




Marking Versus Overmarking: Spatial and Behavioral Patterns of Scent Marking in Wild Diademed Sifaka (*Propithecus diadema*)



Longondraza Miaritsoa¹ · Andrea Cascella¹ · Luigi Vadàla¹ · Daria Valente^{1,2} · Chiara De Gregorio¹ · Valeria Torti¹ · Ivan Norscia¹ · Jonah Ratsimbazafy³ · Olivier Friard¹ · Cristina Giacoma¹ · Marco Gamba¹ 

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Abstract

In mammals, olfactory communication plays an essential role in territorial and mating dynamics. Scent depositions in various species, including lemurs, can be placed via marking or overmarking (marking over previous depositions). We focused on the role that marking and overmarking play in territorial defence and intrasexual competition. We investigated these aspects in diademed sifaka (*Propithecus diadema*) in the primary rainforest of Maromizaha (eastern Madagascar). We collected scent marking data for five groups from April to November 2018 and from May to December 2019. We aimed to understand whether the lemurs deposited scent marks homogeneously across the home range and whether sex, rank, and occurrence of intergroup encounters affected the lemur's deposition rate. We also asked whether males overmarked adult females more often than other depositions, and the marking and overmarking rates changed between the migration and non-migration seasons. We found that scent marking was performed higher in peripheral and overlapping areas than in the home range central areas. In addition, males had higher scent marking rates, but intergroup encounters did not affect deposition rates. Males showed higher rates of overmarking and primarily targeted dominant females' depositions, particularly during the “migration” season (including pre-mating and mating seasons). Our findings suggest a border-marking strategy in *Propithecus diadema*. More frequent scent marking in the “migration” season suggests intrasexual competition in males. Our results suggest that marking is associated with territorial and resource defence, suggesting that it plays a role in monopolizing females using a mate-guarding strategy and may also serve for males' self-advertisement to females and subordinate depositors.

Keywords Lemurs · Olfactory signals · Intraspecific communication · Territorial defence · Ranging patterns

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Cristina Giacoma and Marco Gamba Joint last authors.

Extended author information available on the last page of the article

Introduction

Olfactory communication is an important part of social behavior for many mammalian species (Ralls, 1971; Enselberg and Kleiman, 1972). Scent marking (deposition of scent signals from urine, faeces, or glandular secretions: Kleiman, 1966) is a distinctive form of olfactory communication (Epple, 1986; Epple & Moulton, 1978; Schilling, 1979) aimed at conveying chemical signals to conspecifics (e.g., group members or neighboring conspecifics). An extensive body of studies shows that scent marks are primarily status signals involved in territorial defence (Allen et al., 1999; Braune et al., 2005; Brown & Macdonald, 1985; Coombes et al., 2018; Gorman & Mills, 1984; Gosling & Roberts, 2001a, 2001b; Lewis, 2006) and intrasexual competition (Gosling & Roberts, 2001a; Muller and Manser, 2008; Kappeler, 1998; Lewis, 2005; Norcia et al., 2009).

In line with the territorial defence hypothesis, the scent marking rate increases on days when intergroup encounters occur (Lledo-Ferrer et al., 2011; Roberts, 2012) and the spatial distribution of scent marks maximizes the probability of detection by an intruder (Gorman & Mills, 1984; Gosling, 1982; Gosling & Roberts, 2001b; Lewis, 2006; Schilling, 1980). This hypothesis suggests that scent marking is related to the size of the home range (Gorman & Mills, 1984). In species living in large home ranges, territory owners may not be able to mark the entire perimeter and may instead intensively mark the central part of the home range using the “hinterland” marking strategy (Roper et al., 1993; Mills et al., 1980; Jordan et al., 2007; Begg et al., 2003, 2005). In contrast, in species living in small home ranges, which are economically defensible and where the boundary that must be patrolled is shorter (Hamilton et al., 1976; Mitani & Rodman, 1979), overlapping and peripheral areas may be intensively marked, as these are the areas with a higher probability of intrusion and where aggressive encounters occur (Brashares & Arcese, 1999; Lewis, 2006; Roberts, 2012; Rylands, 1990). Several studies of primates have reported that the spatial distribution of scent marking supports a territorial defence function (Roberts, 2012; Lewis, 2006; Mertl-Millhollen, 1979; Ryland, 1990). It was argued that *Saguinus fuscicollis* used a “border marking strategy” by showing a higher scent marking rate at the peripheral and shared area of their home range (Roberts, 2012). Lemurs also scent marked areas close to the home range perimeter more than they did in the core area (*Propithecus verreauxi*: Lewis, 2006) and deposited a higher proportion of scent marks in overlapping areas than in the interior (*Lemur catta*, and *P. verreauxi*: Mertl-Millhollen, 1986). These studies supported the territorial defence hypothesis, which suggests that scent marks are essential to signal territorial boundaries to conspecifics (Mertl-Millhollen, 1986; Lewis, 2006).

Because scent marking provides honest signals about the depositors' quality (Charpentier et al., 2008; Harris et al., 2018; Pochron et al., 2005b), the individual and temporal patterns of scent marking also can inform conspecifics about signal function (Lewis, 2006; Pochron et al., 2005a, 2005b). Because males often are the sex with the highest intrasexual competition for access to mates (Kraus et al., 1999) and mark at higher rates than females (Heymann, 2006; Pochron et al., 2005a; Gould & Overdoff, 2002), scent marking also has been suggested to play a critical

role in intrasexual competition (Kappeler, 1990, 1998; Lewis, 2005). In line with this hypothesis, high-ranking males, who are highly engaged in reproduction and intrasexual competition, scent mark at higher rates than subordinates to advertise their status to conspecific competitors (*Lemur catta*: Kappeler, 1998; Oda, 1999; *P. verreauxi*: Kraus et al., 1999; Lewis & Van Schaik, 2007; Dall'Olio et al., 2012; *P. edwardsi*: Pochron et al., 2005a, 2005b). Scent marking also increases at specific times for the purpose of intrasexual competition. For example, a study of *P. edwardsi* found an increased rate of scent marking during lactation and before the mating season when the dispersal of adult males occurs (Pochron et al., 2004, 2005b).

The rate of overmarking (placement of a scent mark directly on top of a previously deposited scent mark) increased before the mating season (Johnston et al., 1994). The males of *Hapalemur meridionalis* overmarked female scent marks more often when younger males were likely to disperse (Eppley et al., 2016). The authors interpreted male lemurs immediately overmarking female depositions to conceal females' reproductive state to competitor males as a mate-guarding strategy (Eppley et al., 2016; Kappeler, 1998; Lewis, 2005; Lewis & Van Schaik, 2007; Palagi & Norscia, 2009).

