



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,

Ramanamanjato, et al., 2015). Most lemuriformes, including *Hapalemur* spp., exhibit seasonal reproduction which is typically entrained by photoperiod (Wright, 1999). It has been reported that close congeners, e.g. *Hapalemur griseus*, mate between June and July, experiencing a gestation length of approximately 130–140 days (Tan, 2006; Wright, 1990). Although we never observed copulation during the study period, infants in the three groups were first observed in mid-November, validating a similar gestation length. We therefore group June–July together as ‘mating season’ as females would probably be sexually receptive at some point during this time, while all other months are allocated to ‘nonmating season’.

Ten adult *H. meridionalis* (five females, five males) across four neighbouring social groups were captured between October and December 2012 by an experienced Malagasy technician via Telinect blow darts containing 4 mg/kg of either Ketamine (ketamine hydrochloride) or Zoletil (tiletamine and zolazepam). Differences in anaesthesia sedatives used were due to the limited quantities available. Only adults without dependent infants were captured and all animals recovered from anaesthesia within 1.5 h at the capture site and were followed for approximately 1 h until they regained full mobility. There were no injuries as a consequence of the captures, nor did we observe any short-term or long-term effects as a result of these manipulations. As this species is highly cryptic and difficult to locate, individuals were fitted with external radiotransmitters (ARC400, Advanced Telemetry Systems, Isanti, MN, U.S.A.) secured via a neoprene collar looped through PVC tubing and fastened with a small nut/bolt. The total weight per transmitter tag and collar attachments was 38 g (ranging from 2.9 to 4.2% of total body mass for the heaviest and lightest individuals, respectively). These tags were slightly larger than standard VHF radiocollars due to their data-logging abilities (see Eppley, Donati, & Ganzhorn, 2015), but they allowed us to expedite the habituation period by making it easier to locate and follow groups (Juarez, Rotundo, Berg, & Fernández-Duque, 2011). In addition, a colour-coded pendant was attached to assist in individual identification. We removed radiocollars at the end of the study in December 2013 following the same protocol.

Behavioural Data

From January to December 2013, we conducted full-day focal follows (from sunrise to sunset) for approximately 5 days/month for three of the social groups, i.e. groups 1, 2 and 4 (Table 1). All individuals were well habituated and so it was rare that a focal subject was out of sight for >5 min. Home range data were collected via GIS coordinates recorded with a Garmin GPSMAP 62S unit every 15 min throughout the focal follow. Conversely, group 3 was located biweekly for approximately 2 h to exclusively collect home range data via the same waypoint sampling; however, behavioural focal sampling was not conducted on this group due to time constraints. All bamboo lemurs were categorized by age/sex class (Table 1) with all adult individuals in each group sampled at least once each month, collecting both instantaneous and continuous focal sampling data for concurrent studies (Altmann, 1974).

During daily follows of a focal subject, all latrine sites visited (i.e. specific locations involving defecation/urination) were flagged and given a unique code. In addition, their GIS coordinates were recorded. As bamboo lemurs travel as a cohesive group, they often arrived and departed from latrine sites at approximately the same time (± 15 s). Thus, we were able to directly observe and to collect the relevant behavioural data on all individuals within the group visiting the latrine site. We also noted whether previous faeces had accumulated here, which could

range from two to more than 50 faecal deposits. These were easily identifiable as *Hapalemur* faeces given the typically green coloration and fibrous content, due to this species' dietary reliance on grasses and lianas (Eppley, Donati, et al., 2015; Eppley et al., 2011); the only similarly sized lemur in this forest (*Eulemur collaris*) does not use latrines (G. Donati, personal observation) while carnivores of similar size are also very rare in this fragmented area. It is possible that the remaining defecation/urination sites were visited less frequently and thus any accumulated faecal material may have been subject to faster degradation and decomposition, an issue that also may be due to habitat differences (i.e. swamp versus littoral forest) within Mandena. Regardless, sites that had no accumulation of faeces yet, but were observed to be used collectively by the entire focal group for defecation/urination, were included in our analyses. Microhabitat data for each of these sites was recorded by T.M.E., specifically noting scientific family, genus and species of the tree from which the latrine was accessed, and its dimensions, e.g. diameter at breast height (DBH), height (m) and crown volume (m^3). Crown volume was estimated as an ellipsoid via the crown height and two crown diameters, i.e. maximum and perpendicular widths.

We sought to determine whether stilt-rooted *Uapaca* spp. trees selected as latrine sites were significantly different in their dimensions from individuals of the same species sampled in our botanical plots. As part of a larger ecological research project, we established 100 m^2 (20 \times 50 m) botanical plots ($N = 20$), using the same metrics described above so as to characterize the Mandena habitats (Henderson, 1999). Plots were then used for comparison with the latrine sites to gain an understanding of site selection preferences by the bamboo lemurs.

