

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 (Epple 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; Epple 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 (Epple et al. 1986), and functions associated with inter- or intragroup aggression and dominance (Epple 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 (Epple 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 (Epple 1986;

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Schilling 1979). 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. 1996). 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 Peyrieras (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.

Aims of this paper.—This paper has 3 purposes. We report new observations of latrine behavior for 2 lemur species in the wild: *Lepilemur* sp. and *Hapalemur griseus*. These include details of behavioral context and evidence of previously undocumented behaviors associated with latrine use. Second, we review all documented cases of latrine behavior in primates and suggest that this behavior may be more widespread among lemurs than is currently recognized. Finally, we present and discuss hypotheses for the function of latrine behavior in lemurs.

MATERIALS AND METHODS

Three of us (MTI, KES, and JLR) led a census expedition to Kalambatritra Special Reserve in June 2000 (details in Irwin et al. 2001). Located in southern central Madagascar, this reserve contains the westernmost rain forest in the country. We conducted censuses in the larger forest block in the northern half of the reserve, Ambalabe (23°23'S, 46°28'E; elevation 1,500–1,600 m). Five lemur species were detected at Kalambatritra (*Eulemur collaris*, *Hapalemur griseus*, *Lepilemur* sp., *Microcebus rufus*, and *Daubentonia madagascariensis*). Although Kalambatritra falls within the range of *Lepilemur microdon* as previously described, we refer to the form we observed as *Lepilemur* sp. because morphometric data collected subsequent to our census suggest that this is a distinct and previously unrecognized taxon. A 6th species, *Cheirogaleus major*, likely exists within the reserve but was not detected as the survey was conducted in the austral winter, when this species enters torpor. Among these, the sportive lemur (*Lepilemur*) appeared to be the most abundant species, with an estimated 72 individuals per square kilometer (more than 15 times the density of the next-most abundant species, the collared brown lemur, *Eulemur collaris*). The main objective of the research was line-transect censuses in order to characterize primate species incidence and population densities. Observations of *Lepilemur* latrines and behavior were made opportunistically during and between censuses by regular monitoring and extended vigils at observed latrine sites and feces dissections.

One of us (PCW) observed wild gentle bamboo lemurs (*Hapalemur griseus griseus*) at Analamazaotra (Perinet) Special Reserve, Andasibe, Madagascar (18°56'S, 48°24'E; elevation 900 m) in June and August 1985 (Wright 1986). Ten primate species occur at this site (*Indri indri*, *Eulemur fulvus fulvus*, *Eulemur rubriventer*, *Hapalemur griseus griseus*, *Lepilemur mustelinus*, *Avahi laniger*, *Cheirogaleus major*, *Microcebus rufus*, *Allocebus trichotis*, and *Daubentonia madagascariensis*). Observations focused on a group of 4 lemurs containing 1 adult male, 1 adult female, 1 subadult, and 1 juvenile; data are from 7 daylong observation periods between 9 and 20 August. Latrine use and its behavioral context were observed at 5 locations.

No lemurs were captured or handled during either study.

RESULTS

Lepilemur at Kalambatritra Special Reserve.—One latrine was encountered on 21 June 2000. It consisted of a large pile of feces (diameter 0.5 m, depth ~5 cm; ~150–200 individual feces) at the base of a Hafitra tree (Malvaceae: *Dombeya*). No trails were visible in the dense undergrowth that would have indicated the habitual passage of a terrestrial animal. This latrine tree, along with several other *Dombeya* trees in the vicinity, displayed several single elongate scratches (1–2 cm long and approximately 2 mm wide, 1–2 m aboveground) that were mainly horizontally oriented but not paired (as expected if produced by left and right canines). To determine whether the

TABLE 1.—Known observations of latrine behavior in primates in Madagascar.

