LEMUR LATRINES: OBSERVATIONS OF LATRINE BEHAVIOR IN WILD PRIMATES AND POSSIBLE ECOLOGICAL SIGNIFICANCE

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Latrine behavior, or the preferential, repeated use of 1 or more specific defecation sites, is well known among mammals and believed to function in olfactory communication among individuals or groups in many circumstances. Primates have reduced their capacity for olfaction in favor of more developed visual systems; however, several prosimian primates regularly use olfactory communication for transmission of social signals, most often using scent gland secretions and urine. Latrine behaviors have been described rarely in primates and have traditionally not been included in reviews of primate olfactory communication, yet we found ample evidence that certain primate species habitually use latrine sites for defecation. Here we review the previous evidence for latrine use in primates and report new and more extensive observations of latrine use in 2 lemuriform primates (Lepilemur sp. and Hapalemur griseus). Based on these new observations, we present and evaluate 4 available hypotheses for the function of latrines (advertisement of sexual cycling, predation avoidance, intragroup spacing, and intergroup resource defense) in lemur taxa for which sufficient evidence of latrine use exists. In all cases, intergroup resource defense is the function most consistent with available observations.

Key words: chemical communication, defecation, latrines, lemurs, Madagascar, primates, resource defense, scent marking, territoriality

An enhanced visual system and reduced emphasis on olfaction (and the vomeronasal organ—Liman and Innan 2003) is generally considered to be one of the hallmarks of primate evolution. However, some authors argue that research has focused on visual and auditory stimuli because they are the most readily detected by human observers. In fact, the use of chemical signals in primate communication is well documented (Epplle 1986; Schilling 1979). Chemical signals convey specific information, such as identity of species or subspecies (Harrington 1979; Schilling 1980a), sex or reproductive condition (Converse et al. 1995; Epplle et al. 1986; Harrington 1977; Ziegler et al. 1993), and individual signatures (Mertl 1975; Schilling 1979, 1980a; Seitz 1969). Specific functions of communication involving olfaction include familiarization with the environment (Schilling 1979; Seitz 1969), territoriality (Charles-Dominique 1977; Mertl-Milhollen 1979, 1988), transmission of information related to reproductive behavior (Epplle et al. 1986), and functions associated with inter- or intragroup aggression and dominance (Epplle 1986; Kappeler 1990, 1998; Ralls 1971; Schilling 1979, 1980a).

Chemical communication via olfaction may have been retained in this predominantly visual group because of the advantage of not being limited in time and space, as is true of optical (and to a lesser extent acoustic) signals (Eisenberg and Kleiman 1972; Schilling 1979). Thus, even in species that rely primarily on optical communication, chemical communication via olfaction may allow individuals to receive signals even when distant from the signal source. In addition, one might expect olfaction to be best developed in nocturnal animals, as optical signals are less efficient at night (Wright 1989). Indeed, nocturnal prosimian primates have better-developed olfactory organs and use olfaction in communication more than the almost exclusively diurnal anthropoids (Epplle 1986).

In primates, the compounds by which chemical signals are transmitted are secretions from scent-producing skin glands, saliva, or waste products, such as urine or feces (Epplle 1986;
Among bodily wastes, urine is widely used by primates in scent marking of substrates or conspecific animals and even in self-anointing (Epple et al. 1986; Schilling 1980a); in contrast, reports of marking with feces are relatively uncommon.

**Latrine behavior in mammals.**—In contrast to primates, many mammalian species in several other orders (most of which are terrestrial) appear to use feces in chemical communication (Gorman 1990; Gorman and Trowbridge 1989; Gosling 1982; Macdonald 1980). Such behaviors usually fall into 1 of 2 categories (Gorman and Trowbridge 1989): frequent marking with small volumes applied to substrates or to animals themselves or the production of latrines, large accumulations of feces resulting from repeated defecations at a single site. In both cases, feces are often deposited in conjunction with scent from anal sacs, anal pouches, or other glands. Latrine behavior is here defined as the nonrandom selection of defecation sites in such a way that feces accumulate in 1 or more specific locations (latrines).