In addition, we distinguished between nondescript latrine sites (i.e. latrine sites that are indistinguishable from other common sites within the forest) and visually conspicuous latrines (i.e. latrine sites that are characterized by horizontal and/or oblique substrates along or just above the ground). In more detail, we classified stilt-rooted *Uapaca* spp. trees, large terrestrial liana tangles and fallen/horizontal trees as visually conspicuous latrine sites.

From June 2013 to December 2013, we recorded two additional behaviours including the act of, and sequential order of individuals, glandular scent marking at latrine sites. Specifically, we recorded instances of scent marking immediately before and/or after defecation/urination at a latrine site, i.e. on the woody substrate directly above or immediately adjacent to the latrine (≤ 2 m). Scent-marking behaviour in *H. meridionalis* is similar to what has been described for *Hapalemur alaotrensis* (Nievergelt et al., 1998), and so we employed the same definition. Although scent marking does occur at nonlatrine sites, we did not record these and are thus unable to include them in our analyses.

Furthermore, we recorded all instances of intergroup agonism, specifically noting when groups defended their home range by vocalizing, chasing and occasionally biting intruding neighbouring groups and roaming/dispersing individuals. These occurrences were analysed monthly so as to gain a greater understanding of intergroup agonism and how this may influence territorial defence.

Data Analyses

All ranging and latrine data were entered into ArcGIS 10.2 (ESRI) using the Geospatial Modelling Environment (GME) spatial ecology interface (Beyer, 2012) with R statistical software version 3.1.2 (R Development Core Team, 2014). We determined each group home range with a 95% kernel density estimate while prescribing a core area as having a 50% kernel density estimate

(Worton, 1989). The location of each latrine site was categorized as either within or outside the core area of each group home range; this allowed us to determine whether the density of latrine distribution was uniform throughout their range. Additionally, using the 95% kernel density estimate we calculated the amount of home range area that overlaps between all groups to understand the degree of territoriality this species exhibits. Furthermore, to examine selection preferences for latrine sites, we used a *t* test to determine whether specific tree metrics differed significantly from those obtained from botanical plots. We then used a nonparametric chi-square to test whether the frequency of use of nondescript and visually conspicuous latrine sites differed from a uniform distribution.

To determine which factors influenced the repeated use of latrine sites, we fitted generalized linear mixed-effects models (GLMM) in R statistical software (R Development Core Team, 2014) using the *glmer* function of the *lme4* package (Bates, Maechler, & Bolker, 2012), with preferred latrines as a binomial dependent variable. We define preference latrines as those sites that are visited multiple times (i.e. more than once) by a focal group. By creating this dichotomy, we were able to investigate specifically what influenced bamboo lemurs to return to latrine sites. As groups are cohesive units, both males and females often visit latrines together, although they do not always display latrine behaviours at each site. Because of this, we tested each sex separately. Male latrine behaviour was perfectly collinear with preference sites as males defecated/urinated on each occasion of visiting a preference latrine. As a result, models to explain variation in preferred latrines were unable to obtain reliable estimates of the conditional standard error (Hauck & Donner, 1977). To circumvent this issue, we ran two separate GLMMs, the first with a data set limited to male-used latrines and the second with the full data set where 'males' was not included as a fixed effect. Fixed effects that were included in various combinations and interactions were location (i.e. noncore area or core area), season (i.e. nonmating or mating season), type (i.e. nondescript or visually conspicuous), and whether at least one adult male (0/1) and/or adult female (0/1) member of the group utilized the visited latrine site. Groups were included as a random effect. We then used the *anova* function to calculate likelihood ratio tests for model comparison and determined which model had the most explanatory power by comparing the Akaike's information criterion (AIC) for all of the possible models.

While latrine behaviour alone may provide chemical communication between individuals and/or groups, we wanted to consider the role of scent marking at latrine sites separately. To do this, we examined which factors influence the use of scent marking by bamboo lemurs during each latrine occurrence. We used the proportion of individuals in a group (limited to adult individuals) that scent-marked at a latrine as a continuous response in linear mixed models (LMMs). Similar to the previously described GLMM, we included location, season, type, male, female

and preference site as fixed effects in various combinations and biologically relevant interactions. To determine whether scent marking was largely driven by males or females, both factors were included separately as fixed effects but never together in the same model. We also included a full model which contained all of the fixed effects and a null model that contained only the random effect, which in this case was the social groups ($N = 3$). The *anova* function was again used to calculate likelihood ratio tests and determine which model best fitted the data by comparing AIC for all possible models. All models were fitted using the *lmer* function of the *lme4* package (Bates et al., 2012) and *P* values were obtained with a likelihood ratio test using the *afex* package (Singmann, 2014), both developed for R statistical software (R Development Core Team, 2014).

Lastly, we examined the potential factors that may influence an individual to overmark the scent-mark of a conspecific from their group. All of our observations were limited to males overmarking female scent-marks. Using each group level latrine occurrence as our unit of analysis, we ran a GLMM to determine which factors best predicted whether overmarking a conspecific scent-mark would occur during a latrine site visit (e.g. at least one male group member overmarking the deposited scent-mark of at least one female group member during the same visit). Our fixed effects included location, season, preference site and latrine type. Once again, group was controlled for as a random effect and we followed the same procedure previously described.