Family	Species	Latrine type	Localities	References
Cheirogaleidae	<i>Cheirogaleus major</i>	Arboreal	Captive	Petter (1962)
			Unknown field locality	Petter (1962)
	<i>Cheirogaleus medius</i>	Arboreal	Ranomafana National Park	L. Martin (pers. comm.)
			Captive	Petter (1962); Schilling (1980b)
			Kirindy Forest	Ganzhorn and Kappeler (1996)
Lepilemuridae	<i>Lepilemur leucopus</i>	Terrestrial	Berenty Private Reserve	Charles-Dominique and Hladik (1971); Russell (1977)
			Beza Mahafaly Special Reserve	L. Nash (pers. comm.)
	<i>Lepilemur microdon</i>	Terrestrial	Manombo Special Reserve	J. Ratsimbazafy (pers. comm.)
	<i>Lepilemur sp. (?microdon)</i>	Terrestrial	Kalambatrira Special Reserve	This study
	<i>Lepilemur ruficaudatus</i>	Terrestrial	Kirindy Forest	J. Ganzhorn (pers. comm.)
Lemuridae	<i>Hapalemur aureus</i>	Terrestrial	Captive: Parc Botanique et Zoologique de Tsimbazaza, Madagascar	G. Rakotoarisoa (pers. comm.)
			Analamazaotra Special Reserve	This study
	<i>Hapalemur griseus</i>	Terrestrial	Captive: Duke University Primate Center, outdoor enclosures	D. Haring (pers. comm.)
			Captive	Petter and Peyrieras (1970)
	<i>Hapalemur simus</i>	Terrestrial	Ranomafana National Park	P. Wright (pers. obs.)
	<i>Lemur catta</i>	Terrestrial	Isalo National Park	J. Jernvall and P. Wright (pers. obs.)

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 antibrachial 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

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 lemurs are arboreal, whereas other mammals using latrines tend to be terrestrial, fossorial, or aquatic.

We suggest that the scratches observed near *Lepilemur* latrines at Kalambatrira are from concurrent scent marking. Some lemur species gouge tree 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 (*Cheirogaleus*, *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 Kalambatrira 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 aerial 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 Kalambatrira 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.

Site	Forest type	Species	Density (ind./km ²), $\bar{X} \pm 95\% CI$	Avahi present	Reference
Masoala National Park	Rain forest (NE)	<i>L. mustelinus</i>	36 ± 6/33 ± 22	+	Sterling and Rakotoarison (1998)
Anjanaharibe-Sud Special Reserve	Rain forest (NE)	<i>L. mustelinus</i>	20.8 ^a	+	Schmid and Smolker (1998)
Analamazaotra Special Reserve	Rain forest (E)	<i>L. microdon</i>	13 ± 9	+	Ganzhorn (1992)
Namahoaka (Ranomafana National Park)	Rain forest (SE)	<i>L. microdon</i>	0 ^b	+	Irwin et al. (2000, unpub. data)
Marofotsy (Ranomafana National Park)	Rain forest (SE)	<i>L. microdon</i>	8.33	+	Irwin et al. (2000, unpub. data)
Midongy-Sud National Park	Rain forest (SE)	<i>L. microdon</i>	11.9	+	Wright (in litt.)
Kalambatritra Special Reserve	Rain forest (SE)	<i>L. sp. (?microdon)</i>	71.8	–	Irwin et al. (2001); this study
Ankarana Special Reserve	Deciduous forest (N)	<i>L. septentrionalis</i>	163 ± 68 (dry forest) 476 (wet forest)	+	Ganzhorn (1992); Hawkins et al. (1990)
Analamera Special Reserve	Deciduous forest (N)	<i>L. septentrionalis</i>	146 ± 48 60	–	Hawkins et al. (1990) D. Meyers (in Mittermeier et al. 1994); Meyers and Ratsirarson (1989)
Ampijoroa (Ankarafantsika Integral Natural Reserve)	Deciduous forest (NW)	<i>L. edwardsi</i>	57 ± 22 500	+	Ganzhorn (1992) Rasoloharijaona et al. (2000)
Marosalaza	Deciduous forest (W)	<i>L. ruficaudatus</i>	180–350	–	Petter et al. (1971)
Mangoky	Deciduous forest (W)	<i>L. ruficaudatus</i>	260	–	Petter et al. (1971)
Kirindy Centre de Formation Professionnelle Forestière	Deciduous forest (W)	<i>L. ruficaudatus</i>	195 ^c	–	Ganzhorn and Kappeler (1996)
Kirindy and Area	Deciduous forest (W)	<i>L. ruficaudatus</i>	136	–	Smith et al. (1997)
Berenty Private Reserve	Dry spiny forest (S)	<i>L. leucopus</i>	200–350 (Didiereaceae forest) 450 (gallery forest)	–	Charles-Dominique and Hladik (1971)
Beza Mahafaly Special Reserve	Dry spiny forest (S)	<i>L. leucopus</i>	Comparable to Berenty	–	Nash (2000, pers. comm.)

