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Review Article

A Review and Interspecific Comparison of Nocturnal and Cathemeral Strepsirhine Primate Olfactory Behavioural Ecology

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This paper provides a comparative review of the known patterns of olfactory behavioural ecology among the nocturnal strepsirhine primates and the cathemeral lemurid genus *Eulemur*. Endemic to Madagascar, all *Eulemur* species exhibit both diurnality and nocturnality (i.e., cathemerality), and are gregarious, making them an interesting group of taxa to compare with the nocturnal strepsirhines. This paper represents the first comparative review of patterns of olfactory communication among the nocturnal strepsirhines and the cathemeral *Eulemur* species. Inductive assessment of these comparative data indicates that olfactory communication serves multiple functions in both groups, including individual recognition, sex recognition, indication of social dominance, and coordination of mating behaviour. However, the urine-washing behaviour characteristic of many nocturnal strepsirhines has no clear homologue among *Eulemur* species (although the latter may use urine droplets in scent marking). Despite sparse and scattered comparative data, it appears that *Eulemur* species exhibit different olfactory communication patterns that are associated with differing social organizations in this genus.

1. Introduction

In their 2004 paper reviewing comparative data on latrine behaviour among lemur species, Irwin and coauthors [1] contended that, "... the use of chemical signals in primate communication is well documented." On this point, they cited two fundamental sources: first, Alain Schilling's 1979 review paper, "Olfactory Communication in Prosimians" [2], and second, Gisela Eppe's 1986 review of primate olfactory behaviour, "Communication by Chemical Signals" [3].

There are two important things to note concerning this pair of key publications on primate olfactory behaviour. The first is that, although it has been 32 and 25 years, respectively, since these works were published, both continue to be required reading in the field of primate olfactory communication. The second is that both these publications predate the 1987 definition of primate species with both diurnal and nocturnal activity patterns as being "cathemeral," or active "through the day" (i.e., through the 24-hour daily cycle) [4]. This definition ushered in the extensive attention the

lemuriform primate genus *Eulemur* has received concerning this distinctive activity pattern, (e.g., [5–7], and references therein).

Genus *Eulemur* and all the other lemuriform primates native to Madagascar, together with the loriform primates of Africa and Asia, represent a major adaptive radiation within the Order Primates—the Suborder Strepsirhini. These primates retain the ancestral mammalian characteristic of the *rhinarium* (or "wet nose"). Strepsirhine primates include all the lemur species of Madagascar and the Comoro Islands, the lorises of south and southeastern Asia, and the pottos and galagos (or, bushbabies) of sub-Saharan Africa. In the closing section of his 1979 paper, Schilling [2] remarked on the apparent distinction between the predominantly deferred olfactory signals of nocturnal strepsirhines and the combined direct olfactory and visual signalling of diurnal strepsirhines, stating, "It would be interesting to study this aspect of olfactory communication *in species that are intermediate between the two types* (emphasis added), that is, which are gregarious to the extent that they live in family groups, and which are more or less nocturnal, like *Haplemur griseus*,

Avahi laniger, and *Lemur mongoz*.” Thus, the present paper represents the first comparative review of olfactory communication exhibited by nocturnal strepsirhine primates and the cathemeral *Eulemur* species. The major aim of this paper is to provide an initial assessment of the types and contexts of olfactory communication of the nocturnal strepsirhines relative to those of the cathemeral genus *Eulemur* (as well as the cathemeral lemurid species *Haplemur griseus*).