All other statistical analyses were performed using PASW 21.0 (IBM, Inc., Armonk, NY, U.S.A.) with significance considered at $P < 0.05$. We tested for the normality of the residuals and the presence of outliers both for the LMM and the *t* tests using the Kolmogorov–Smirnov test. Data for the *t* tests were entered into parametric analyses after log transformation as they were not all normally distributed.

RESULTS

General Latrine Behaviour

Focal observations of *H. meridionalis* totalled 1762 h across the three groups, during which time we recorded latrine behaviour 429 times across 282 latrine sites. Of these, 92.55% were observed to have previous faeces, e.g. piled, hardened and/or decomposing fibrous material. Females initiated latrine use on 52.45% of occasions, males initiated use on 25.87% and juvenile individuals initiated use on 21.68% of all occurrences. Bamboo lemurs frequently visited latrine sites as a cohesive group; however, we only included those individuals that defecated/urinated at a specific site as having displayed latrine behaviour. Considering this, 73.43% of all latrine site observations included more than one individual, while 36.36% included greater than or equal to half of group individuals. Furthermore, 29.79% of the latrine sites were visited more than once, constituting 53.85% of observed defecations during the study. The mean (\pm SE) height of *H. meridionalis* defecation was 0.41 ± 0.02 m ($N = 429$), with 95.57% of observations occurring between 0 and ≤ 1 m from the ground. Interestingly, 6.10% of the total latrine occurrences involved the lemurs descending directly onto the ground.

Antipredator and Defence from Climatic Event Hypothesis

Southern bamboo lemurs were highly selective when choosing latrine sites, with conspicuous latrine sites (i.e. *Uapaca* spp. trees, large terrestrial liana tangles and fallen trees) constituting 86.62% of all sites, while the remaining 13.38% of latrine sites were nondescript. The lemurs appeared to favour visually conspicuous

Table 1
Group composition of habituated *H. meridionalis* in Mandena

Group	Total	Adult ♀	Adult ♂	Juvenile ♀	Juvenile ♂	Infant ^a
1	3–5	3	1	1		2
2	3–4	1	1		1	1
3	4–5		3	2		
4	8–9	2	2	1	2	2

Total column represents the number of animals within the social group observed each month from January to December 2013.

^a Infant refers to dependent offspring.

latrine sites compared to nondescript latrine sites ($\chi^2_1 = 150.48$, $P < 0.001$). Furthermore, *Uapaca* tree latrine sites were found to have a significantly larger DBH ($t_{134} = 3.783$, $P < 0.001$), height ($t_{134} = 2.241$, $P = 0.027$) and crown volume ($t_{134} = 2.135$, $P = 0.035$) compared to the *Uapaca* spp. metrics obtained from our botanical plots. In fact, *Uapaca* spp. presence within the Mandena littoral forest constituted only 1.51% ($N = 22$) of trees in our botanical plots.

Territorial Defence Hypothesis

We used 95% kernel analysis and found that home range sizes varied: group 1 = 18.39 ha; group 2 = 17.66 ha; group 3 = 6.60 ha; group 4 = 10.43 ha. Home range overlap between groups was minimal, yet all of these overlapping areas did contain latrines, some of which were mutually utilized by groups (Table 2). It is plausible that group 4 shared a few latrines with group 3; however, since we did not conduct true focal follows on group 3 we cannot be certain that they visited these latrine sites that fell within their buffer zone.

Core areas (50% kernel estimate) were analysed for group 1 (7.76 ha), group 2 (3.74 ha) and group 4 (2.09 ha). For each of these areas, multiple latrines were found within the core areas of each group, constituting 29.9% of all latrines in group 1, 35.1% of latrines in group 2 and 36.1% of latrines in group 4. However, the density of latrine sites was higher in the core areas (8.54 ± 3.83 latrines/ha) than in the noncore areas (3.98 ± 0.21 latrines/ha) of group home ranges.

From January to December 2013, only 13 intergroup agonistic conflicts were recorded, resulting in an overall monthly average (\pm SE) of 0.008 ± 0.002 intergroup agonistic events/h. Monthly averages (\pm SE) of intergroup agonism were very low across all three groups (group 1: 0.01 ± 0.004 /h; group 2: 0.007 ± 0.003 /h; group 4: 0.007 ± 0.004 /h).

Preference Site

The best-fit model to explain the repeated use of a latrine site by male lemurs included location and type as significant predictors (AIC = 509.65, $\chi^2_1 = 12.05$, $P < 0.001$). The male-visited preference sites were significantly more likely to occur in the core area of the group home range, while males also appeared to select the nondescript latrine type more often (Table 3).