^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 Kalambatritra, *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 Kalambatritra 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, *Haplemur* 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 Tongoalahy (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 sécrétions 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 sur 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 lémuriformes dont on a assez d'évidence. Dans tous les cas, la défense des ressources entre les groupes est la fonction la plus concordante avec les observations.

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LITERATURE CITED

- AMICO G., AND M. A. AIZEN. 2000. Mistletoe seed dispersal by a marsupial. *Nature* 408:929–930.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- ANDREWS, J., P. ANTILAHIMENA, AND C. R. BIRKINSHAW. 1998. Use of a day resting box by a wild sportive lemur, *Lepilemur dorsalis*, on Nosy Be, north-western Madagascar. *Folia Primatologica* 69:18–21.
- BOONSTRA, R., C. J. KREBS, AND A. KENNEY. 1996. Why lemmings have indoor plumbing in summer. *Canadian Journal of Zoology* 74:1947–1949.
- CHARLES-DOMINIQUE, P. 1977. Urine marking and territoriality in *Galago alleni* (Waterhouse, 1837—Lorisoidae, Primates)—a field study by radio-telemetry. *Zeitschrift für Tierpsychologie* 43:113–138.
- CHARLES-DOMINIQUE, P., AND C. M. HLADIK. 1971. Le *Lepilemur* du sud de Madagascar: écologie, alimentation, et vie sociale. *Revue d'Écologie (La Terre et la Vie)* 25:3–66.
- CLEVENGER, A. P. 1996. Frugivory of *Martes martes* and *Genetta genetta* in an insular Mediterranean habitat. *Revue d'Écologie (Terre et Vie)* 51:19–28.
- CONVERSE, L. J., A. A. CARLSON, T. E. ZIEGLER, AND C. T. SNOWDON. 1995. Communication of ovulatory state to mates by female pygmy marmosets, *Cebuella pygmaea*. *Animal Behaviour* 49:615–621.
- DINERSTEIN, E. 1991. Seed dispersal by greater one-horned rhinoceros (*Rhinoceros unicornis*) and the flora of *Rhinoceros* latrines. *Mammalia* 55:355–362.
- DONCASTER, C. P., AND R. WOODROFFE. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* 66:88–93.
- EISENBERG, J. F., AND D. G. KLEIMAN. 1972. Olfactory communication in mammals. *Annual Review of Ecology and Systematics* 3:1–32.
- EPPLER, G. 1986. Communication by chemical signals. Pp. 531–580 in *Comparative primate biology, volume 2A: behavior, conservation and ecology* (G. Mitchell and J. Erwin, eds.). Alan R. Liss, New York.
- EPPLER, G., A. M. BELCHER, AND A. B. SMITH III. 1986. Chemical signals in callitrichid monkeys—a comparative review. Pp. 653–673 in *Chemical signals in vertebrates 4: ecology, evolution and comparative biology* (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, eds.). Plenum Press, New York.
- GANZHORN, J. U. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests: test of a hypothesis. *Oecologia* 91:540–547.
- GANZHORN, J. U. 1993. Flexibility and constraints of *Lepilemur* ecology. Pp. 153–166 in *Lemur social systems and their ecological basis* (P. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.
- GANZHORN, J. U., AND P. M. KAPPELER. 1996. Lemurs of the Kirindy forest. Pp. 257–274 in *Ecology and economy of a tropical dry forest in Madagascar* (Primate Report 46-1; J. U. Ganzhorn and J.-P. Sorg, eds.). Erich Goltze GmbH and Co, Göttingen, Germany.
- GILBERT, K. A. 1997. Red howling monkey use of specific defecation sites as a parasite avoidance strategy. *Animal Behaviour* 54:451–455.