Investigating lemurs for marking and overmarking is particularly interesting, because they are smell-oriented primates and possess specialized scent glands that show differences between males and females (Greene et al., 2019; del Barco-Trillo et al., 2012; Charpentier et al., 2010; Elwell et al., 2021). *Propithecus diadema* belongs to the family Indriidae and is one of the largest extant lemurs (Mittermeier et al., 2010). It lives in mid-altitude, dense, humid rainforests in central-eastern Madagascar (Powzyk & Mowry, 2003). It is a Critically Endangered lemur that lives in multimale–multifemale groups (Irwin, 2020; Rasolonjatovo & Irwin, 2020), occupies a home range of 21–83 ha, and travels on average 837–987 m per day depending on habitat quality (Irwin, 2008). Each group comprises a dominant adult male and a dominant adult female, with subordinate adults, subadults, and juvenile individuals, where females dominate males (Rasolonjatovo and Irwin, 2019). We chose *Propithecus diadema* (Irwin, 2020), as a suitable species to investigate scent deposition patterns in their natural habitat. The species exhibits complex scent marking behaviour by depositing scent odors from urine, faeces, and glandular secretions (sternal and anogenital glands) on different substrates (e.g., branches, trunks), either in sequence or singularly.

We investigated the spatial and behavioural patterns of both marking and overmarking in wild *Propithecus diadema* in the light of territorial defence and intrasexual competition. We tested the following hypotheses. Assuming that *Propithecus diadema* home ranges are economically defensible, we hypothesized that a long daily travel path is helpful for the animals to patrol the whole perimeter, and we predict they will increase the rate of scent marking (marking and overmarking) in peripheral and overlapping areas. Second, we hypothesized that if scent marking is linked to territorial defence (Lledo-Ferrer et al., 2011; Roberts, 2012), we predict to observe an increased scent marking rate (marking and overmarking) during the days of the intergroup encounters. Third, we hypothesized that if male lemurs, including dominant males, are subjected to intrasexual competition for mates, scent marking rate (marking and overmarking) is highest in adult and dominant male depositors than in adult females and

subordinates males. Fourth, as sifaka overmark females' scent marks (intrasexual competition by mate guarding), we predict males will immediately overmark females' depositions to conceal females' reproductive state against male competitors. Fifth, lemurs increase vigilance during the migration period, where the bond formation of the reproductive couple occurs. Thus, we predicted that *Propithecus diadema* increases the scent marking rate (marking and overmarking) to deter migrating males.

Methods

Study Site and Study Groups

We conducted field research in the Maromizaha New Protected Area in eastern Madagascar, 6.5 km from the junction to Andasibe (18° 56' S, 48° 27' E) and accessible through the village of Anevoka. Maromizaha is a mid-altitude primary rainforest, covering 2,150 ha and part of the Ankeniheny Zahamena corridor (Randrianarison et al., 2015), harbouring 12 lemur species, including our study species. Group sizes range from 4 to 11 in Maromizaha.

We studied five habituated groups of *Propithecus diadema*, focusing on patterns of scent marking. The study lasted for more than 14 months during two research periods: April–November 2018 and May–December 2019. For a total of 108 days (870.50 ± 1.06 h, mean = 8.03 ± 1.06 h per day), we collected scent mark behavioural data from 35 individuals: 21 males and 14 females (Table 1). We considered three age classes. Individuals born during the study period were designated as young, and animals older than 1 year but less than 2 years old at the beginning of the data collection were considered subadults. The remaining individuals were aged of 3.5 years and above, in line with the species interbirth interval (1.5 years: Weir, 2014), they were assigned as adults. We assigned the season based on the species reproductive schedule (Weir, 2014); Mating/Migration: November–January; Lactating/Migration: August–October; Birth: June–July; Gestation: February–May. We observed mating attempts during late lactation (September–October: 2 cases) and early mating season (November: 1 case). In addition, we observed two immigration/emigration cases during the study periods (1 case occurred in early lactation season and 1 in mating season). Thus, we labelled events recorded during the lactation/migration and mating/migration as part of the MIGRATION season; events occurring gestation and birth season, during which we observed no immigration, were labelled as the NON-MIGRATION season.

Operational Definitions and Behavioral Data Collection

We defined “marking” as the act of depositing scent signals where no other scent mark had been deposited the same day on the same spot by any group member (Lewis, 2005). We defined “overmarking” when the mark overlapped a previous scent mark by another group member entirely or partially (Johnston et al., 1994; Jordan et al., 2010; Lewis, 2005; Pochron et al., 2005b). We used “scent mark”

Table 1 Details of the Propithecus diadema study groups in the Maromizaha New Protected Area (April–November 2018 and May–December 2019). We include only individuals aged more than 6 months. #Females that gave birth at least once during the study period; *Individuals born during the study; [+ 18] and [+ 19] respectively indicate individuals that joined the group, and [– 18] and [– 19] those that left the group in 2018 and 2019. AD: adult; SA: subadult and Y: young; DOM: dominant, SUB: subordinate; M: Male, F: Female, NA: not available as the individual was not yet present in the group

Group	Individual	Sex	Age	Rank	Days	MARKING (rate per hour)				OVERMARKING (rate per hour)			
						Nonmigration season		Migration season		Nonmigration season		Migration season	
						Mean	SD	Mean	SD	Mean	SD	Mean	SD
2PD-MZ	Kaly [– 18]	M	AD	DOM	3	NA	NA	1.800	1.740	NA	NA	0.900	0.660
	Gigi [+ 18]	M	AD	DOM	21	0.007	0.360	1.860	1.140	0.360	0.300	0.720	0.300
	Joby	M	AD	SUB	25	0.300	0.180	0.420	0.480	0.180	0.060	0.240	0.180
	Tsikivy	M	AD	SUB	25	0.240	0.180	0.300	0.300	0.000	0.000	0.060	0.000
	Blue	M	SA	SUB	25	0.120	0.060	0.180	0.060	0.000	0.000	0.000	0.000
	Tandra#	F	AD	DOM	25	0.360	0.180	0.660	0.300	0.240	0.000	0.180	0.060
	Onja#	F	AD	SUB	25	0.300	0.180	0.540	0.420	0.060	0.000	0.120	0.000
	Kintana	F	AD	SUB	25	0.300	0.180	0.120	0.060	0.000	0.000	0.000	0.000
	Voa	F	AD	SUB	25	0.120	0.000	0.060	0.000	0.000	0.000	0.000	0.000
	Green	F	SA	SUB	25	0.180	0.060	0.180	0.060	0.000	0.000	0.000	0.000
3PD-MZ	Fotsiloha [– 19]	M	AD	DOM	15	0.660	0.360	1.140	0.840	0.480	0.300	0.600	0.360
	Andry [+ 19]	M	AD	DOM	7	NA	NA	1.680	1.080	NA	NA	1.140	0.540
	Mike	M	AD	SUB	24	0.360	0.240	0.720	0.780	0.000	0.000	0.420	0.360
	Bisky	M	AD	SUB	24	0.180	0.060	0.300	0.420	0.180	0.000	0.240	0.000
	Pink	M	SA	SUB	24	0.120	0.000	0.120	0.060	0.000	0.000	0.120	0.000
	Orchide#	F	AD	DOM	24	0.480	0.300	1.260	0.900	0.000	0.000	0.180	0.000
	Siramamy#	F	AD	SUB	24	0.180	0.120	0.300	0.120	0.000	0.000	0.180	0.060
	Rahona [– 19]	F	AD	SUB	15	0.240	0.120	0.060	0.000	0.000	0.000	0.000	0.000

