposition of olfactory cues (i.e. faeces, urine, glandular secretions) at visually conspicuous sites may convey information to neighbouring conspecifics, thus reducing the need for intergroup agonism. Overall, latrine behaviour acts as a multimodal means of intergroup communication.

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Latrine behaviour is defined as the repeated use of specific sites for defecation/urination in such a way that excretory waste products accumulate either on arboreal, terrestrial or subterranean substrates (Irwin, Samonds, Raharison, & Wright, 2004). Utilization of latrine sites is often understood as a means of olfactory communication (Brown & MacDonald, 1985; Gorman & Trowbridge, 1989; Kleiman, 1966), with recent evidence suggesting it is an ancestral communicatory strategy predating mammalian synapsids (Fiorelli et al., 2013). Today, many mammals retain this behaviour (reviewed in Dröscher & Kappeler, 2014), including carnivores (e.g. Ben-David et al., 2005; Darden, Steffensen, & Dabelsteen, 2008; Gorman & Mills, 1984; Gorman & Trowbridge,

1989; Hulsman et al., 2010; Jordan, Cherry, & Manser, 2007; Kilshaw, Newman, Buesching, Bunyan, & MacDonald, 2009; MacDonald, 1980; Nel & Bothma, 2002; Oldham & Black, 2009; Roper et al., 1993), herbivores (e.g. Black-Decima & Santana, 2011; Brashares & Arcese, 1999; Linklater, Mayer, & Swaisgood, 2013; Marnewick, 2013; Wronski, Apio, & Plath, 2006; Wronski & Plath, 2010), marsupials (e.g. Oakwood, 2002; Ruibal, Peakall, & Claridge, 2011; Runcie, 2004) and rodents (e.g. Francescoli, 2000; Woodroffe & Lawton, 1990), but it is rare among primates (e.g. Dröscher & Kappeler, 2014; Irwin et al., 2004). Chemical communication (via olfaction) is the most commonly postulated function for latrine use (Dawkins & Krebs, 1978; Dröscher & Kappeler, 2014; Eisenberg & Kleiman, 1972; Schilling, 1979). Adaptive reasons for latrine use include intra- and interspecific communication (Gorman & Trowbridge, 1989; Jordan et al., 2007), improving reproductive success (Jordan, 2007; Ruibal et al., 2011), avoidance

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of endoparasite transmission/reinfestation (Ezenwa, 2004) and avoidance of detection by predators (Boonstra, Krebs, & Kenney, 1996).

Although primates primarily rely on visual and auditory communication, olfaction also appears to be important for strepsirrhine primates, allowing individuals to receive chemical information from a conspecific signaller who may no longer be present in the immediate area (Alberts, 1992; Colquhoun, 2011; Eppele, 1986). Similar to other mammals, strepsirrhine chemical signals are transmitted via secretions from scent-producing skin glands, saliva, faeces and/or urine deposited on substrates, conspecifics and/or self-anointed (Colquhoun, 2011; Eppele, 1986; Lewis, 2005; Nievergelt, Mutschler, & Feistner, 1998; Schilling, 1979, 1980), and can occur in conjunction with latrine use (Dröscher & Kappeler, 2014; Irwin et al., 2004). Thus far, observations of latrine use have been recorded in three distinct strepsirrhine genera, i.e. *Cheirogaleus* (Ganzhorn & Kappeler, 1996; Petter, 1962), *Lepilemur* (Charles-Dominique & Hladik, 1971; Dröscher & Kappeler, 2014; Irwin et al., 2004) and *Hapalemur* (Eppley & Donati, 2010; Irwin et al., 2004).