Latrines described in the literature vary in location (arboreal, terrestrial, or subterranean), volume of feces, spatial distribution, and behaviors associated with defecation and seem to vary in the functions they serve. Chemical communication is the most commonly invoked function for latrine use, although alternative explanations include avoidance of parasite transmission (Gilbert 1997) and avoidance of detection by predators (Boonstra et al. 1997). Within the realm of chemical communication, most studies have pointed to territoriality as the likeliest function (in contrast to the diverse functions ascribed to other forms of scent marking—Gorman and Trowbridge 1989).

**Previous reports of primate latrines.**—The use of latrines has been mentioned for 3 lemuriform genera. Charles-Dominique and Hladik (1971) first noted the use of a terrestrial latrine by a male *Lepilemur leucopus* at Berenty but later suggested these latrines may have been an inadvertent result of the animals remaining stationary at specific surveillance points at the periphery of their home range while monitoring conspecific animals (Schilling 1979:470). Russell (1977:59) also implied latrine formation by this species, noting habitual use of “specific trees for urination or defecation” leading to a “layer of fossil feces beneath these trees.”

Petter and Peyrières (1970) reported the use of terrestrial latrines in semi free–ranging and captive *Hapalemur griseus*, and Petter (1962) described arboreal latrines in wild and captive *Cheirogaleus*. In *Cheirogaleus*, feces are smeared on branches during repeated walking defecation, resulting in a thick, homogeneous accumulation (up to 40 cm long) adhering to the branch. This behavior has since been specifically investigated in captive *C. medius* (Schilling 1979, 1980b) and noted in wild *C. medius* (Ganzhorn and Kappeler 1996).

In general, primate latrines have only been mentioned in passing within works of much broader scope; latrines are not mentioned in current reviews of lemur behavior and social organization (Harcourt and Thornback 1990; Mittermeier et al. 1994). Further, no studies have offered specific hypotheses for the function of latrines or fecal marking in general in primates. However, when one considers the extensive comparative data available for other mammals, it seems plausible that these latrines may act in chemical communication.
The latrine was active, we covered it with leaves at 1830 h on 21 June. Fifteen new fecal deposits were discovered at the latrine at 0815 h on 22 June, and 12 more were deposited between 1055 h and 1915 h on 23 June. A dissection of 5 scats revealed 100% leaf content, consistent with production by the folivorous *Lepilemur* and inconsistent with production by other lemur species known to be present.

A single *Lepilemur* was observed at the latrine at 1802 h on 24 June. The animal vocalized, moved rapidly around the latrine, and defecated nearby (feces matched those of the latrine in size and form). Finally, new scats were discovered on the mornings of 25 June (7) and 26 June (26). These observations indicate that the latrine was produced by *Lepilemur* and was used frequently (at least once per night), but it remains unclear how many individuals participated or to which age or sex class they belonged.

A second, older latrine was found approximately 1 km from the first. It was at the base of a tree with numerous scratches similar to those previously observed. Finally, a 3rd set of similar scratches were found approximately 450 m away. Taken together, these 3 sites indicate that latrine behavior in this population is not unique to a single individual or group but is more widespread.

**Hapalemur griseus at Analamazaotra (Perinet) Special Reserve.**—The 1st latrine was used on 9 August 1985 at 1435 h and on 17 August at 0855 h. The feces mound below the tree was ~12 cm deep and was ~20 m from a sleep tree (a tree regularly but not exclusively used for sleeping at night). All 4 members of the group traveled to the latrine and defecated in succession from a horizontal branch 5 m above the ground.

The 2nd latrine was used on 10 August at 1420 h. The male left the site where he was resting and moved to a horizontal branch 4 m aboveground. Subsequently the male, female, and subadult defecated in turn from the same place. Many sets of feces were evident at the latrine (older feces were darker brown, fresh feces were shiny and green).