2. Strepsirhine Olfactory Biology in Comparative Perspective

Before comparing patterns of olfactory communication amongst nocturnal and cathemeral strepsirhine primates, it is useful to first consider strepsirhine olfactory biology in broader primate and mammalian comparative contexts. Relative to many other mammalian orders (e.g., rodents, artiodactyls, perissodactyls, carnivores), primates have historically been regarded as microsmatic [8–10]. But the olfactory systems of strepsirhine and haplorhine primates also exhibit considerable differences in the relative proportions and complexities of their anatomical structures [10–19]. Early work in this area produced the proposal that those primate species possessing functional vomeronasal organs (VNOs) might be regarded as relatively macrosmatic while those primate species without functional VNOs could be considered microsmatic, (e.g., [8]). Further, these comparative anatomical data have also been interpreted as indicating, in general, relatively sensitive olfaction among strepsirhines, tarsiers, and platyrrhines, and less keen olfactory abilities among catarrhine primates (i.e., Old World cercopithecoïd monkeys and hominoids); these latter taxa are considered more visually adapted, exhibiting specializations such as trichromatic vision [8–12, 14, 19–26]. More recently, however, this interpretation and classification schema has been discarded due to mounting evidence that there is not a direct correspondence between the presence or relative sizes of olfactory structures and olfactory function, (e.g., [10, 19, 27, 28]).

In terms of comparative anatomy, the extant strepsirhine primates (together with the extinct adapoid primates of the Eocene epoch) are considered to have retained the primitive eutherian mammal “nasal ground plan” [10]. All strepsirhine primates possess the rhinarium, the naked, moist tissue surrounding the nostrils, which is also found in many other mammalian taxa but has been lost in all haplorhine primates (i.e., New World monkeys, Old World monkeys, and hominoids [10, 29]). The available comparative anatomical data for members of the Order Primates indicate that both the VNO and the entire vomeronasal complex (VNC) are most fully developed in strepsirhines [13, 14, 30], and likely play critical roles in discrimination among chemical classes of odourants [19] and in pheromonal communication [20]. The available anatomical data on species in the haplorhine infraorders Tarsiiformes (tarsiers) and Platyrrhini (New World, or platyrrhine, monkeys) indicate that these taxa also possess VNCs that are “structurally comparable” [30] to those found in strepsirhines [10, 14, 17, 18, 30]; however,

the functional role of the VNC has not been fully examined across these former taxa [21, 30].

The accessory olfactory bulb (AOB) of the accessory olfactory system (AOS) is described as large to very large relative to body size in those strepsirhine species that have been examined [15]. There is considerable variation in AOB size relative to body size in those strepsirhine and platyrrhine species for which there are data [15]. The AOB is described as relatively well developed in platyrrhine species, but the available comparative data also indicate that AOBs in New World monkeys are generally reduced in absolute size compared to those of strepsirhine species [15]. In those Old World monkey species (Cercopithecoïdeia) studied thus far, the AOS is absent in adults [10, 21, 30]. In the ape species (Hominoïdeia) that have been studied, including humans, the AOB is absent in adults [10, 15]. If the VNO is present in hominoid species (again, including humans), it appears vestigial in structure and is thought to likely be nonfunctional [10, 13–16, 19, 20, 22–24, 30]. Among the strepsirhines studied to date, nocturnal strepsirhines are reported to both have larger AOBs [15], and larger olfactory bulbs (OBs) [10] than diurnal strepsirhines. Barton and colleagues [12] reported that among nocturnal strepsirhines, there is a positive correlation between the proportion of fruit in the overall diet and the relative size of the OB, (see also [25]). Haplorhine primates, by contrast, have relatively small OBs in comparison to most other mammals [19, 26].

There have been several reports noting that olfaction in primates is relatively under-studied and remains poorly understood (e.g., [10, 20, 21, 26]). Recently, the view has also been expressed that interpreting primate olfactory reception and processing as being functionally divided between the main olfactory system (MOS) and the AOS is too simplistic [8, 10, 19, 20, 27, 28]. Specifically, the complexity of primate olfaction is not reflected in a functional interpretation that sees the MOS primarily detecting airborne volatile odours from a variety of stimuli in the environment, such as food or predators [19, 27], and the AOS being primarily sensitive to heavy, nonvolatile, fluid-borne chemical stimuli, such as urine and scent-marks, as well as pheromones, that communicate sociosexual information [10, 19, 27]. Rather, the emerging view is that there must be a degree of overlap, or integration, in the functioning of the MOS and AOS [8, 10, 19, 20, 27, 28].