- GOODMAN, S. M., S. O'CONNOR, AND O. LANGRAND. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. Pp. 51–66 in *Lemur social systems and their ecological basis* (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.
- GORMAN, M. L. 1990. Scent marking strategies in mammals. *Revue Suisse de Zoologie* 97:3–30.
- GORMAN, M. L., AND B. J. TROWBRIDGE. 1989. The role of odor in the social lives of carnivores. Pp. 57–88 in *Carnivore behavior, ecology, and evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.
- GOSLING, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie* 60:89–118.
- GOSLING, L. M. 1986. Economic consequences of scent marking in mammalian territoriality. Pp. 385–395 in *Chemical signals in vertebrates 4: ecology, evolution and comparative biology* (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, eds.). Plenum Press, New York.
- GOSLING, L. M. 1990. Scent marking by resource holders: alternative mechanisms for advertising the costs of competition. Pp. 315–328 in *Chemical signals in vertebrates 5*. (D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, eds.). Oxford University Press, Oxford, United Kingdom.
- GRASSI, C. 2001. The behavioral ecology of *Haplemur griseus griseus*: the influences of microhabitat and population density on this small-bodied prosimian folivore. Ph.D. dissertation, University of Texas at Austin.
- HARCOURT, C., AND J. THORNBACK. 1990. Lemurs of Madagascar and the Comoros: the IUCN red data book. IUCN, Gland, Switzerland.
- HARRINGTON, J. E. 1977. Discrimination between males and females by scent in *Lemur fulvus*. *Animal Behaviour* 25:147–151.
- HARRINGTON, J. E. 1979. Responses of *Lemur fulvus* to scents of different subspecies of *Lemur fulvus* and to scents of different species of lemuriforms. *Zeitschrift für Tierpsychologie* 49:1–9.
- HAWKINS, A. F. A., P. CHAPMAN, J. U. GANZHORN, Q. M. C. BLOZAM, S. C. BARLOW, AND S. J. TONGE. 1990. Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. *Biological Conservation* 54:83–110.
- IRWIN, M. T., T. M. SMITH, AND P. C. WRIGHT. 2000. Census of three eastern rainforest sites north of Ranomafana National Park: preliminary results and implications for lemur conservation. *Lemur News* 5:20–22.
- IRWIN, M. T., K. E. SAMONDS, AND J.-L. RAHARISON. 2001. A biological inventory of the lemur community of Réserve Spéciale de Kalambatritra, South-Central Madagascar. *Lemur News* 6:24–28.
- JOLLY, A. 1966. Lemur behavior. University of Chicago Press, Chicago, Illinois.
- KAPPELER, P. M. 1990. Social status and scent-marking behaviour in *Lemur catta*. *Animal Behaviour* 40:774–776.
- KAPPELER, P. M. 1998. To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. *Behavioral Ecology and Sociobiology* 42:411–421.
- KARPANTY, S. M., AND R. GRELLA. 2001. Lemur responses to diurnal raptor calls in Ranomafana National Park, Madagascar. *Folia Primatologica* 72:100–103.
- KRISHNAMANI, R., AND W. C. MAHANEY. 2000. Geophagy among primates: adaptive significance and ecological consequences. *Animal Behaviour* 59:899–915.
- KRUK, H. 1992. Scent marking by otters (*Lutra lutra*): signaling the use of resources. *Behavioral Ecology* 3:133–140.