The 3rd latrine was discovered on 13 August. It was under a horizontal branch with no vegetation below and located ~20 m from another sleep tree. At 1530 h, each animal defecated in turn; the large mound of feces indicated a long period of use. Also on 13 August, the juvenile defecated at what appeared to be a latrine. At 1505 h, this individual stopped feeding and traveled to a horizontal branch 10 m away. After defecating from a height of 6 m, he returned and continued eating. The defecation site contained new, small green feces and several older, drier sets of small red-brown feces, suggesting previous use by the juvenile only.

The 4th latrine, used on 15 August at 1400 h, was located below a horizontal branch that was 3 m above the ground with no vegetation below the branch. The 3 adult-sized individuals were seen to urinate then defecate in turn. A mound of feces (~6 cm in depth) was noted.

Finally, a 5th latrine was used on 20 August at 1230 h; the adult female and juvenile defecated at a latrine of ~4 cm depth. Five minutes after the defecation, the adult male, adult female, and juvenile ate soil from an uprooted tree about 10 m from the latrine.

In summary, 5 latrines were used by adult group members, and the group exhibited a characteristic order of sequential defecation (adults preceded immatures). Another possible latrine was inferred to have been used at least twice by the 9-month-old individual. Latrines were fairly evenly spaced throughout the 8-ha territory (each ~100 m distant from its closest neighbor) and were not preferentially located at the periphery of the home range; however, some were adjacent to sleep sites or sites of geophagy. On 2 occasions, the adult male scent marked using antebrachial glands before defecating at latrines.

**Discussion**

**Latrine behavior in lemurs.**—Latrine behavior appears to be widespread in some lemur genera (Table 1) but varies within

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Latrine type</th>
<th>Localities</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cheirogaleidae</td>
<td><em>Cheirogaleus major</em></td>
<td>Arboreal</td>
<td>Captive</td>
<td>Petter (1962); Petter (1962); L. Martin (pers. comm.)</td>
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<td></td>
<td></td>
<td></td>
<td>Unknown field locality</td>
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<td>Ranomafana National Park</td>
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<tr>
<td></td>
<td><em>Cheirogaleus medius</em></td>
<td>Arboreal</td>
<td>Captive</td>
<td>Petter (1962); Schilling (1980b)</td>
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<td></td>
<td></td>
<td></td>
<td>Kirindy Forest</td>
<td>Ganzhorn and Kappeler (1996)</td>
</tr>
<tr>
<td>Lepilemuridae</td>
<td><em>Lepilemur leucopus</em></td>
<td>Terrestrial</td>
<td>Berenty Private Reserve</td>
<td>Charles-Dominique and Hladik (1971);</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Russell (1977)</td>
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<td></td>
<td><em>Lepilemur microdon</em></td>
<td>Terrestrial</td>
<td>Beza Mahafaly Special Reserve</td>
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<td><em>Lepilemur sp. (?microdon)</em></td>
<td>Terrestrial</td>
<td>Manombo Special Reserve</td>
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<tr>
<td></td>
<td><em>Lepilemur ruficaudatus</em></td>
<td>Terrestrial</td>
<td>Kalambatrita Special Reserve</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>L. Nash (pers. comm.)</td>
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<td></td>
<td></td>
<td></td>
<td>J. Ratsimbazafy (pers. comm.)</td>
</tr>
<tr>
<td>Lemuridae</td>
<td><em>Hapalemur aureus</em></td>
<td>Terrestrial</td>
<td>Captive: Parc Botanique et Zoologique Tsimbazaza, Madagascar</td>
<td>G. Rakotoarisoa (pers. comm.)</td>
</tr>
<tr>
<td></td>
<td><em>Hapalemur griseus</em></td>
<td>Terrestrial</td>
<td>Captive: Duke University Primate Center, outdoor enclosures</td>
<td>D. Haring (pers. comm.)</td>
</tr>
<tr>
<td></td>
<td><em>Lemur catta</em></td>
<td>Terrestrial</td>
<td>Captive</td>
<td>P. Wright (pers. obs.)</td>
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<td></td>
<td></td>
<td>Ranomafana National Park</td>
<td>J. Jernvall and P. Wright (pers. obs.)</td>
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<td>Isalo National Park</td>
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</table>
genera and even among conspecific populations. Latrines were observed in *H. griseus* at Analamazaotra (this study) but were not reported in 2 long-term studies of 5 groups of *H. griseus* at Ranomafana (Grassi 2001; Tan 2000); however, animals in 3 of these groups almost always defecated from horizontal or oblique branches less than 1 m above ground (C. Grassi, pers. comm.). Similarly, *Lemur catta* latrines were observed at Isalo but have not been described in other long-term studies (Jolly 1966). Finally, latrine behavior was not observed in *Lepilemur* at Analamazaotra but has been witnessed in this study and at Kirindy (J. Ganzhorn, pers. comm.).