This more nuanced interpretation of primate olfaction has been pushed ahead by innovative studies that have made novel applications of research techniques. For example, advances in genomic analyses have made possible the comparison of olfactory receptor (OR) gene families coding for olfactory receptor proteins (ORPs) in different primate species and other mammals, (e.g., [9, 11, 18, 19, 23, 24, 28]). Advances have also been realized in several recent studies of primate olfaction through the use of gas chromatography-mass spectrometry (GC-MS) to identify both the volatile components of the glandular secretions used in scent marking, (e.g., [31–34]), and the chemical composition of urine [35].

Notably, genetic studies have provided new insights into primate olfactory function. Although testing across the

Order Primates has not been exhaustive to this point, the V1R and V2R olfactory receptor (OR) gene families and the TRP2 gene (which is crucial for pheromone signal transduction in the VNO) have been examined across several primate genera. These preliminary assessments of the genetics of olfaction have shown that catarrhine primates, with their trichromatic vision, exhibit a significantly higher proportion of nonfunctional OR pseudogenes than do either platyrrhine monkeys or strepsirhines [9, 11, 18, 19, 23, 24]. An exception to this taxonomic pattern is the platyrrhine genus *Alouatta*, the howler monkeys, which have evolved trichromatic vision via convergent evolution and exhibit a level of OR pseudogenization similar to that among catarrhine taxa [11]. Yet, this does not mean that cercopithecoids and hominoids (or *Alouatta*, for that matter) do not use, or respond to, olfactory communication [19, 29, 36]. Despite lacking the AOS as adults, some cercopithecoid monkeys do exhibit scent-marking behaviour (e.g., [37, 38]). Although scent-marking behaviour has not been recorded among hominoid taxa [10, 39, 40], available comparative data show that specialized cutaneous scent glands, such as the axillary apocrine glands, are known in all hominoid genera [10, 39, 40]; this provides a likely channel for interindividual olfactory communication and individual recognition in hominoids, including humans [27, 39–42]. Similarly, recent GC-MS analyses of the volatile components in mandrill (*Mandrillus sphinx*) scent marks indicated that, despite the mandrill apparently lacking a functional AOS, individual odour profiles convey information about the signaller, including age, sex, dominance rank of adult males, and perhaps identity of the signaller [43]. Additionally, odour similarity between signaller and receiver is related to major histocompatibility (MHC) concordance, and represents a potential mechanism for mate selection by females in favour of MHC-diverse males [44]. These new insights into olfactory communication in a catarrhine primate seem to provide an example of the suggestion that, even without functional AOSs or VNOs, catarrhines can still detect and respond to sociosexual odour cues and pheromonal stimuli through ORPs that are expressed in the main olfactory epithelium [10, 19, 20, 22, 27, 28].

So, while we have an emerging picture of humans and other catarrhine primates being capable of responding to an array of odour cues, including chemosensory responses to volatile components of some odours [10, 19, 20, 27, 28, 43, 44], the available comparative data on strepsirhine primates (where we find species that exhibit retention of the rhinarium, well-developed AOSs, relatively large AOBs, functional VNOs, intact OR gene families coding for functional ORPs, plus functional integration of the AOSs and the MOSs), indicate that strepsirhine primate taxa experience considerable complexity in their olfactory communication [10, 19, 20, 28, 35]. The important role of scent marking and olfactory communication in strepsirhine behavioural ecology, particularly in regard to reproductive behaviour, has been recognized for decades, (e.g., [45]). Yet, despite this, and despite important comparative works like those by Schilling [2] and Epple [3], it is surprising how little-studied strepsirhine olfactory communication remains and how little we know with certainty about strepsirhine