- LACHER, T. E., JR., G. A. B. DA FONSECA, C. ALVES, JR., AND B. MAGALHÃES-CASTRO. 1981. Exudate-eating, scent-marking, and territoriality in wild populations of marmosets. *Animal Behaviour* 29:306–307.
- LIMAN, E. R., AND H. INNAN. 2003. Relaxed selective pressure on an essential component of pheromone transduction in primate evolution. *Proceedings of the National Academy of Sciences* 100:3328–3332.
- MACDONALD, D. W. 1980. Patterns of scent marking with urine and faeces amongst carnivore communities. *Symposia of the Zoological Society of London* 45:107–139.
- MERTL, A. S. 1975. Discrimination of individuals by scent in a primate. *Behavioral Biology* 14:505–509.
- MERTL-MILHOLLEN, A. S. 1979. Olfactory demarcation of territorial boundaries by a primate—*Propithecus verreauxi*. *Folia Primatologica* 32:35–42.
- MERTL-MILHOLLEN, A. S. 1988. Olfactory demarcation of territorial but not home range boundaries by *Lemur catta*. *Folia Primatologica* 50:175–187.
- MEYERS, D. M., AND J. RATSIRARSON. 1989. Distribution and conservation of two endangered sifakas in northern Madagascar. *Primate Conservation* 10:81–86.
- MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington, D.C.
- NASH, L. 2000. Encounter rate estimates on *Lepilemur leucopus* and *Microcebus murinus* at Beza Mahafaly Special Reserve, southwestern Madagascar. *Lemur News* 5:38–40.
- PETTER, J.-J. 1962. Recherches sur l'écologie et l'éthologie des lémuriers malgaches. *Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie* 27:1–146.
- PETTER J.-J., R. ALBIGNAC, AND Y. RUMPLER. 1977. Faune de Madagascar 44: mammifères lémuriers (Primates Prosimiens). ORSTROM/CNRS, Paris, France.
- PETTER J.-J., AND A. PEYRIERAS. 1970. Observations éco-éthologiques sur les lémuriers malgaches du genre *Haplemur*. *Revue d'Écologie (La Terre et la Vie)* 24:356–382.
- PETTER, J.-J., A. SCHILLING, AND G. PARIENTE. 1971. Observations éco-éthologiques sur deux lémuriers malgaches nocturnes: *Phaner furcifer* et *Microcebus coquereli*. *Revue d'Écologie (La Terre et la Vie)* 25:287–327.
- PIGOZZI, G. 1992. Frugivory and seed dispersal by the European badger in a Mediterranean habitat. *Journal of Mammalogy* 73:630–639.
- PORTER, L. M. 1998. Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. *Folia Primatologica* 69:172–176.
- QUIROGA-CASTRO, V., AND A. I. ROLDÁN. 2001. The fate of *Attalea phalerata* (Palmae) seeds dispersed to a tapir latrine. *Biotropica* 33:472–477.
- RALLS, K. 1971. Mammalian scent marking. *Science* 171:443–449.
- RASOLOHARIJAONA, S., B. RAKOTOSAMIMANANA, AND E. ZIMMERMAN. 2000. Infanticide by a male Milne-Edwards' sportive Lemur (*Lepilemur edwardsi*) in Ampijoroa, NW Madagascar. *International Journal of Primatology* 21:41–45.
- RICHARD, A. F., R. E. DEWAR, M. SCHWARTZ, AND J. RATSIRARSON. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution* 39: 381–391.
- ROPER, T. J. 1993. Badger setts as a limiting resource. Pp. 26–34 in *The badger* (T. J. Hayden, ed.). Royal Irish Academy, Dublin, Ireland.
- ROPER, T. J., D. J. SHEPHERDSON, AND J. M. DAVIES. 1986. Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* 97:94–117.