The arboreal fecal marking of *Cheirogaleus* seems to be unique (Petter 1962; Schilling 1980b). However, the latrines of *Lepilemur* and *Hapalemur griseus* observed in this study were all terrestrial latrines produced by defecation from arboreal substrates and seem consistent with latrines known for other mammals. The major difference is that these lemuris are arboreal, whereas other mammals using latrines tend to be terrestrial, fossorial, or aquatic.

We suggest that the scratches observed near *Lepilemur* latrines at Kalambahrita are from concurrent scent marking. Some lemur species gove bark with their teeth as they scent mark (e.g., *Propithecus diadema*), and male *Lemur catta* use a horny keratinized spur adjacent to the antebrachial gland on the forearm (Schilling 1974). The marks we observed may have been caused by tooth gouging or using the grooming claw of the 2nd pedal digit. Further observations will be required to determine the age and sex classes of latrine users and scent markers. *Lepilemur* females have no scent glands, but males have paired glands behind the scrotum (Petter et al. 1977). Scent-marking behavior by males, usually accompanied by urination, has been observed in the wild but is usually discrete and less well developed than in other lemurs (Petter et al. 1977).

Observations of latrine behavior pertain to 4 phylogenetically distant and ecologically diverse lemur genera (*Cheirogales*, *Lepilemur*, *Hapalemur*, and *Lemur*). Therefore, latrine use either is an ancestral trait lost in many lineages or was acquired independently through convergence. As scent marking is widespread in primates (Epple 1986), latrines may be an extension of these preexisting behaviors.

*Function of latrine behavior in lemurs.—* The systematic and repeated nature of latrine behavior and the uniformity of latrines argue against them resulting inadvertently from other behaviors (contra Zollner et al. 1996). We discuss 4 possible functions of latrines in *Lepilemur* and *Hapalemur*.

Woodroffe et al. (1990) suggest that latrines in a population of water voles (*Arvicola terrestris*) serve to signal sexual activity. No other studies point to this function for mammalian latrines, but most female terrestrial mammals do transmit information about their reproductive condition chemically (Converse et al. 1995; Eisenberg and Kleiman 1972; Epple 1986; Ziegler et al. 1993), and such information could be transmitted using feces or associated scent marks. If so, latrines should be accessible to potential mates and/or used more frequently in the breeding season. The *Lepilemur* latrine at Kalambahrita was observed to be used in the mating season, but it appeared to be a product of long-term use; *L. ruficaudatus* at Kirindy uses latrines year-round (J. Ganzhorn, pers. comm.). The *Hapalemur griseus* latrine we observed was used after the mating season and appeared to be the product of long-term use. We conclude that lemur latrines do not serve solely to advertise sexual receptivity, although this could be 1 of multiple functions.

In some species, defecation sites may be located in a concealed place where they afford protection from predators simply by impairing the ability of predators to detect populations (Boonstra et al. 1996; Viitala et al. 1995). Repeated use of concealed defecation sites can lead to latrine formation. Lemurs have arial and terrestrial predators (Goodman et al. 1993; Karpanty and Grella 2001; Wright et al. 1997), but our observations indicated that latrines were placed in prominent locations rather than hidden from sight.