olfactory behavioural ecology. This relates to the general point raised repeatedly in the literature that research into primate olfaction lags far behind that on primate visual and vocal systems, for example, [10, 20, 21, 26]. For example, the comments of Rowell [46] over 30 years ago remain surprisingly current: “Prosimians are smelly animals... olfactory communication occurs both at a distance and in body contact, but monitoring the “conversation” presents difficulties for our olfactorily unsophisticated species and proceeds slowly.” Over the last decade, for every peer-reviewed paper dealing with primate olfaction, 115 dealing with primate vision have been published (e.g., see the PrimateLit database: <http://primatelit.library.wisc.edu>; see also [26]). From this, we can appreciate why Heymann [26] concluded that, “Thus, it is appropriate to consider olfaction as a sense that is still neglected in the study of nonhuman primates.”

All this is by way of pointing out that the present, and any other, comparative review of olfactory behavioural ecology across strepsirhine primate species must rely on a body of information that is fragmentary and scattered. Thus, this review must be regarded as entirely preliminary. Recent taxonomies recognize at least 26 loriform strepsirhine species (i.e., the lorises, pottos, and galagos, or bushbabies; see [47]) while the number of recognized lemuriform strepsirhine species endemic to Madagascar approaches 100 and is still climbing [48–50]. For most of these loriform and lemuriform taxa, however, there is no information available on the behavioural ecology of their olfactory communication.

3. Nocturnal and Cathemeral Strepsirhines: Comparative Data

In order to review the literature relating to strepsirhine primate olfactory behavioural ecology as completely as possible, and given the scant literature that deals explicitly with primate olfaction (see above), it was also necessary to consult reports, on strepsirhine primate species, that have dealt primarily with other topics (such as social organization, social behaviour, ranging ecology, etc.), and glean whatever material could be found concerning olfactory communication. This entailed having to pull information from a sentence here or an anecdote there, in a literature that is very scattered (relevant material was found in publications that focused on primatology, anthropology, behaviour, chemical ecology, mammalogy, and zoology). This simply underscores the fact that the behavioural ecology of strepsirhine primate olfaction and olfactory behaviour remains both a poorly researched and poorly understood dimension of the overall behavioural ecology of these taxa. It also points to this area being an extremely fertile and promising area for future research on the behavioural ecology of strepsirhine primates (moreover, the same applies to the study of primate olfactory behavioural ecology in general, as several recent publications reflect, e.g., [20, 26–28, 42, 43, 51]).

3.1. Nocturnal Lemuriforms

3.1.1. Genus *Microcebus*: The Mouse Lemurs. *Microcebus murinus*, the gray mouse lemur, is the lemuriform species for which the accessory olfactory system (AOS), including the vomeronasal organ, has most fully been investigated [52]. In *M. murinus*, male-male, male-female, and female-female socio-sexual interactions are mediated and coordinated by urinary chemosensory cues [53–55]. Studies of *M. murinus* in captivity have shown that male urinary marking behaviour decreases with age [56, 57]. The suite of scent-marking behaviours known for the gray mouse lemur includes punctuated urine marking (sometimes with “perineal wiping”), head rubbing and muzzle or lip wiping, branch chewing with salivary deposition, and, especially, “urine washing” (where individuals purposefully urinate on their hands and feet), which accounts for over 80% of all scent-marking behaviours performed [2, 3, 58–61]. In a recent field study of the golden brown mouse lemur (*M. ravelobensis*), Braune and colleagues [62] recognized two forms of scent marking: urine washing, and mouth wiping (sometimes with face and/or head rubbing).

3.1.2. Genus *Mirza*: The “Giant” Mouse Lemurs. Olfactory communication among *Mirza* during reproductive behaviour includes nasonasal, nasobody and nasogenital contact [63]. Both punctuated urine marking and urine trail marking occur, and experimental work indicates males can discriminate among the urine marks of conspecifics [3, 58]. Both males and females anogenital scent mark, and, like *Microcebus*, *Mirza* also engages in salivary marking [59]. Notably, *Mirza* would also appear to exhibit flehmen (see photo Figure 8 in [59]—the caption reads, “The typical posture for smelling a mark of a conspecific; note the open mouth, and retracted tongue,” emphasis added; cf. [64]).