Considering the entire data set for preference latrine sites and using the same fixed effects (now including females but removing males), the best-fit model included location and female use as significant predictors (AIC = 544.97, $\chi^2_1 = 10.14$, $P = 0.001$). Similar to males and thus not driven by one sex, females were shown to significantly return to preference latrine sites, and overall these sites were characterized by occurring within the core areas of group territories (Fig. 1). Unlike the male-used latrines, the latrine type had no significant influence on whether a site would be more likely

to be used multiple times (Table 4). Season had no effect on whether lemurs would utilize a preference site.

Advertising Sexual Condition Hypothesis

Glandular scent-marks were often observed to be deposited along the stilt-root of a *Uapaca* tree or a portion of liana within a large terrestrial liana tangle that was located directly over the accumulated faeces. Bamboo lemurs damage a substrate (e.g. the bark of a stilt-root from a *Uapaca* tree) by scratching it with their lower front dentition. In the case of male individuals, they then rub their antebrachial glands against their brachial glands, followed by smearing their antebrachial glands across the damaged spot (e.g. the scrape or notch) that exists on the woody substrate. Females have less pronounced antebrachial and brachial glands, and instead mark the substrate with their anogenital region by sitting several times along the substrate, while on rare occasions depositing urine in conjunction. Scent marking was observed during 71.53% of the 281 latrine behaviour occurrences between June and December 2013. The average frequency (\pm SD) of scent marking occurring at a latrine site during the nonmating season was 0.46 ± 0.17 compared to an average frequency (\pm SD) of 0.40 ± 0.18 during the mating season. We used a linear mixed model (LMM) to determine which factors best predicted a greater proportion of group individuals to scent-mark at a latrine site. The best-fit model for increased proportion of scent-marking group members at latrine sites (AIC = -66.222, $\chi^2_1 = 181.75$, $P < 0.001$) was predicted by nonmating season and was largely driven by males (Table 5).

Mate-Guarding Hypothesis

Bamboo lemurs were observed to overmark, occasionally referred to as counter-marking, whereby an individual scent-marks directly on top of a previously deposited glandular scent-mark. Of the observed latrine occurrences between June and December 2013, males overmarked 40.79% of the sites previously scent-marked by females. This involved one or more males immediately counter-marking directly on top of a female scent-mark, whereas we never observed the reciprocal direction. A comparison of the overmarking events at latrine sites shows an average frequency (\pm SD) of 0.15 ± 0.11 overmarks during the mating season whereas we observed an average frequency (\pm SD) of 0.39 ± 0.18 overmarks during the nonmating season. To determine which factor or combination of factors and interactions best predicted this behaviour, we performed a GLMM. The model with the best predictive value (AIC = 311.15, $\chi^2_1 = 22.63$, $P < 0.001$) shows that overmarking was more likely to occur in the nonmating season (Table 6) while the other fixed effects and/or interactions played little to no role.

Table 2

Percentage of territorial overlap between groups, number of latrine sites within overlap area and number of latrine sites utilized by both groups

Groups	Overlap area 95% kernel (ha)	Unique latrines			Shared latrines	
		Group 1	Group 2	Group 4	N	Times used
1 & 2	0.42	2	2	–	3	12
1 & 4	1.40	14	–	11	5	18
3 & 4	0.30	–	–	4	–	–

There was no area of overlap between groups 1 & 3 and 2 & 4.

Table 3

Generalized linear mixed model with the best explanatory predictors for returning to a latrine site multiple times relative to males

Variable	β	SE	Z	P
Fixed effects ^a				
Intercept	0.6336	0.3758	1.686	0.092
Location	0.7763	0.2268	3.424	<0.001
Season	0.3342	0.2545	1.313	0.189
Type	-0.7162	0.3499	-2.047	0.041
Random effects				
Group	Variance	0.3496		

Bold indicates factors significant at $P < 0.05$.

^a Data set limited to male-visited latrine sites as the fixed effect 'Male' was perfectly collinear with preference site latrines.