Kruuk (1992) has suggested that latrines advertise local resource use within groups and aid in interindividual spacing. Such latrines are found within territories rather than along borders and tend to be deposited before, during, and after feeding bouts (Kruuk 1992). Rather than compete for a currently occupied or recently depleted patch, individuals detecting a latrine would seek resources elsewhere. This hypothesis is unlikely to apply in lemurs for 2 reasons. First, although adult *Lepilemur* tend to forage alone (Charles-Dominique and Hladik 1971; Russell 1977; Warren and Crompton 1997), their food resources (leaves) are fairly uniformly distributed. Moreover, *Hapalemur griseus* lives in cohesive groups (Grassi 2001) and would not need to signal resource use among group members. Finally, latrines of both species were used over long periods and are therefore unlikely to signal short-term depletion of food.

Finally, many studies have suggested that latrines serve to advertise to conspecifics the continued presence of an individual or group and a willingness to defend its resources. Latrines need not be situated at territorial boundaries to serve these functions because the resource could be specific food patches (e.g., Lacher et al. 1981), mates (Roper et al. 1986, 1993; Woodroffe et al. 1990), or breeding and/or sleeping sites (Doncaster and Woodroffe 1993; Roper 1993). Such signals may protect resources either by deterring intruders or by encouraging them to avoid conflict when territory owners are encountered (Gosling 1982, 1986, 1990). Our observations are consistent with this hypothesis.

Latrine sites of *Hapalemur* at Analamazaotra were distributed throughout the territory rather than at territorial boundaries; 2 were close to sleep trees, and 2 were near fallen trees where the animals ate soil (Krishnamani and Mahaney 2000), suggesting possible defense of these sites. The proximity of *Lepilemur* latrines to defendable resources at Kalambahrita is unknown, but *Lepilemur* at other localities is reported to defecate near (but not directly below) sleep trees and not at home range boundaries (L. Nash, pers. comm.; Russell 1977). The repeated, high-fidelity use of naturally occurring tree holes as sleep sites in this genus (Andrews et al. 1998; Porter 1998) makes these sites likely locations to advertise resource defense. Ranging patterns also vary substantially within this genus:
TABLE 2.—Population density of *Lepilemur* species at various localities in Madagascar (letters following forest type indicate region of Madagascar). Presence of woolly lemurs (*Avahi*) may depress *Lepilemur* density, as both are small nocturnal folivores. Localities known to have high levels of hunting or disturbance are excluded.