3.1.3. Genus *Cheirogaleus*: The Dwarf Lemurs. Data on olfactory communication are available for the greater dwarf lemur (*Cheirogaleus major*) and the fat-tailed dwarf lemur (*C. medius*). Both species exhibit punctuated urine marking and urine trail marking, as well as anogenital scent marking [2, 58], but the dwarf lemurs are notable for their specialized fecal marking of branches [2, 65], which Irwin and colleagues [1] identify as arboreal latrine behaviour. Dwarf lemur fecal marking may be related to territorial advertisement.

3.1.4. Genus *Phaner*: The fork-Marked Lemurs. *Phaner* stands out amongst the nocturnal lemuriforms because of the apparent absence of any form of urine marking in this genus [2, 66]. Males may rarely scent mark branches with their throat gland [67]; more often, males use their throat gland to scent mark females during allogrooming bouts [66].

3.1.5. Genus *Lepilemur*: The Sportive Lemurs. Like most other nocturnal strepsirhines studied to date, sportive lemurs exhibit urine marking [2, 3, 58]. Only males are reported to anogenital scent mark [1–3]. Although *Lepilemur* species

are totally arboreal, patterns of defecation produce terrestrial latrines that seem to be linked to resource defence [1–3, 68].

3.1.6. Genus *Daubentonia*: The Aye-Aye. Both sexes exhibit anogenital scent marking [2, 69], and female anogenital scent marking increases during estrus [70]. Aye-ayes also engage in urine trail marking [2, 71, 72].

3.1.7. Genus *Avahi*: The Woolly Lemurs. The woolly lemurs are not at all well-studied; there is a dearth of research on their behavioural ecology. I could not find any published information on the olfactory behavioural ecology of *Avahi*.

3.2. The *Lorisiformes*. All taxa that have been studied in this nocturnal primate infraorder (that is, the lorises, pottos, and galagos, or bushbabies) scent mark extensively with urine [58], and urine marking is much more frequent than glandular scent marking. Together with the lorisine genus *Loris*, all galagine primates studied to date (except the galago genus *Euoticus*) exhibit both urine washing and punctuated urine marking (or “rhythmic micturition”) [73–76]. Urine washing can occur in a variety of contexts, including mobbing behaviour, moving into an unfamiliar area, during agonistic and aggressive encounters, and, in social interactions, especially when a female is in estrus [76–78]. Greater galagos (*Otolemur crassicaudatus*) have been shown experimentally to differentiate scent marks by sex and by individual [78, 79]. Allen’s galago (*Sciurocheirus alleni*) shows high frequencies of urine marking in territorial boundary zones [80]. Scent marking seems also to function as a stress-reducing mechanism in the small-eared bushbaby (*Otolemur garnettii*) [81]. Urine washing in *Loris*, the slender loris, has been reported to often occur in the context of consuming noxious insect prey, both before catching the prey and after consuming the prey; urine washing would also occur if a loris was stung by an insect [82]. *Loris* females have also been observed to urine wash before they groom their infants—this has been proposed to possibly have an anti-predator function when females “park” their infants while they forage (i.e., the possible anti-predator function of a female urine washing and then grooming her infant could be either that it provides an olfactory screen or barrier against potential predators, or that it acts as a form of predator mimicry while the infant is “parked”) [82].