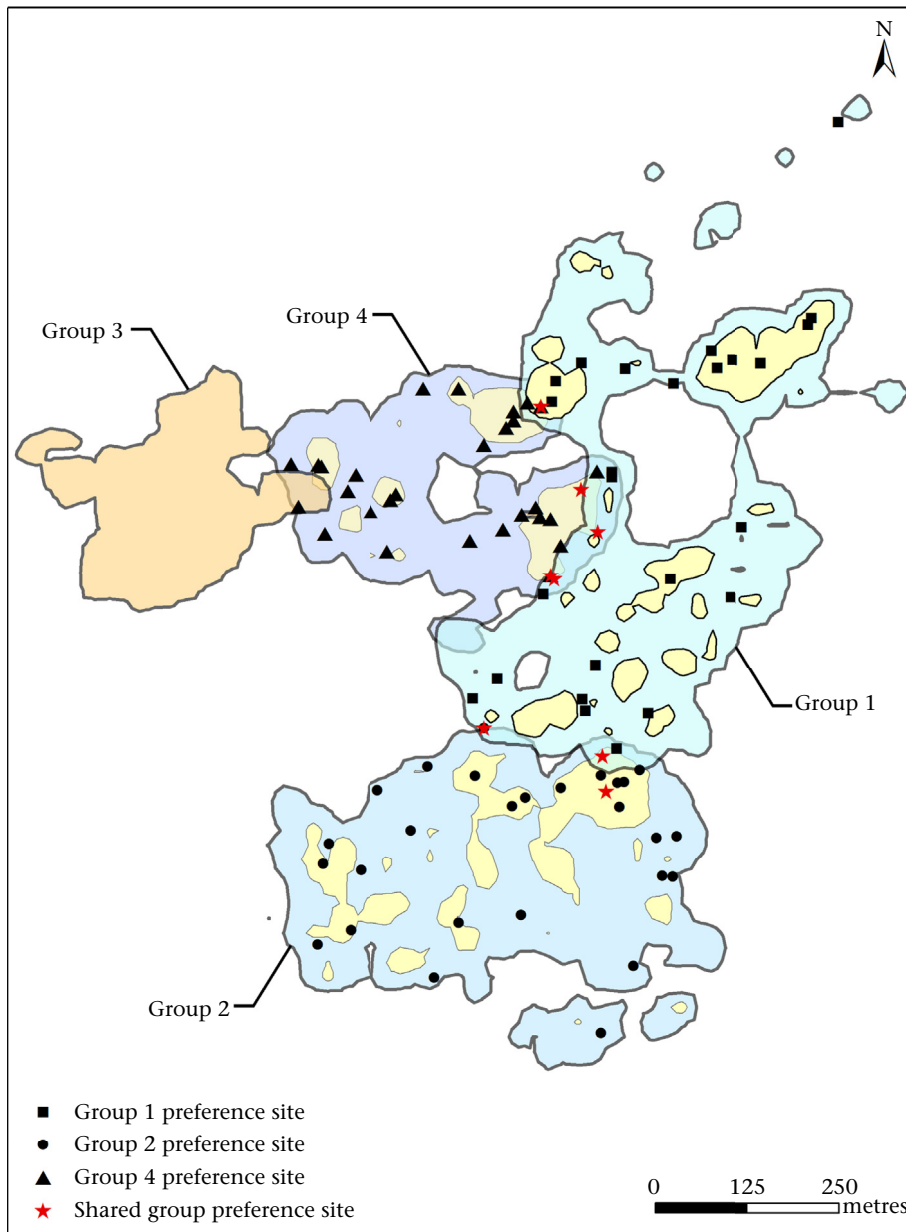


Figure 1. Home ranges (95% kernel) and core areas (50% kernel) of *Hapalemur meridionalis* focal groups at Mandena between January and December 2013. Various points indicate latrine preference sites for each group as well as latrine sites shared between groups. Group 3 is included here to display the degree of home range overlap.

Table 4
Generalized linear mixed model for latrine preference sites

Variable	β	SE	Z	P
Fixed effects				
Intercept	-1.0902	0.4892	-2.229	0.026
Location	0.6947	0.2200	3.158	0.002
Season	0.1715	0.2402	0.714	0.475
Type	-0.5610	0.3322	-1.689	0.091
Female	1.6710	0.3549	4.708	<0.001
Random effects				
Group	Variance	0.3895		

Bold indicates factors significant at $P < 0.05$.

Table 5
Linear mixed model predicting proportion of adult group members scent marking at latrine sites

Variable	β	SE	95% CI	t	P
Fixed effects					
Intercept	0.076	0.115	-0.16–0.31	0.659	0.54
Preference site	0.084	0.069	-0.05–0.22	1.218	0.65
Type	0.043	0.066	-0.08–0.17	0.659	0.45
Season	-0.029	0.041	-0.11–0.05	-0.699	0.003
Male	0.507	0.037	0.44–0.58	13.75	<0.001
Preference site*type	-0.079	0.074	-0.22–0.06	-1.072	0.33
Season*male	-0.158	0.054	-0.26– -0.05	-2.918	0.70
Random effects					
Group	Variance	0.158			
Residual	Variance	0.206			

Fixed effects that were not part of the best-fit model (location, female) are not included in this table. P values (significant at $P < 0.05$, indicated in bold) were obtained using likelihood-ratio test. CI: confidence interval.

Table 6
GLMM best fit model for occurrence of male overmarking female scent-marks at latrine sites

Variable	β	SE	Z	P
Fixed effects				
Intercept	−0.3070	0.4058	−0.757	0.449
Location	−0.4257	0.2953	−1.442	0.149
Season	−1.3575	0.3184	−4.263	<0.001
Random effects				
Group	Variance	0.6106		

Fixed effects that were not part of the best-fit model (preference site, type) are not included in this table. Bold indicates factors significant at $P < 0.05$.