Table 1 (continued)

Group	Individual	Sex	Age	Rank	Days	MARKING (rate per hour)				OVERMARKING (rate per hour)				
						Nonmigration season		Migration season		Nonmigration season		Migration season		
						Mean	SD	Mean	SD	Mean	SD	Mean	SD	
4PD-MZ	Feno	M	AD	DOM	24	0.720	0.360	1.260	0.720	0.360	0.360	0.300	0.780	0.480
	Tantely	M	AD	SUB	24	0.600	0.540	0.600	0.540	0.180	0.060	0.060	0.240	0.120
	Faly	M	AD	SUB	24	0.300	0.180	0.420	0.420	0.120	0.000	0.000	0.180	0.060
6PD-MZ	Faniry	M	SA	SUB	24	0.240	0.120	0.240	0.060	0.000	0.000	0.000	0.180	0.000
	Volana [#]	F	AD	DOM	24	0.780	0.420	1.320	0.840	0.120	0.000	0.000	0.120	0.060
	Hery	M	AD	DOM	19	0.960	0.600	1.260	0.960	0.780	0.480	0.480	0.660	0.540
	Hasina	M	SA	SUB	19	0.180	0.180	0.540	0.420	0.180	0.000	0.000	0.000	0.000
	Akondro [*]	M	Y	SUB	6	0.120	0.000	0.120	0.000	0.000	0.000	0.000	0.000	0.000
	Masina [#]	F	AD	DOM	19	0.540	0.360	0.540	0.120	0.120	0.000	0.000	0.000	0.000
	Diane [#]	F	AD	SUB	19	0.480	0.360	0.780	0.480	0.000	0.000	0.000	0.120	0.000
8PD-MZ	Gavo [*]	F	Y	SUB	6	0.120	0.000	0.120	0.000	0.000	0.000	0.000	0.000	0.000
	Tafta	M	AD	DOM	16	0.780	0.540	1.620	1.560	0.240	0.180	0.180	0.420	0.300
	Lova	M	AD	SUB	16	0.420	0.240	0.480	0.000	0.120	0.000	0.000	0.000	0.000
	Tia	M	AD	SUB	16	0.180	0.060	0.660	0.780	0.000	0.000	0.000	0.000	0.000
	Papay [*]	M	Y	SUB	6	0.240	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Litchi	Afaka [#]	F	AD	DOM	16	0.420	0.300	0.540	0.300	0.000	0.000	0.000	0.000	0.000
	Litchi	F	SA	SUB	10	0.180	0.000	0.000	0.000	0.120	0.000	0.000	0.000	0.000

to indicate both marking and overmarking depositions (Lewis, 2005). We define as an “event” any sequence of scent marking deposition, without interruption at the same spot on a given substrate, through chest rubbing, anogenital rubbing, and urine, or faecal deposition. We indicated as scent mark each single marking behaviour (e.g., anogenital rubbing, chest rubbing, and urination) in a scent marking event. Thus, each marking “event” can be composed of one or multiple marking “acts” (Heymann, 2000; Lledo-Ferrer et al., 2011).

We used all occurrences sampling (Altmann, 1974), collecting data across all individuals in the group to maximize data collection on these relatively infrequent behavioural events. We focused on one group for 3–4 consecutive days per week. On each sampling day, we reached the group between 6:00 and 7:30 AM (before the start of the animals’ activity) and followed it until dusk (4:00 to 5:30 PM) when the animals went to sleep. For each scent marking event, we recorded depositor identity, the target substrate part (trunk or branch), and the time at which the lemur deposited a scent mark. We also monitored whether another individual followed, inspected, and scent marked on the same spot. Indeed, after any scent mark event, two observers monitored the other individuals’ behaviour until the group members left the spot. We also recorded the timing of the overmarking, whether it occurred within one minute, within or after 5 min of scent deposition. Thus, we could identify the overmarker (followers) and the first depositor.

Propithecus diadema use tree trunks and occupies the lower part of the forest (Powzyk, 1997), allowing good visibility during scent marking deposition. We used natural marks, such as permanent scars and pelage variation, to distinguish individuals. Two researchers and two research guides collected data simultaneously, following different animals, to ensure that all group members were visible at any time. If two or more observers witnessed a scent marking deposition, we reached a consensus on the depositors’ identity and the sequence of scent marking acts immediately after the observation. If an observer had doubts about the depositor’s identity, he or she asked the others to achieve consensus on identification. Four of five groups were small, with 4–6 individuals and 3–5 adults per group, and we could detect each group member individually. The largest group (2PD-MZ) was more widely spread than other groups (up to 40 m). If we could not keep all group members in sight, and if we did not observe adults, dominant, or reproductive individuals, we excluded this day from the behavioural and spatial analysis of scent marking, but we still considered it for the group home-range estimation.

We also observed the behaviour of the group members during intergroup encounters and on the following day to compare days with and without intergroup encounters. If we could not observe the group on the following day, we used data from the day before the encounter in our comparison instead (Lledo-Ferrer et al., 2011). In addition to scent marking, we recorded aggressive interactions between group members to determine the dominance hierarchy among individuals, using all occurrences sampling (Altmann, 1974).

Spatial Data Collection

We tracked and geo-referenced specific behaviors performed by the animals, including feeding, intergroup encounters, locomotion, and scent marking events (marking and overmarking), on a Garmin GPS MAP 78 S, with precision ranging 3–10 m. In addition, we recorded a new GPS point every time the group members interrupted their activities and moved 20–50 m away from their previous location and engaged in the same or different behavior (Bonadonna et al., 2017, 2020). When different behaviors occurred at one GPS waypoint (from the same or different individuals), we coded the point accordingly (example: feeding then marking). We recorded only one GPS waypoint from if we observed several scent mark events at a single location (e.g., deposited within a distance of less than 20 m from the previous GPS waypoint) by one or more individuals (e.g., in the case of overmarking). Our points were not equally weighted since time spent at each location changed according to the behaviors performed in each location.

Spatial Analysis

We analyzed spatial data in QGIS (QGIS development team, 2018) coupled with ArcGis (ESRI, 2016). We performed all statistical analyses using R software (R Core Team, 2018; version 3.6.1).

Home Range Size

We first estimated each group's home range and identified overlapping areas (the portion of the home range used by two or more adjacent groups) using the Characteristic Hull Polygon method (95% CHP: Downs & Horner, 2009). We used 95% CHP, because both the Minimum Convex Polygon (MCP) and Kernel Density Estimation (KDE) tend to overestimate home range size (Downs & Horner, 2009; MCP: Burgman & Fox, 2003; KDE: Walter et al., 2011). Next, we calculated the home ranges with QGIS software (QGIS development team, 2018) using spatial data collected during the 154 days of following (mean \pm SD = 30 ± 4 days per group; range: 23–35 days), analyzing 2,281 GPS waypoints (mean \pm SD = 456.20 ± 54.75 per group). We assessed whether the number of days with spatial data collection was enough to compute the groups' home ranges by plotting the home range size against the number of days of observation for each group. We extracted 10,000 random combinations for each number of days and calculated the mean and standard deviation of the Characteristic Hull Polygons (CHP). There is a slowdown in the curve slope from left to right (group 3PD-MZ, 8PD-MZ, and 4PD-MZ), indicating that the home range will not increase significantly even if additional data are provided, except for 6PD-MZ and 2PD-MZ that seem still climbing (Fig. 1).