All lorisine primates studied thus far exhibit urine trail marking in addition to punctuated urine marking [2, 58, 76, 83]. In *Loris*, inter-sexual social interactions often see males either sniffing the muzzle or anogenital region of females [82, 84]. During allogrooming bouts, *Loris* males and females will lick and rub a specialized brachial gland on their own face and body and on the body of the grooming partner [82]. *Perodicticus*, the potto, exhibits “genital scratch grooming” during which grooming partners of both sexes scent mark each other—this behaviour is not linked to reproduction [85]. In *Perodicticus*, urine marking may accompany allogrooming [86]. During allogrooming, pottos also mark each other with saliva and genital secretions [87]. *Arctocebus*,

TABLE 1: Comparative interspecific profiles of scent marking behaviours among nocturnal strepsirhine genera (i.e., lemuriforms, galagines, and lorises) and the cathemeral lemurid genera *Eulemur* and *Hapalemur*, as derived from the published literature on these taxa [1–3, 52–112]. Scent-marking behaviours: 1, urine washing; 2, punctuated urine marking; 3, urine-trail marking; 4, muzzle wipe/branch chewing (saliva deposition); 5, flehmen; 6, fecal marking; 7, latrine behaviour; 8, anogenital scent marking; 9, head marking (males).

Strepsirhine taxon (refs)	Scent-marking behaviours								
	1	2	3	4	5	6	7	8	9
Nocturnal lemuriforms									
<i>Microcebus</i> [2, 3, 52–62]]	+	+	–	+	?	–	–	–	+
<i>Mirza</i> [3, 58, 59, 63, 64]	–	+	+	+	+	–	–	(Both sexes)	?
<i>Cheirogaleus</i> [1, 2, 58, 65]	–	+	+	?	?	+	–	+	?
<i>Phaner</i> [2, 6, 66, 67]	–	?	?	?	?	–	–	– (?)	(Male throat gland)
<i>Lepilemur</i> [1–3, 58, 68]	–	+	–	?	?	–	+	(Males)	?
<i>Daubentonia</i> [2, 68, 69, 71, 72]	–	?	+	?	?	–	–	+	–
<i>Avahi</i> (no refs.)	– (?)	?	?	?	?	– (?)	– (?)	+(?)	?
Galagines [58, 73–83]									
<i>Galagoides</i>	+	+	–	?	?	–	–	?	?
<i>Galago</i>	+	+	–	?	?	–	–	?	?
<i>Euoticus</i>	–	–	–	?	?	–	–	?	?
<i>Sciurocheirus</i>	+	+	–	?	?	–	–	?	?
<i>Otolemur</i>	+	+	–	?	?	–	–	+	?
Lorisines [2, 58, 76, 82, 84–89]									
<i>Loris</i>	+	+	+	?	+	–	–	+*	–
<i>Nycticebus</i>	–	+	+	?	?	–	–	?	–
<i>Perodicticus</i>	–	+	+	?	+	–	–	+*	–
<i>Arctocebus</i>	–	+	+	?	?	–	–	+* = “passing over”	–
Cathemeral lemuriforms [1–3, 90–113]									
<i>Eulemur</i>	–	+	–	+	+	–	–	+	+
<i>Hapalemur</i>	–	+	–	+	?	–	+	+	–

the golden potto, exhibits distinctive “passing over” scent-marking behaviour, where the male straddles the female and scent-marks her dorsum [85]. “Passing over” has also been observed in *Loris* and *Perodicticus* [82]. Flehmen behaviour has recently been described in these two genera [82]; in *Loris*, it followed the licking of a urine mark while in *Perodicticus* it followed a male sniffing a substrate in a female’s home range [82]. *Nycticebus*, the slow loris, apparently possesses a “fear scent” (an “Angstgeruch”), and this has also been suggested for *Perodicticus* and *Arctocebus* (especially in the context of mother-infant alarm communication [86]); similarly, *Loris* has been suggested to have an anti-predator “alarm pheromone” [82]. Male pygmy slow lorises (*N. pygmaeus*) countermark, with urine, on both male and female urine

marks. Males countermark the urine marks of other males with significant amounts of urine. In this species, estrus females appear to prefer countermarking males [88], and males whose scent-mark odours are already familiar to them [89].