<table>
<thead>
<tr>
<th>Site</th>
<th>Forest type</th>
<th>Species</th>
<th>Density (ind./km²), (\bar{X}) ± 95% CI</th>
<th>Avahi present</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Masoala National Park</td>
<td>Rain forest (NE)</td>
<td><em>L. mustelinus</em></td>
<td>36 ± 6/33 ± 22</td>
<td>+</td>
<td>Sterling and Rakotoarison (1998)</td>
</tr>
<tr>
<td>Anjanaharibe-Sud Special Reserve</td>
<td>Rain forest (NE)</td>
<td><em>L. mustelinus</em></td>
<td>20.8(^*)</td>
<td>+</td>
<td>Schmid and Smolker (1998)</td>
</tr>
<tr>
<td>Analamazoatra Special Reserve</td>
<td>Rain forest (E)</td>
<td><em>L. microdon</em></td>
<td>13 ± 9</td>
<td>+</td>
<td>Ganzhorn (1992)</td>
</tr>
<tr>
<td>Namahaoka (Ranomafana National Park)</td>
<td>Rain forest (SE)</td>
<td><em>L. microdon</em></td>
<td>0(^b)</td>
<td>+</td>
<td>Irwin et al. (2000, unpub. data)</td>
</tr>
<tr>
<td>Marofotsy (Ranomafana National Park)</td>
<td>Rain forest (SE)</td>
<td><em>L. microdon</em></td>
<td>8.33</td>
<td>+</td>
<td>Irwin et al. (2000, unpub. data)</td>
</tr>
<tr>
<td>Midongy-Sud National Park</td>
<td>Rain forest (SE)</td>
<td><em>L. microdon</em></td>
<td>11.9</td>
<td>+</td>
<td>Wright (in litt.)</td>
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<td>Kalambatiratra Special Reserve</td>
<td>Rain forest (SE)</td>
<td>*L. sp. (?microdon)</td>
<td>71.8</td>
<td>–</td>
<td>Irwin et al. (2001); this study</td>
</tr>
<tr>
<td>Ankaranana Special Reserve</td>
<td>Deciduous forest (N)</td>
<td><em>L. septentrionalis</em></td>
<td>163 ± 68 (dry forest) 476 (wet forest)</td>
<td>+</td>
<td>Ganzhorn (1992); Hawkins et al. (1990)</td>
</tr>
<tr>
<td>Analamazaotra Special Reserve</td>
<td>Deciduous forest (N)</td>
<td><em>L. septentrionalis</em></td>
<td>146 ± 48</td>
<td>–</td>
<td>Hawkins (1990)</td>
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<tr>
<td>Ampijoroa (Ankafantiska Integral Natural Reserve)</td>
<td>Deciduous forest (NW)</td>
<td><em>L. edwardsi</em></td>
<td>57 ± 22</td>
<td>+</td>
<td>Ganzhorn (1992)</td>
</tr>
<tr>
<td>Marosalaza</td>
<td>Deciduous forest (W)</td>
<td><em>L. ruficaudatus</em></td>
<td>180–350</td>
<td>–</td>
<td>Petter et al. (1971)</td>
</tr>
<tr>
<td>Mangoky</td>
<td>Deciduous forest (W)</td>
<td><em>L. ruficaudatus</em></td>
<td>260</td>
<td>–</td>
<td>Petter et al. (1971)</td>
</tr>
<tr>
<td>Kirindy Centre de Formation</td>
<td>Deciduous forest (W)</td>
<td><em>L. ruficaudatus</em></td>
<td>195(^c)</td>
<td>–</td>
<td>Ganzhorn and Kappeler (1996)</td>
</tr>
<tr>
<td>Professional Forestière</td>
<td>Deciduous forest (W)</td>
<td><em>L. ruficaudatus</em></td>
<td>136</td>
<td>–</td>
<td>Smith et al. (1997)</td>
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<tr>
<td>Kirindy and Area</td>
<td>Deciduous forest (W)</td>
<td><em>L. ruficaudatus</em></td>
<td>36</td>
<td>–</td>
<td>Charles-Dominique and Hladik (1971)</td>
</tr>
<tr>
<td>Be Mentarya Private Reserve</td>
<td>Dry spiny forest (S)</td>
<td><em>L. leucopus</em></td>
<td>200–350 (Didiereaceae forest)</td>
<td>–</td>
<td>Charles-Dominique and Hladik (1971)</td>
</tr>
<tr>
<td>Beza Mahafaly Special Reserve</td>
<td>Dry spiny forest (S)</td>
<td><em>L. leucopus</em></td>
<td>Comparable to Be Mentarya</td>
<td>–</td>
<td>Nash (2000, pers. comm.)</td>
</tr>
</tbody>
</table>

\(^a\) Calculated using published sighting rates and a strip width of 24 m (obtained for other censuses of *Lepilemur* in rain-forest habitats: Irwin et al. 2000).

\(^b\) Not detected during census but known to exist in study area; inferred to be rare.

\(^c\) Arithmetic mean of 10 census sites; from data in Ganzhorn and Kappeler (1996).

some populations defend exclusive territories, and others overlap extensively (Charles-Dominique and Hladik 1971; Russell 1977; Warren and Crompton 1997); this variation might affect presence or placement of latrines.