Among the possible functions of latrine use by lemurs, several nonmutually exclusive hypotheses have been proposed (Irwin et al., 2004). The first hypothesis postulates that the repeated use of concealed defecation sites may act as an antipredator strategy by impairing the ability of a potential predator to detect prey (Boonstra et al., 1996; Viitala, Korpimäki, Palokangas, & Koivula, 1995); alternatively, obscured sites may be used to prolong the duration of the signal by protecting the excretory waste products from climatic events (Crowley, Johnson, & Hodder, 2012). A second hypothesis states that they provide a system of territorial demarcation, whereby faecal/urine deposits are placed around home range boundaries to act as a delineation of the territory, i.e. intergroup spacing (Brashares & Arcese, 1999; Stewart, MacDonald, Newman, & Cheeseman, 2001), similar to glandular scent-marking strategies observed in some lemur genera (Mertl-Millhollen, 1979, 2006). Although many mammalian species use latrines with the functional role of providing territorial defence, the deposition of glandular secretions in addition to faeces/urine can provide additional chemical information (Brown & MacDonald, 1985; Gorman, 1990; Gorman & Trowbridge, 1989; Gosling, 1982; MacDonald, 1980). As such, a third hypothesis is that latrines may strategically serve to advertise sexual condition via olfactory cues (Gorman, 1990; Woodroffe & Lawton, 1990). Specifically, females have been shown to increase their use of, and subsequent scent marking at, latrine sites during periods when they were sexually receptive (Kruuk, 1978; Peters & Mech, 1975; Roper, Shepherdson, & Davies, 1986; Stewart, MacDonald, Newman, & Tattersall, 2002). Among meerkats, *Suricata suricatta*, evidence of male-biased glandular scent marking at latrines suggests that they serve a subsidiary role in mate defence. Male meerkats not only scent-mark more than females but also preferentially overmark female scent-marks (Jordan, 2007; Jordan et al., 2007). As a fourth hypothesis, 'overmarking', i.e. a secondary scent marking, involves placing a glandular scent-mark directly on top of a previous mark so as to potentially disguise the presence of females in the territory from neighbouring or dispersing males, acting as a mate-guarding strategy (Jordan et al., 2007; Lewis, 2005; Rich & Hurst, 1998). Similar behaviour has been observed in both European badgers, *Meles meles*, and honey badgers, *Mellivora capensis*, showing distinct sex and seasonal differences (Begg, Begg, Du Toit, & Mills, 2003; Kruuk, 1978; Roper et al., 1986, 1993). Lastly, a fifth hypothesis states that advertising local resource use may assist intragroup spacing (Kruuk, 1992); however, this is unlikely within cohesive groups as there would be no need to signal resource use (Irwin et al., 2004).

While systematic tests on the functional role of terrestrial latrines in lemurs are available for solitary foragers (Dröscher & Kappeler, 2014), the possible function of this behaviour for group-living species, such as bamboo lemurs (*Hapalemur* spp.), remains little understood (Eppley & Donati, 2010; Irwin et al., 2004; Petter & Peyrieras, 1970). We therefore aimed to test predictions for the function of latrines via the first systematic study of latrine behaviour by a group-living strepsirrhine, the southern bamboo lemur, *Hapalemur meridionalis*. Eppley and Donati (2010) previously noted *H. meridionalis* displaying a preference for utilizing large stilt-rooted trees, specifically within the genus *Uapaca* (Family Euphorbiaceae), as latrine sites. As such, (1) if latrine sites are intended to be hidden from potential predators or climatic events, we would predict a significant portion of defecation/urination to occur under stilt-rooted trees and other horizontal substrates (i.e. liana tangles, fallen trees) so as to obscure the accumulated excretory wastes. Furthermore, (2) if latrines and/or glandular scent marking at latrines are used for territorial defence, we would expect them to be located in larger proportions throughout the noncore areas rather than concentrated in the core areas of their home ranges. Conversely, the establishment of latrine sites in equal proportions, i.e. densities, in core and non-core areas of bamboo lemur home ranges may be a strategy to increase the likelihood with which neighbouring or intruding individuals encounter the latrine sites (Gosling, 1981). (3) If latrine use and glandular scent marking function in advertising sexual condition, we would predict an increase in these behaviours by females near or during the mating season (June–July) when southern bamboo lemur females become sexually receptive. Additionally, (4) if overmarking glandular scent-marks functions in mate guarding, we would predict directional male–female overmarking to occur during the mating season so as to deter intruding males.

METHODS

Ethical Note

All data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. This research was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherche N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

Study Site and Species

Our study was conducted in Mandena (24°95'S 46°99'E) in the extreme southeast of Madagascar, approximately 10 km north of Fort-Dauphin (Tolagnaro). This protected area consists of 148 ha of fragmented and degraded littoral forest with approximately 82 ha of interspersed, seasonally inundated swamp (Ganzhorn et al., 2007). Littoral forests occur within 3 km of the coast, characterized by a typically low canopy growing on sandy substrate (Dumetz, 1999).

Southern bamboo lemurs are medium-sized (1.072 ± 0.107 kg) cathemeral lemurs characterized by folivory and female dominance (Eppley, Ganzhorn, & Donati, 2015; Eppley, Hall, Donati, & Ganzhorn, 2015; Eppley, Verjans, & Donati, 2011). They maintain small social groups with typically one to two adult males and one to two breeding adult females that are generally in constant daily contact with one another. In Mandena, southern bamboo lemur groups average (±SD) 5.6 ± 1.5 individuals ($N = 5$; Eppley, Donati,

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