3.3. *The Cathemeral Lemurids.* Comparative data on the olfactory communication of cathemeral lemurids, a good deal of it from field research reported since 1990, reveals both broad similarities with nocturnal strepsirhines (see Table 1; [1–3, 52–113]), as well as interesting, and unforeseen, distinctions among the cathemeral lemurids themselves (see Table 2; [1–3, 90–113]). In addition to anogenital scent-marking, most cathemeral lemurid species also make use

TABLE 2: Comparative interspecific profiles of scent marking behaviours among lemurid species of the genera *Eulemur* and *Hapalemur*, as derived from the published literature on these taxa [1–3, 90–113]. The patterns seen in the two pair-bonded *Eulemur* species, *E. mongoz* and *E. rubriventer*, are very similar to each other, and contrast in significant ways to the patterns exhibited amongst the *Eulemur* taxa that occur in multimale, multifemale social groups (i.e., the *E. fulvus* group of taxa, *E. macaco*, and *E. coronatus*).

Scent-marking behaviours	<i>E. fulvus</i> group	<i>E. macaco</i>	<i>E. coronatus</i>	<i>E. mongoz</i>	<i>E. rubriventer</i>	<i>Hapalemur</i>
Anogenital scent-mark surfaces	+	+	+	+	+	+
Urine mark	+	+	+	+	?	+
Bite mark (saliva deposition) males	+	+	+	Cheek rubbing	Teeth grinding during inter-group encounters	+
Anogenital mark Conspecifics	M → F	M → F	M → F	M → F F → M	M → F F → M	M → F
HeadMarking (males)	+	+	+	+	+	–
Hand/palmarmarking (males)	+	+	+	+	+	Antebrachial gland marking
Anogenital sniff (M → F)	+	+	+	+	+	+
Self-marking	Observed in captivity	Observed in captivity	–	–	–	M marks tail with antebrachial glands to “stink fight” other Ms
Marking during inter-group encounters	Variable. Vocal & visual displays; some marking	Vocal and visual displays	Vocal & visual displays	+	+	+
					(Incl. F overmarking of M anogen marks)	(Both substrate and self-marking)
Flehmen	?	+	?	?	?	?
		(pers. obs.)				
Latrine behaviour	–	–	–	–	–	+

of punctuated urine marking (deposited concurrently with the anogenital scent mark—cf. [35], where lemurids, including several *Eulemur* taxa, are characterized as “nonurine marking” species). I could not find any report, however, of punctuated urine marking in *Eulemur rubriventer*, the red-bellied lemur (also, Tecot, personal communication). Urine washing has never been reported in any cathemeral strepsirrhine. Head marking by males occurs across the entire genus *Eulemur*.

Notably, the mongoose lemur (*E. mongoz*) and the red-bellied lemur (*E. rubriventer*), which are both pair-bonded and territorial species, share similar patterns of olfactory communication [90–94]. These two *Eulemur* species contrast in their patterns of scent-marking behaviour vis-à-vis their congeners that exhibit multi-male, multi-female social organization: the crowned lemur (*E. coronatus*) [95, 96], the black lemurs (*E. macaco* and *E. flavifrons*) [97–101], and the brown lemur taxa (*E. fulvus*, *E. rufus*, *E. sanfordi*, *E. albifrons*, *E. rufifrons*, *E. collaris*, and *E. cinereiceps*) [102–109]. I could not find any report of male “bite marking” (a behaviour in which a male chews a branch and deposits a salivary mark) in either mongoose or red-bellied lemurs. Although male bite marking has not been reported in these two species, male mongoose lemurs have been observed to cheek rub branches [91]; whether or not saliva is deposited

in this process is unclear. In both of these pair-bonded *Eulemur* species, anogenital scent marking of conspecifics of the opposite sex is performed by both sexes, rather than only males anogenitally scent marking females (a pattern seen in the multi-male, multi-female group-living *Eulemur* species). Scent marking also figures prominently during intergroup encounters with conspecific groups in both *E. mongoz* and *E. rubriventer*, including females overmarking male anogenital marks in *E. rubriventer* [93, 94]. These differential patterns of scent-marking behaviour were only uncovered as emergent patterns because of this comparative review of olfactory communication in the genus *Eulemur* and other strepsirrhine primates.