- ROPER, T. J., L. CONRADT, J. BUTLER, S. E. CHRISTIAN, J. OSTLER, AND T. K. SCHMID. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour* 127:289–307.
- RUSSELL, R. J. 1977. The behavior, ecology and environmental physiology of a nocturnal primate, *Lepilemur mustelinus* (Strepsirhini, Lemuriformes, Lepilemuridae). Ph.D. dissertation, Duke University, Durham, North Carolina.
- SCHILLING, A. 1974. A study of marking behavior in *Lemur catta*. Pp. 347–362 in *Prosimian biology* (R. D. Martin, G. A. Doyle, and A. C. Walker, eds.). Duckworth, London, United Kingdom.
- SCHILLING, A. 1979. Olfactory communication in primates. Pp. 461–542 in *The study of prosimian behavior* (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.
- SCHILLING, A. 1980a. The possible role of urine in territoriality of some nocturnal prosimians. *Symposia of the Zoological Society of London* 45:165–193.
- SCHILLING, A. 1980b. Seasonal variation in the fecal marking of *Cheirogaleus medius* in simulated climatic conditions. Pp. 181–190 in *Nocturnal Malagasy primates: ecology, physiology and behavior* (P. Charles-Dominique et al., eds.). Academic Press, New York.
- SCHMID, J., AND R. SMOLKER. 1998. Lemurs of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. *Fieldiana: Zoology* 90:227–238.
- SEITZ, E. 1969. Die Bedeutung geruchlicher Orientierung beim Plumpflori *Nycticebus coucang* Boddaert 1785 (Prosimii, Lorisidae). *Zeitschrift für Tierpsychologie* 26:73–103.
- SMITH, A. P., N. HORNING, AND D. MOORE. 1997. Regional biodiversity planning and lemur conservation with GIS in western Madagascar. *Conservation Biology* 11:498–512.
- STERLING, E. J., AND N. RAKOTOARISON. 1998. Rapid assessment of richness and density of primate species on the Masoala Peninsula, Eastern Madagascar. *Folia Primatologica* 69:109–116.
- TAN, C. 2000. Behavior and ecology of three sympatric bamboo lemur species (genus *Haplemur*) in Ranomafana National Park, Madagascar. Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook.
- VIITALA, J., E. KORPIMÄKI, P. PALOKANGAS, AND M. KOIVULA. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* 373:425–427.
- WARREN, R. D., AND R. H. CROMPTON. 1997. A comparative study of the ranging behavior, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *Journal of Zoology (London)* 243:397–415.
- WOODROFFE, G. L., J. H. LAWTON, AND W. L. DAVIDSON. 1990. Patterns in the production of latrines by water voles (*Arvicola terrestris*) and their use as indices of abundance in population surveys. *Journal of Zoology (London)* 220:439–445.
- WRIGHT, P. C. 1986. Diet, ranging behavior and activity pattern of the gentle lemur (*Haplemur griseus*) in Madagascar. *American Journal of Physical Anthropology* 70:283.
- WRIGHT, P. C. 1989. The nocturnal primate niche in the New World. *Journal of Human Evolution* 18:635–658.
- WRIGHT, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yearbook of Physical Anthropology* 42:31–72.
- WRIGHT, P. C., S. K. HECKSCHER, AND A. E. DUNHAM. 1997. Predation of Milne-Edward's sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia Primatologica* 68:34–43.
- WRIGHT, P. C., AND L. B. MARTIN. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. Pp. 45–60 in *Creatures of the dark: the nocturnal prosimians* (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.
- ZIEGLER, T. E., G. EPPLE, C. T. SNOWDON, T. A. PORTER, A. M. BELCHER, AND I. KÜDERLING. 1993. Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Animal Behaviour* 45:313–322.
- ZOLLNER, P. A., W. P. SMITH, AND L. A. BRENNAN. 1996. Characteristics and adaptive significance of latrines of swamp rabbit (*Sylvilagus aquaticus*). *Journal of Mammalogy* 77:1049–1058.

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