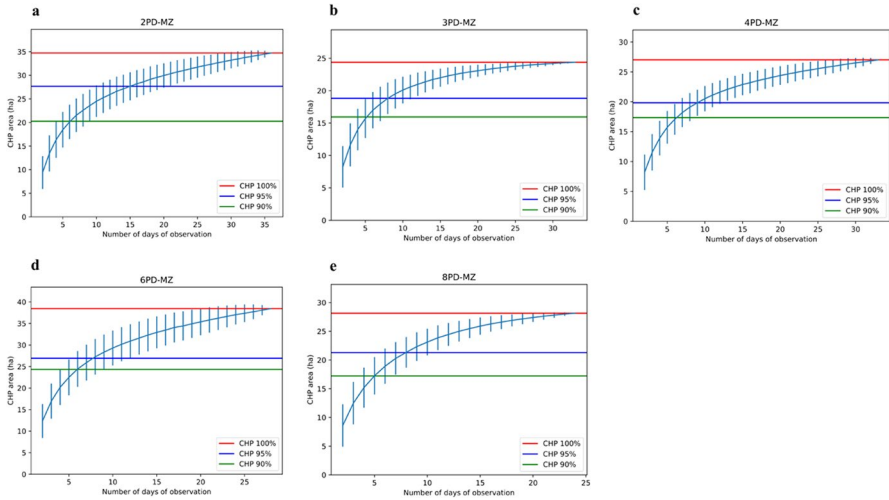


Fig. 1 Accumulation curve computed by plotting the home range size (ha) against the number of days of observations using the Characteristic Hull Polygon method for five groups of diademed sifaka (*Protophthalmus diadema*) in Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019) (a–e). We computed the curve using 10,000 random combinations for each number of days.

Home Range Defendability

Home range defendability depends on an animal’s ability to monitor the perimeter of its range to detect potential intruders (Hamilton et al., 1976; Mitani & Rodman, 1979). The defendability index (D) is defined as the ratio of observed daily path length (d) to an area equal to the diameter (d’) of a circle with an area equivalent to the home range area of the animal ($D = d/d'$). The term d’ is defined by the formula: $(4A/\pi)^{0.5}$, where A represents the area of the home range of a given group; thus, $D = d/\sqrt{(4A/\pi)}$. When the index value is less than 1, the territory is considered not defendable, whereas when the index value is equal to or higher than 1, the home range is considered defendable (Mitani & Rodman, 1979). We applied this formula to define the defendability index of each group’s home range. To do so, we first measured each group’s daily travel path length (d) using ArcGIS software (ESRI, 2016), considering only days when we followed the group for the whole day (total of 136 days), with a mean of 17 points per day (range: 7–32).

Use of the Home Range

To assess the pattern of home range usage, we applied the gridding technique (Bona-donna et al., 2020). First, we established a 0.216 ha network of hexagons for each home range using the data management tools in QGIS (QGIS development team, 2018). As we recorded a new GPS point every 20–50 m, the size of 0.216 ha is

appropriate to aggregate at least two waypoints per hexagon. Then, we aggregated the hours spent by the group at each point location when engaging in a particular behavior in each hexagon (Bonadonna et al., 2020) and the time between two successive GPS points.

To define the central and peripheral area of the home range, we extracted the centroid of each hexagon using the QGIS geoprocessing tool options. We defined hexagons with a centroid more than 50 m away from the home range boundary as the “central area” and hexagons with a centroid less than 50 m from the boundary as “peripheral areas.” We focused on four groups that had at least one inter-group encounter during data collection to identify the overlapping area. We defined hexagons that were included at least in part in the shared area between two or more adjacent groups as “overlapping areas.” We defined all the other hexagons as “nonoverlapping areas.”

Spatial Distribution of Scent Marking

We pooled an individual’s scent marking (marking and overmarking events) per GPS waypoint location. We then mapped the pooled geo-referenced scent marks onto the groups’ home range. Next, we counted the marking and overmarking events performed by each individual in each home range hexagon and for central, peripheral, overlapping and nonoverlapping areas using the QGIS analyst tool. We then calculated the rate (events per hour) by dividing the scent marking count by the time spent in each area. We calculated the timeframe by extracting the time that passed between two successive GPS points.

To assess whether the scent marking changed depending on an individuals’ position in the home range, we compared the rate of scent marking: 1) between the central area and peripheral area (all 5 groups), and 2) between overlapping and nonoverlapping areas (4 adjacent groups: 2PD-MZ, 4PD-MZ, 6PD-MZ, and 8PD-MZ). Where the data were not normally distributed (Kolmogorov–Smirnov: $P < 0.05$) we used a Wilcoxon matched-pairs signed-ranks test (hereafter, Wilcoxon test; Mundry & Fischer, 1998; Siegel & Castellan, 1988). When data were normally distributed, we used a paired *t*-test. We excluded one adult male from analysis because he left the group (2PD-MZ) when we had sampled it for just 3 days.

Analysis of the Behavioral Data

First, we ran a steepness analysis to evaluate dominance hierarchy among individuals. We calculate the David’s Score for each lemur (*i*) by summing the proportion of its wins during interactions with another individual divided by the number of interactions with the other individual (*w*) with w_2 (e.g., the summed *w* values of those individuals with which *i* interacted). We then subtracted *l*, which represents the sum of that particular individual’s losses against the other individual, and l_2 , which represents the summed *l* values of those individuals with whom *i* interacted (Shizuka & McDonald, 2012). As females dominate males (Rasolonjatovo and Irwin, 2019), we

analyzed males' agonistic interactions (chase, bite, fight) separately from those of females. We defined the individuals with the highest value of David's score as dominant and those with lower scores as subordinates (Shizuka & McDonald, 2012).

When intergroup encounter occurred, we quantified scent marking for each individual during the day of the intergroup encounter and calculated the rate by dividing the total count by the individual observation time. We analyzed three groups, namely 2PD-MZ, 6PD-MZ, and 8PD-MZ. We excluded an individual not sampled during the intergroup encounters from the analysis. We also extracted the rate of scent marking recorded on the following day (or the day before if data on the following day were not available) and compared the rates. The data were not normally distributed (Kolmogorov–Smirnov, $P < 0.05$), and the sample size was limited, so we used a Wilcoxon matched-pairs, signed-ranks test (Mundry & Fischer, 1998; Siegel & Castellan, 1988) to compare scent marking rates on the day of encounter to those on the day with no such encounter.