DISCUSSION

Antipredator and Defence from Climatic Event Hypothesis

While the cryptic nature (Tan, 2006) and cathemeral activity pattern of *Haplemur* spp. (Eppley, Ganzhorn, et al., 2015; Mutschler, 1999) may result in an effective antipredator strategy, latrines may also constitute a similar strategy. Our data showed an overwhelming majority of latrine sites situated under a low, horizontal substrate, possibly concealing their faeces/urine. While this may theoretically act as a safeguard against predation by impairing the ability of potential predators to detect the prey population (Boonstra et al., 1996; Viitala et al., 1995), it cannot be ruled out that these latrine locations were selected to protect the accompanying chemical cues from environmental influences (e.g. sun and/or rain), thereby prolonging its olfactory impact (Crowley, Johnson, & Hodder, 2012).

Territorial Defence Hypothesis

Our findings do not support latrine behaviour, nor glandular scent marking at latrines, among *H. meridionalis* as a means for territorial defence by having latrine sites disproportionately concentrated in the core areas of group home ranges. Additionally, our best-fit models predict that latrines within the core area of a group home range are more likely to be visited multiple times, i.e. preference sites. This was not influenced by one sex; rather both males and females visited these sites significantly more often than nonpreference sites. While these data lack support for previous assertions that latrines would be placed in the noncore areas so as to demarcate mammalian territories (Brashares & Arcese, 1999; Jordan et al., 2007; Stewart et al., 2001), their utilization within both areas of the home range may be better understood when considering other factors, specifically the latrine type.

Bamboo lemurs often selected visually conspicuous locations to function as their latrine sites, specifically, stilt-rooted *Uapaca* spp. trees, large terrestrial liana tangles and fallen/horizontal trees from which they defecated/urinated. These latrine sites maintain a distinguishable structure characterized by horizontal and/or oblique substrates along or just above the ground, and would all be readily noticed from a distance by visually oriented mammals when traversing through the forest, and possibly enhance their detection by conspecifics (Barja & List, 2006; Gosling, 1981). Interestingly, it may be speculated that due to the low density of *Uapaca* trees, males preferentially returned to nondescript sites so as to increase the deposited faecal matter making the latrine site potentially more conspicuous to nongroup conspecifics. Nevertheless, despite the increased density of latrine sites concentrated in core areas, *H. meridionalis* groups maintained minimal home range overlap, low rates of intergroup agonism and even occasionally utilized shared latrines.

Furthermore, it has been well-established in mammals that scent marking regulates territorial spacing by increasing chances of intercepting conspecific intruders (Barja, 2009; Gosling, 1981), for example, along territorial borders (Brashares & Arcese, 1999; Kruuk, 1978; Rosell, Bergan, & Parker, 1998), at trail junctions (Barja, de Miguel, & Bárcena, 2004) or concentrated around key resources (Gorman & Mills, 1984; Mills & Gorman, 1987). However, as we did not record scent-marks at sites other than latrines, we cannot say whether general glandular scent marking played a role in territorial defence.

Advertising Sexual Condition Hypothesis

Seasons, i.e. mating and nonmating, were not shown to influence bamboo lemur groups (analysed separately for adult males and females) to return to latrine sites, while the proportion of group individuals scent marking at latrine sites was influenced by the nonmating season. We found no support for the sexual advertising hypothesis as females were found to glandular scent-mark at consistent rates from June to December 2013. This is also similar to observations of scent marking by *Propithecus verreauxi* (Lewis, 2005), *Eulemur fulvus*, *Eulemur macaco* (Fornasieri & Roeder, 1992), *Eulemur rufifrons* (Gould & Overdorff, 2002) and *Lemur catta* (Mertl-Millhollen, 2006), but in contrast to other studies of *L. catta* (Gould & Overdorff, 2002; Kappeler, 1998) and *Propithecus diadema* (Powzyk, 1997) which showed an increase in scent marking during their reproductive season. This also occurs in platyrrhine primates, e.g. *Cebuella pygmaea* (Converse, Carlson, Ziegler, & Snowden, 1995) and *Saguinus mystax* (Heymann, 1998), as well as other mammals, e.g. bushbuck, *Tragelaphus scriptus* (Wronski et al., 2006), and meerkat (Jordan, 2007).