If latrines serve a territorial role, they may be more common in dense populations. Indeed, at Kalambatiratra, *Lepilemur* exists at higher population density than any other rain-forest site (Table 2), possibly because of the unusual absence of both *Avahi* and *Propithecus*, the only other folivores with which it might compete for food (Ganzhorn 1993; Mittermeier et al. 1994).

We have insufficient information on latrines of *Cheirogaleus* in the wild to suggest how they function. However, observations of captive individuals suggest a possible territorial role, as most fecal marking occurs in novel areas created by the opening up of a partition, and initial fecal marking is concentrated at the “periphery of the core area most frequently used by the animals” (Schilling 1979:526).

Latrines at Kalambatiratra and Analamazaotra seem to be composite signals. Feces were deposited in conjunction with scent marks, so either or both may be sources of chemical or optical signals. Chemical signals are important to both diurnal nocturnal lemurs, while optical signals may be most useful in diurnal species. Among the genera discussed here, *Hapalemur* and *Lemur* are diurnal, but *Lepilemur* and *Cheirogaleus* are strictly nocturnal (Mittermeier et al. 1994). In examining the social functions of latrines, it will be important to consider all forms of communication used at latrine sites.

Latrine use seems to fit into the overall picture of lemur behavior relative to that of other primates. Specifically, the energy frugality hypothesis (Richard et al. 2000; Wright 1999) invokes the relatively low productivity and resource quality of Malagasy forests as causal factors influencing the evolution of lemur social systems, including female social dominance and low rates of agonism. Latrines would seem to fit this paradigm, being a similar low-energy behavioral response to the ecological challenge of defending resources without escalated contest.

Finally, latrines may be important for seed dispersal in some lemur species (Clevenger 1996; Dinerstein 1991; Pigozzi 1992; Quiroga-Castro and Roldán 2001). For example, *Cheirogaleus medius* at Kirindy may disperse the seeds of an epiphytic mistletoe (*Viscum*—Ganzhorn and Kappeler 1996; see also Amico and Aizen 2000). A similar process may exist in the eastern rain forests, as *C. major* at Ranomafana National Park consumes fruit of the epiphytic Tongoaalaly (*Loranthaceae: Bakerella*—Wright and Martin 1995).

More detailed information on latrine density and distribution, seasonality, age and sex of users, sociosexual context, food resource distribution, and interpopulation differences would shed light on latrine functions in lemurs. If latrines function
mainly for resource defense, as we suggest, one would predict locations near territorial boundaries with regular visitation by members of neighboring social groups or near sleep sites or food resources (the latter particularly at times or places of food scarcity). Finally, future work should consider the possibility that distribution of some plants may be tied to spatial or seasonal patterns of latrines.

**Résumé**

Le comportement latrine, ou l’usage préférentiel et répété de certains endroits de défécation, est bien connu dans au moins sept ordres de mammifères, et dans quelques groupes, on pense qu’il y a une fonction de communication olfactive. En général, les primates ont réduit leur capacité de communication olfactive en faveur des systèmes de communication visuelles plus développés; néanmoins, beaucoup de primates prosimiens utilisent la communication olfactive pour transmettre des signaux sociaux, plus souvent avec des secretions glandulaires ou d’urine. Les comportements latrine n’ont été décrits que rarement chez les primates, et n’ont pas été inclus dans les revues concernant la communication olfactive de ce groupe, mais nous avons trouvé que quelques espèces utilisent fréquemment ces latrines. Ici, nous présentons des évidences préexistantes de l’usage des latrines chez les primates, et les nouvelles observations plus extensives de l’usage des latrines chez deux primates lemuriformes (*Lepilemur* sp. et *Hapalemur griseus*). En utilisant ces nouvelles observations, nous pouvons évaluer 4 hypothèses pour la fonction de ces latrines (annonce de l’état sexuel, action d’éviter les prédateurs, espacement des membres du groupe, et défense des ressources entre les groupes voisins) dans les espèces de lémuriens dont on a assez d’observations. Dans tous les cas, la défense des ressources entre les groupes est la fonction la plus concordante avec les observations.

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