We then pooled the daily scent marking observations for each individual. Next, we calculated the rate of marking and overmarking per hour by dividing the scent marking counts by individuals' daily observation time. Using these rates as the response variables, we built Generalized Linear Mixed Effects Models (GLMMs) using the *glmmTMB* package that can handle zero-inflated data (Brook et al., 2017) in R studio (R Core Team, 2018; version 3.6.1) on data for all five study groups. Our goal was to test whether the rate of occurrence is affected by sex, social rank, or season considering only adults. We removed two adult males sampled on fewer than 8 days or sampled for one season only from the analysis. We also excluded one adult female, because including her values caused residuals to deviate from a normal distribution. We used the *glmmTMB* function to perform the model with the beta family distribution. We built a full and a null model in which we set the scent marking rates as the response variable (*rate_min*). We set the depositor's sex (male, female), rank (dominant, subordinate), and season (migration, nonmigration) as fixed factors and depositor identity ($N_{\text{levels}} = 23$), group ($N_{\text{levels}} = 5$), and day of sampling ($N_{\text{levels}} = 108$) as random factors. We also assessed the interaction between social rank and season. We retained depositor sex, and the interaction between social rank and season as fixed factors. We examined the variance inflation factors (VIF package; Fox & Weisberg, 2011) to exclude collinear predictors. We used an inclusion threshold of $VIF < 5$, because $VIF \geq 5$ may indicate considerable collinearity (Chatterjee & Simonoff, 2013; James et al., 2017).

We tested the full model's significance (Forstmeier & Schielzeth, 2011) by comparing it against the null model, using a likelihood ratio test (ANOVA with argument test *Chisq*; Dobson, 2002). We used the R function "*drop1*" (Barr et al., 2013) to calculate *P* values for each predictor based on likelihood ratio tests between the full and the null model. We checked whether the residuals were normally distributed and homogeneous by looking at a *qqplot* curve and the distribution of the residuals plotted against the fitted values (DHARMA R package: Hartig, 2016).

Because we did not assess the interaction between sex and season, we ran a further analysis to compare the marking rate for adult males and females across the seasons (NONMIGRATION vs. MIGRATION). Because we could not fit a GLMM model to assess the factors affecting the overmarking rate due to the limited number

of depositors (the model would not converge and the distribution of the residuals highly deviated from a normal distribution), we also compared the male overmarking rate targeting either male and female scent depositions between the NONMIGRATION and MIGRATION seasons. Because the data were not normally distributed (Kolmogorov–Smirnov, $P < 0.05$), we used Wilcoxon matched-pairs, signed-rank tests for two paired samples (Mundry & Fischer, 1998; Siegel & Castellan, 1988). We included only individuals that we observed for both periods in the analysis. Finally, we used a Man-Whitney U test to compare the rate of overmarking between sexes.

Ethical Note

We performed this study in the Maromizaha Protected Area, Central Eastern-Madagascar, with research permits 91/18/MEF/SG/DGF/DSAP/SCB: 118/19/MEDD/SG/DGEF/DSAP/DGRNE, 284/19/MEDD/SG/DGEF/DSAP/DGRNE and 338/19/MEDD/SG/DGEF/DSAP/DGRNE, delivered by the Ministère de l'Environnement et du Développement Durable (MEDD). During the study, we conducted only behavioral observations without manipulating animals. All the information reported in this paper result from our own data. The findings are not reported anywhere else. We also declare that the data collection procedure conformed to the national legislation and international regulation regarding animal welfare.

Results

Home Range of the Study Groups

The study groups occupied economically defensible home ranges with a mean size of 20.7 ± 4 ha (SD). Group 6PD-MZ had the largest home range (95% CHP: 25.5 ha) and shared 25.5% (6.5 ha) of its home range with at least three adjacent groups (4PD-MZ, 8PD-MZ, and 2PD-MZ; Fig. 2). Group 3PD-MZ had the smallest home range ($HRS_{\text{MEAN}} \pm \text{SD}$: 16.6 ha) and did not overlap with the other study groups. Overall, the study groups traveled a mean daily travel path length of 720.1 ± 106 m. The home range defendability index (D) across all groups was 1.4 ± 0.2 . Only 1 of 5 adjacent groups did not share part of its home range with any of the other study groups.

The mean home range overlap between four adjacent groups was $13 \pm 12\%$ (Fig. 2b), and 10 intergroup encounters occurred in these overlapping areas. Each group used an area of 17.7 ± 1.5 ha exclusively.

Scent Marking Spatial Distribution Pattern

Overall, the rate of marking deposition was significantly higher in the peripheral area than the central area of the home range (Matched-Wilcoxon test: $N = 25$,

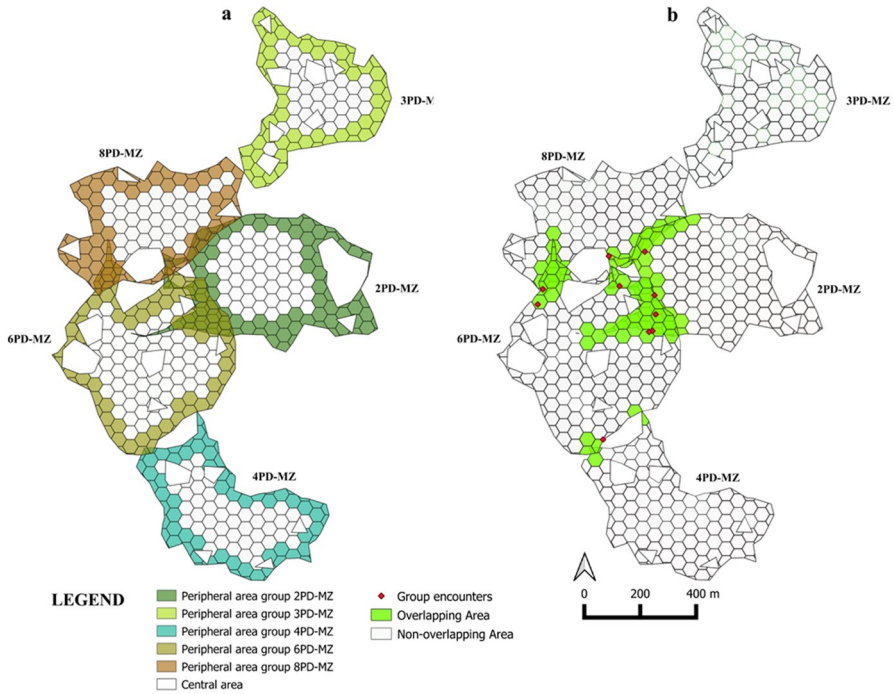


Fig. 2 Maps of home ranges (95% Characteristic Hull method) and home range overlaps of five adjacent groups of diademed sifaka (*Propithecus diadema*) in Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019). **(a)** Peripheral areas are in different colors for each study group and the central area is represented by empty hexagons. **(b)** Overlapping hexagons are in light green and non-overlapping areas are in white. The irregular shapes in each home range are not part of the home range.