Mate-guarding Hypothesis

Males overmarked female glandular scent-marks at latrine sites often, a behaviour that was influenced by the nonmating season. Overmarking occurs when one individual places its scent-mark directly on top of the scent-mark of another individual (Johnston, Chaing, & Tung, 1994), and observations suggest that it is widespread among mammals (Ferkin & Pierce, 2007). Overmarking appears to be associated with the acquisition and defence of mates and mating opportunities (Johnston, Sorokin, & Ferkin, 1997a,b), with males typically scent marking on top of the scent-marks of their mates (Begg et al., 2003; Jordan, 2007; Kruuk, 1978; Roper et al., 1986, 1993). In contrast, female *Eulemur rubriventer* overmark male anogenital scent marking (Overdorff & Tecot, 2006), although intrasexual overmarking by females is relatively rare (but see Hurst, 1990; Jordan et al., 2011; Wolff, Mech, & Thomas, 2002). Similar to male *H. meridionalis* in Mandena overmarking female groupmates, males of *P. verreauxi*, another lemur species, preferentially overmark female scent-marks (Lewis, 2005). One explanation may be that this is an olfactory form of mate guarding whereby the overmark masks, i.e. reduces the effectiveness of, the original scent (Ferkin, 1999a,b; Johnston et al., 1994; Johnston, Munver, & Tung, 1995), which may allow the male to disguise the presence of the female (Jordan, 2007; Roper et al., 1986; Wronski, Apio, Plath, & Ziege, 2013). Although bamboo lemur overmarking in Mandena occurs mainly during the nonmating season, our mate-guarding hypothesis appears to be supported as individual dispersal (emigration/immigration) was also found to occur often during this time, specifically between September and December (T.M. Eppley, personal observation).

Latrine observations of the congener *H. griseus* from Analamazaotra Special Reserve described a sequential order of defecation, with adults preceding juvenile individuals (Irwin et al., 2004), and

Eppley and Donati (2010) made a similar observation with *H. meridionalis* in Mandena. While females initiated more than half of latrine utilizations, a behavioural characteristic that is presumed to be due to females often initiating travel in female-dominated congeners (Tan, 2006; Waeber & Hemelrijk, 2003), our data set suggests, however, that this is not the rule as juvenile individuals were observed to initiate latrine utilization just slightly less often than males. This shows that latrine sites are recognized (either via olfaction or vision) by all age/sex classes.

Thus, the use of certain latrines by more than one group (i.e. the eight latrines within or immediately adjacent to overlapping territorial zones) indicates that these may also convey chemical information to neighbouring groups about female and/or male presence. This latter strategy is based on the observation of both males and females dispersing from their natal group (Eppley, n.d.). In early November 2012, the only two adult males from group 1 dispersed, leaving only females within the group. By December, a new male was present in the group. It seems likely that the role of a male covering the females' scent markings at each latrine site may act as a mate-guarding strategy whereby the male's scent will mask the presence of the female (Jordan, 2007; Roper et al., 1986; Wrónski et al., 2013).

Potential Ecological Consequences of Latrine Use

Various mammalian latrines have been shown to play a key role in ecosystem dynamics, having a direct impact on plant populations via soil fertility and seed dispersal (Ben-David, Bowyer, Duffy, Roby, & Schell, 1998; Clevenger, 1996; Dinerstein, 1991; Pigozzi, 1992; Quiroga-Castro & Roldan, 2001), a finding that has been similarly observed in some New World primate species (Feeley, 2005; González-Zamora et al., 2012; Pouvelle, Jouard, Feer, Tully, & Ponge, 2009) and potentially among lemurs (Ganzhorn & Kappeler, 1996; Wright & Martin, 1995). It has been shown that red howler monkey, *Alouatta seniculus*, latrines not only increase the surrounding soil fertility (Feeley, 2005; Neves, Feer, Samlo, Chateil, & Ponge, 2010), but also increase the viability of defecated seeds (Pouvelle et al., 2009). These examples, however, include the selection of various fruit-producing tree species, whereas *H. meridionalis* selected significantly for the stilt-rooted *Uapaca* spp. as latrine sites, potentially suggesting a mutual relationship. While the low density of *Uapaca* trees in the forest and their large stilt-roots make them visibly conspicuous latrine sites, the lemur faeces probably provide fertilizer for the tree, thereby increasing canopy volume and potentially increased fruit production (Bravo, 2012; Neves et al., 2010). In turn, *H. meridionalis* selected heavily for these fruits during the biannual fruiting periods (July–August and December), ingesting the seeds whole in addition to the pulp (Eppley, Donati, et al., 2015). While it has been shown that swallowing seeds by a frugivorous lemur is an effective method of germination and increasing seed viability (Razafindratsima & Martinez, 2012), it is unknown whether this role can be fulfilled by a folivore, although their heavy reliance on this fruit is intriguing.

As a large portion of the bamboo lemur annual diet in Mandena is terrestrial graminoids (Eppley, Donati, et al., 2015; Eppley et al., 2011), it is interesting to discuss the potential benefit of their latrine behaviour. In fact, the utilization of latrines, especially a majority of which confine the faecal matter in a tangled web of stilt-roots and lianas, may assist bamboo lemurs in avoiding potential contact with excretory waste products (Gilbert, 1997). Conversely, defecation in random locations may lead to occasional contact with old faeces for (semi-) terrestrial species, potentially influencing parasite transmission/infection (Loudon & Sauther, 2013). Bamboo lemurs were never observed to graze immediately

adjacent to latrine sites; thus the chances of ingesting faecal matter and/or parasitic larvae derived from faeces would be minimized. Although this may be a secondary benefit of these latrine locations, previous studies have found no support for this hypothesis among nonprimate mammals (Apio, Plath, & Wrónski, 2006; Lamoot et al., 2004; Logiudice, 2003; Page, Swihart, & Kazacos, 1999).