In contrast to mongoose and red-bellied lemurs (i.e., the two *Eulemur* species that exhibit pair bonding), there is a tendency among the crowned, black, and brown lemurs (i.e., the *Eulemur* taxa that exhibit multi-male, multi-female social groups), to engage in vigorous visual and vocal intergroup displays rather than intergroup displays involving concerted scent marking. In captivity, however, adjacently housed groups of brown lemurs have been observed to exhibit scent marking in addition to the aforementioned visual and vocal inter-group displays. Self-marking has been reported in captive brown lemurs (*E. fulvus*) [2], and the gray gentle lemur *Hapalemur griseus* [113]. Male *Hapalemur griseus* rub

their antebrachial glands on their tail in advance of facing off against other males in tail-waving “stink fights”; these are similar in nature to the “stink fight” displays of male ring-tailed lemurs (*Lemur catta*) [44]. I have observed a captive male black lemur (*E. macaco*) self-mark by repeatedly making palmar markings over his tail. Flehmen behaviour has been reported in the diurnal *L. catta* ([64]; personal observation). I have also observed a wild male black lemur (*E. macaco*) exhibit flehmen during the breeding season—once when he exhibited the characteristic facial grimace associated with flehmen after actively sniffing the air, and a second time after the same male sniffed a tree branch while in proximity to a juvenile male from another social group [100]. The latrine behaviour reported in *Hapalemur* [1] is unique among the cathemeral lemurids.

4. Conclusions

In broad terms, cathemeral lemurids exhibit many forms of olfactory communication that are the same as, or similar to, those seen in nocturnal strepsirhine species, including punctuated urine marking, anogenital scent marking of conspecifics, male overmarking of female scent marks, and, in the two pair-bonded *Eulemur* species, scent marking in territorial boundary zones. Within these broadly similar patterns of olfactory communication across strepsirhine primate species, there are notable distinctions in olfactory communication within the cathemeral genus *Eulemur*. One pattern is exhibited by the two pair-bonding and territorial *Eulemur* species (i.e., *E. mongoz* and *E. rubriventer*); a second pattern is seen in the *Eulemur* taxa that occur in larger multi-male, multi-female social groups. Although it should have been within the power of socioecological theory to generate predictions regarding differences in the olfactory behavioural ecology of *Eulemur* species with differing forms of social organization, it is also notable that such differences were uncovered by an intensive inductive review process. Indeed, although many gaps persist in our knowledge of the strepsirhine primates, further inductive collation of both published quantitative data on, and descriptive observations of, these species could well uncover other previously unrecognized emergent patterns in their behavioural ecology.

While key insights on strepsirhine behavioural ecology have come from increased field research on these taxa over the last 20 years, it is telling that much fundamental information on strepsirhine olfactory communication still derives from research conducted in the 1970s and early 1980s. This highlights the extent to which our understanding of the olfactory behavioural ecology of *Eulemur* species in particular, and strepsirhine primates more generally, is still only in a preliminary state. Future fieldwork should strive to record as much contextual data as possible regarding where and when various forms of olfactory communication are used (for example, what forms of olfactory communication may be exclusive to breeding behaviour? Are there types of olfactory communication that may occur primarily during inter-group encounters in zones of home range overlap or at territorial boundaries?). Additional insights on similarities

and differences among strepsirhine primate species in their chemosensory biology and olfactory communication can be expected from future studies that link odour, genetics, behaviour, and ecology [20, 26, 35, 50, 114].

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