$V=23$, $P<0.001$). In particular, dominant males deposited scent marks at higher rates at the home range border (paired t -test: $t(5) = -3.097$; $P_{adj}=0.027$) (Fig. 3a). In contrast, dominant females ($N=5$; $V=0$, $P_{adj}=0.062$; Fig. 3b), subordinate males ($N=8$, $V=7$, $P_{adj}=0.148$), and subordinate females ($N=6$, $V=3$, $P_{adj}=0.156$) did not show a significant preference for either peripheral or central areas (Figs. 3c–d).

Overall, males overmarked more in the peripheral than in the central zone of the home range (matched Wilcoxon test: $N=14$, $V=13$, $P_{adj}=0.025$). In particular, dominant males overmarked at a significantly lower rate in the central area (Fig. 3e) than the peripheral area ($N=6$, $V=0$, $P_{adj}=0.031$). This was not the case for subordinate individuals (Fig. 3f), which did not differ significantly in the rate of overmarking across all areas ($N=8$, $V=13$, $P_{adj}=0.933$).

Individuals also marked at a significantly higher rate in the overlapping than in the nonoverlapping area (matched Wilcoxon test: $N=18$, $V=17.5$, $P_{adj}=0.003$). We observed a similar pattern for male ($N=10$, $V=17$, $P_{adj}=0.048$) and female depositors ($N=8$, $V=2.5$, $P_{adj}=0.035$) (Figs. 4a–b). In particular, dominant depositors

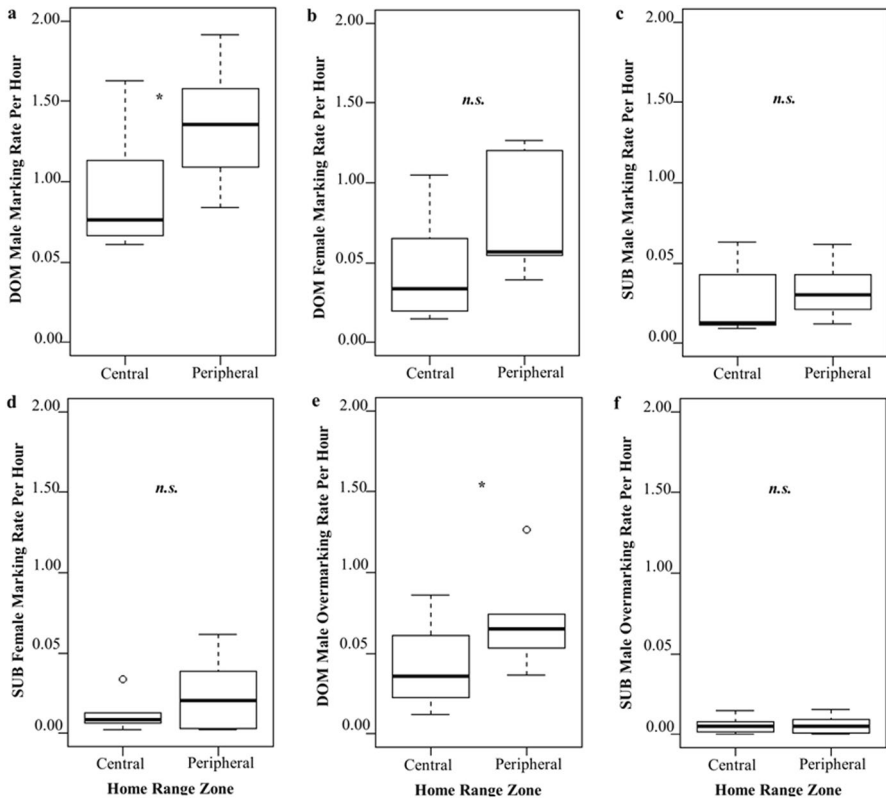


Fig. 3 Rate of marking (a–d) and overmarking (e–f) between central and peripheral areas in five adjacent groups of diademed sifaka (*Propithecus diadema*) at the Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019). Plots show scent marking rates for dominant males (a and e), dominant females (b), subordinate males (c and f), and subordinate females (d). Whiskers indicate 5th/95th percentiles, the horizontal line gives the median, the box the 25th/75th percentiles, and open circles outliers. DOM: dominant depositors; SUB: subordinate depositors; *n.s.*: non-significant.

of both sexes showed higher rates of marking in the overlapping area than the non-overlapping areas (Fig. 4c; $N=8$, $V=1.5$, $P_{adj}=0.025$). In contrast, we did not find a significant difference (Fig. 4d) between these two areas for subordinate individuals ($N=10$, $V=10$, $P_{adj}=0.084$). There was no significant difference in the overmarking rate between overlapping and nonoverlapping areas for adult males (Wilcoxon test: $N=9$; $V=6$, $P_{adj}=0.055$; Fig. 4e).

Effect of Intergroup Encounter on Scent Marking Behaviour

We observed ten intergroup encounters, of which only one ended in an aggressive confrontation, including chasing and biting, and nine consisted of distant confrontation, including jumping between branches and vocal displays

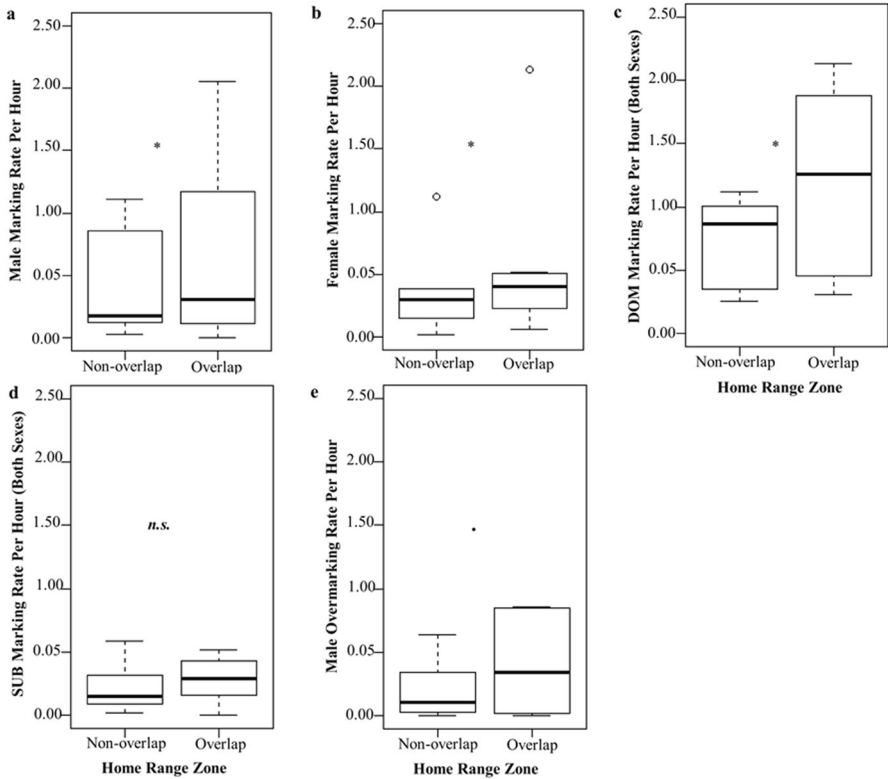


Fig. 4 Rate of marking (**a-d**) and overmarking event occurrence (**e**) between the overlapping and non-overlapping areas in four adjacent groups of diademed sifaka (*Propithecus diadema*) at the Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019). Presented are the rate of scent marking event in adult males (**a** and **e**), adult females (**b**), in dominant (**c**), and subordinate (**d**) individuals from both sexes, and the rate of overmarking in adult males (**e**). Significant results (with P value < 0.05) are highlighted with single star (*), result with P -value = 0.05 is highlighted with single full stop (.) and nonsignificant results (with P value > 0.05) are represented by *n.s.* Whiskers indicate 5th/95th percentiles; the horizontal line gives the median, and the box gives the 25th/75th percentiles, and open circles denote outliers. DOM: dominant depositors; SUB: subordinate depositors.