Interestingly, we made additional observations of *H. meridionalis* using visually conspicuous *Uapaca* spp. trees as latrine sites at the lowland rainforest site of Ampasy (24°34'S, 47°09'E, Tsitongambarika) approximately 50 km north of Mandena. This suggests that their selection of conspicuous latrine sites is not limited to Mandena, but may be more widespread throughout the species range. Also, considering the cryptic nature of *Hapalemur* spp., searching these conspicuous sites for latrines (i.e. accumulated faeces) may provide conservationists with a nontraditional sampling method with which to indicate species presence (Balestrieri, Remonti, & Prigioni, 2009; Tuytens et al., 2001; Wilson, Delahay, de Leeuw, Spyvee, & Handoll, 2003; Wrónski & Plath, 2010).

Energy Frugality Hypothesis

Drawing from the energy conservation hypothesis (Jolly, 1966, 1984; Pereira, Strohecker, Cavigelli, Hughes, & Pearson, 1999; Richard, 1987), the energy frugality hypothesis postulates that the relatively low productivity and resource quality of forests in Madagascar may act as causal factors influencing the evolution of lemur social systems and behavioural adaptations, e.g. female dominance and low rates of agonism (Wright, 1999; but see Curtis, 2004). Irwin et al. (2004) later suggested that latrine behaviours (including scent marking) appear to fit this paradigm whereby they act as a low-energy behavioural response to the ecological challenge of defending resources without increasing agonism and/or vigilance (Kappeler, 1990; Mertl, 1975, 1977; Mertl-Millhollen, 1979). While the distribution of latrine densities does not support territorial demarcation, the preferential utilization of visually conspicuous latrine sites appears to play a functional role. Similar to the large terrestrial liana tangles and dead/fallen trees, *Uapaca* trees are exceptionally conspicuous as they are the only stilt-rooted tree within the Mandena littoral forest. These latrine site types are favoured as they provide low (i.e. ≤ 1 m) horizontal and/or oblique perches from which lemurs can defecate/urinate, as opposed to simply any tree branch or liana tangle in the canopy. The selection of visually conspicuous sites by *H. meridionalis* may function to supplement the olfactory signal (i.e. defecation/urination and scent marking) by creating a visual landmark (Barja, 2009; Barja et al., 2004; Barja, de Miguel, & Bárcena, 2005; Bowyer, Ballenberghe, & Rock, 1994; Clapham, Nevin, Ramsey, & Rosell, 2013; Gorman & Mills, 1984; Nie et al., 2012; Piñeiro & Barja, 2012). This strategy stands to increase the likelihood of detection while reducing the potential fitness cost to the signalling group by minimizing both time and energy investment (Barja, 2009; Gosling, 1981; Gosling & Roberts, 2001).

The latrine behaviour of *H. meridionalis* includes composite signals whereby faeces/urine and scent-marks provide chemical information via olfaction; visual cues are provided via the unique structure of the specified latrine, the scrapes/notches in the substrates where scent marking occurs, as well as the physical accumulation of faeces. Although urine seems to be the more important component than faeces in *Lepilemur leucopus* latrines in terms of olfactory signalling (Dröscher & Kappeler, 2014), and *H. meridionalis* urinate often in conjunction with defecating at latrine sites, urinating in conjunction with anogenital scent marking occurs very rarely as we only observed this a few times. While chemical signals are important to both diurnal and nocturnal

primates, visual signals appear to be most beneficial to diurnal species (Gilad, Wiebe, Przeworski, Lancet, & Pääbo, 2004; Semple & Higham, 2013). The southern bamboo lemurs exhibit a cathemeral activity pattern, that is, they can be active during both the light and dark phases of the diel period (Eppley, Ganzhorn, et al., 2015), and thus the utilization of multisensorial cues would be highly efficient in signalling to conspecifics (Bearder, Nekaris, & Curtis, 2006).

In conclusion, our results present a complex picture of latrine use by *H. meridionalis*. Latrine density comparisons did not support the use of latrines for territorial defence, a finding in line with the preferred utilization and glandular scent marking of latrine sites in the core area, largely driven by male bamboo lemurs. The advertisement of sexual cycling at latrine sites by females is not supported by our data. Directional male overmarking of female scent-marks provides plausible support for mate guarding. It should again, however, be noted that glandular scent marking by southern bamboo lemurs is not limited to latrine sites, and so these results should be considered prudently. Consistent with the predictions of the energy frugality hypothesis, bamboo lemur latrine behaviour appears to play a functional role as a multimodal means for providing intergroup communication, whereby the continued selection of visually conspicuous latrine sites maintains territorial home ranges and low rates of intergroup agonism.

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