as Zzuss and Zzuss-Tsk (Valente et al., 2022). Only adult individuals of both sexes participated in the physical confrontation and scent marking deposition. Although individuals marked more frequently on intergroup encounter days than on days without an intergroup encounter, this comparison was not significant (matched Wilcoxon test: $N = 14$, $V = 32$, $Padj = 0.217$). Neither dominant ($N = 6$, $V = 3$, $Padj = 0.156$) nor subordinate adults ($N = 8$, $V = 9$, $Padj = 0.250$) increased their marking rate significantly on days with intergroup encounters. Intergroup encounters did not affect the overmarking rate ($N = 14$, $V = 13$, $Padj = 0.523$). However, resident adult males often overmarked adult male intruders' and resident females' deposition (e.g., 3 of 4

scent marks deposited by intruder males from group 2PD-MZ were overmarked by adult male in the group 8PD-MZ).

Effects of Sex, Dominance Rank, and Season on Marking and Overmarking

For marking, the full model significantly differed from the null model (full vs. null: $\chi^2=62.788$, $df=4$, $P_{adj}<0.001$; Table II). We found a significant difference in marking rate between sexes with males marking more frequently than females (Table II). The model also showed that marking was influenced by the social rank of depositors with dominant individuals marking at significantly higher rates than subordinates (Table II). There was clear seasonality in marking, which occurred more frequently in the MIGRATION season than in the NONMIGRATION season (Table II). Unlike dominant depositors, the marking of subordinates did not differ between seasons (Pairwise Tukey-test: DOM.MIGRATION—DOM.NONMIGRATION, *Estimate*=0.585; *SE*=0.097, *Z*=6.004, $P<0.001$; SUB.MIGRATION—SUB.NONMIGRATION; *Estimate*=0.113, *SE*=0.118; *Z*=0.965, $P_{adj}=0.760$).

Both males and females showed a seasonal pattern of marking. The marking rate was significantly higher during MIGRATION than NON-MIGRATION season in both males (matched Wilcoxon test: $N=13$, $V=0$, $P_{adj}=0.002$) and females ($N=10$, $V=3$, $P_{adj}=0.042$).

We found a significant difference between the sexes with males overmarking more often than females (Mann–Whitney *U* test: $N_{Male}=15$, $N_{Female}=11$; $W=25$, $P_{adj}=0.003$): 96% of overmarking events ($N=544$) were performed by males, whereas only in 4% ($N=25$) were by females. Moreover, males preferentially targeted female scent marks (Table III). Overall, the vast majority of females' depositions were overmarked by dominant males (Table III). Overmarking of female scent marks by males typically happened very quickly, within the first 60 s after deposition (> 82% of cases) and rarely more than 5 min after deposition (< 3.5%; Fig. 5). Adult male overmarking rates on adult female scent depositions also were higher in the MIGRATION than in the NONMIGRATION season (matched Wilcoxon test: $N=13$, $V=7$, $P_{adj}=0.041$).

Table II Influence of fixed factors on marking rate of *Propithecus diadema* at the Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019): results of a reduced model including only significant interaction (full vs. null: $\chi^2=62.788$, $df=4$, $P_{adj}<0.001$). *na*: Not shown as has no meaningful interpretation

	<i>Estimate</i>	<i>SE</i>	<i>df</i>	Likelihood ratio test	<i>P</i>
<i>Intercept</i>	-4.703	0.106	<i>na</i>	<i>na</i>	<0.001
<i>SexMALE</i>	0.237	0.102	1	4.709	0.020
<i>rankSUB</i>	-0.510	0.118	1	13.766	<0.001
<i>Season MIGRATION</i>	0.585	0.097	1	13.766	<0.001
<i>rankSUB:seasonMIGRATION</i>	0.471	0.125	1	13.766	<0.001

Table III Absolute frequency and percentage of scent marking being overmarked, overmarked by adult and by dominant males across seasons for *Propithecus diadema* at the Maromizaha New Protected Area, Madagascar (April–November 2018 and May–December 2019). The first line is a count and the second line with bold text is a percentage (%) of scent markings being overmarked

SM depositors	Season	# scent marking events	Number (%) of overmarked scent marks			
			Overall	By male	By dominant male	
Adult female	NONMIGRATION	322	155 (48.1)	154 (99.4)	145 (93.5)	Count %
	MIGRATION	528	317 (60.0)	314 (99.1)	274 (86.4)	Count %
Breeding female	NONMIGRATION	292	151 (51.7)	150 (99.3)	141 (93.4)	Count %
	MIGRATION	521	317 (60.8)	314 (99.1)	274 (86.4)	Count %
Dominant female	NONMIGRATION	204	113 (55.4)	113 (100.0)	107 (94.7)	Count %
	MIGRATION	417	270 (64.7)	269 (99.6)	234 (86.7)	Count %
Adult male	BOTH PERIODS	1863	80 (4.3)	61 (76.3)	37 (46.3)	Count %

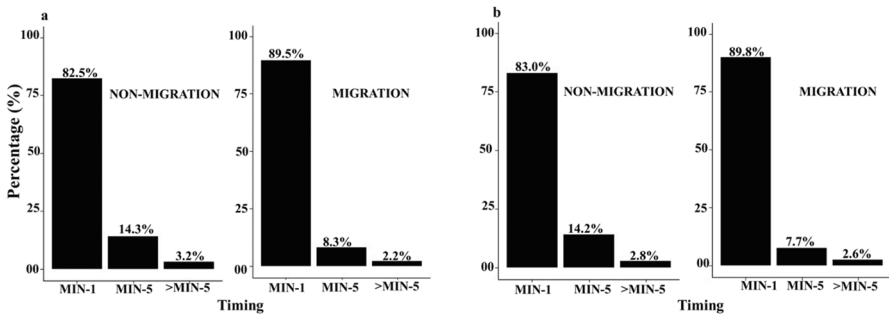


Fig. 5 Percentage of overmarkings of female scent depositions happening within 60 s (MIN-1), the first 5 min (MIN-5), and after the first 5 min (>MIN-5) after scent deposition in NONMIGRATION and MIGRATION seasons. **(a)** Adult female scent marks overmarked by adult males and **(b)** reproductive female scent marks overmarked by dominant males.

Discussion

Marking rates in *Propithecus diadema* differed significantly between the peripheral and central areas of the home range, and between the exclusive areas and areas shared with neighbouring groups. These findings support our first prediction, that scent marking targets the area with a higher probability of signal detection by

neighbouring groups like in the periphery or zones of overlap with neighbouring groups. We also found that *P. diadema* occupied economically defensible home ranges in Maromizaha. These findings are consistent with a border-marking strategy (Gorman & Mills, 1984) and in line with studies reporting that Verreaux's sifaka (*Propithecus verreauxi*) scent marked the boundaries of their home range more frequently than the core area (Mertl-Millhollen, 1979; Lewis, 2006). However, when analysed by sex, we found that the differences in marking at the territory's borders or in the central area are significant only for males but not for females. This finding agrees with observations suggesting that motivation may differ between individuals (Lewis, 2006).

Females may scent marks to advertise their reproductive status to extra-group males (Lewis, 2006) or claim ownership of feeding resources (Palagi & Norscia, 2009). Our data suggest that subordinate individuals make scent marks across the home range to advertise their presence. Overall, our findings are consistent with the territorial defence hypothesis (Lewis, 2005; Pochron et al., 2005a, 2005b). They also agree with studies of saddleback tamarins (*Saguinus fuscicollis*) that exhibited a clear border-marking strategy by intensely marking the home range's peripheral and overlapping areas (Roberts, 2012). Our results showed that overmarking rates also differed significantly between the peripheral and central areas but not between areas shared and not shared with neighboring groups. This difference suggests a different role for marking and overmarking. This finding also is in line with previous studies of lemurs suggesting that the spatial distribution of overmarkings indicate a male tactic related to intrasexual competition (Lewis & Van Schaik, 2007; Norscia et al., 2009). Because previous studies suggested that dominant males are more often mating successfully with dominant females (Kappeler & Schäffler, 2008; Norscia et al., 2009), they may specifically target female depositions if placed at the home range border to conceal female reproductive status from male competitors. Future studies with a larger sample size are needed to test this hypothesis.

In contrast with our second hypothesis, we did not find evidence that scent marking rate increased on days on which intergroup encounters happened (Lledo-Ferrer et al., 2011), possibly because direct competition for resources is only partially based on the olfactory signals or because differences in the daily occurrence of marking did not reflect on the daily rate.

In support of our third hypothesis, we found a clear intersexual difference in the amount of scent marking events, with males depositing markings and overmarkings at higher rates than females. This is in line with previous findings. For example, in Milne-Edwards' sifaka (*Propithecus edwardsi*), males scent marked almost twice as often as females (Pochron et al., 2005a, 2005b). Male *Propithecus verreauxi* also scent marked significantly more often than females (Lewis, 2005). Such evidence has been linked to the intrasexual competition hypothesis, in which the sex that competes more strongly for mates, scent marks more often than the other sex (Heymann, 2006). In line with our prediction, our study also provided evidence that dominant individuals mark at higher rates than subordinate individuals, as observed in several other primate species, and in lemurs in particular. For example, studies of *Propithecus verreauxi* (Lewis, 2005), and *Propithecus edwardsi* (Pochron et al., 2005a, 2005b) reported that either dominant males or females scent marked more

often than subordinates. In *Lemur catta*, dominant individuals also showed a higher rate of scent marking than subordinates (Kappeler, 1990, 1998). Other studies found that dominant sifaka are highly involved in reproductive and intrasexual competition (Lewis & van Schaik, 2007), because they sire the large majority (>90%) of offspring (Kappeler & Schäffler, 2008). In our study, dominant males also overmarked significantly more often than subordinates. Previous findings on the biological market of mating in *P. verreauxi* found that dominant males who overmarked more were more likely to succeed in mating with reproductive females (Norscia et al., 2009). Dominant adult male *P. verreauxi* had a higher rate of chest marking and copulated more frequently with reproductive females than clean chested (mostly subordinate) males (Dall'Olivo et al., 2012). In conclusion, our findings, like those of other studies, suggest an influence of sex and especially social rank on scent marking and odor-mediated intrasexual competition in hierarchical lemur societies.

Supporting our fourth prediction, adult and dominant males also overmarked adult and breeding female scent depositions more frequently, but not male depositions. This intersexual difference in performing and receiving overmarking aligns with the intrasexual competition hypothesis. In *Propithecus verreauxi*, males immediately overmarked female scent marks, and researchers interpreted this behavior as a form of mate competition between males (Lewis & Van Schaik, 2007). In other primate species, males actively overmark mostly female scent depositions, which suggests a mate-guarding function (*Lemur catta*: Kappeler, 1998; *Saguinus fuscicollis*: Lledo-Ferrer et al., 2010; southern bamboo lemur, *Hapalemur meridionalis*, Eppley et al., 2016). In *P. diadema* male overmarking occurred mainly within the first 60 s of female scent deposition. This behavior may serve to claim ownership of the female or to conceal the female's odor from male competitors. Thus, by scent marking, females may advertise themselves as available for mating, whereas males' scent marking and overmarking may allow males to assess the competitive abilities of other males (Kappeler, 1990), playing a role in intrasexual competition.

Finally, marking and overmarking showed seasonal differences, in agreement with the hypothesis that they may play a critical role in advertising intersexual competition for mates. This difference supporting our fifth prediction by showing that adult dominant males and females scent marked at significantly higher rates in the MIGRATION season. Scent marking may serve different functions in the two sexes (Lewis, 2006; Pochron et al., 2005b). For our focal species, the fact that adult and dominant males showed the highest marking rate in the migration period could serve to intimidate and deter migrating adult male competitors (Pochron et al., 2005b). The increase in the rate of overmarking also is in line with intrasexual competition for mates, because it may serve the defence of reproductive females from migrating same-sex competitors. This interpretation does not exclude territorial defence as a function of scent marking because additional markings deposited in the migration period (premating/mating season) may prevent competitors from neighbouring groups and immigrants from using the resources present in the home range and occupying the home range when successful reproduction is at stake. Both sexes scent marked significantly more in the migration season than in the non-migration season. Such an increase may be further associated with other factors. For example, during late lactation and the early

mating season, females may need more energetic resources to secure reproduction success. Consequently, females may invest more in defending feeding resources by increasing the scent marking rate. In addition, the offspring are closer at weaning and become more independent during the early mating season, so they may find beneficial to scent mark more often to communicate their identity to conspecifics (e.g., to receive provisioning from their mothers).

Conclusions

Both forms of scent marking (marking and overmarking) are deposited nonrandomly in the home range and follow a distribution pattern that may optimize signal detection, possibly because depositions are a limited resource and energetically expensive (Gorman & Mills, 1984; Roberts & Lowen, 1997). Furthermore, the intrasexual competition hypothesis may explain the functional convergence of marking and overmarking in males. Overall, this study contributes to understanding the possible functional divergence of scent marking between lemur males and females and is evidence of the multifunctional complexity of olfactory signalling in lemurs.

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Author Contributions L.M, I.N, D.V., C.D.G., M.G., O.F., and V.T. designed the research protocol. L.M, A.C, I.N., O.F., and M.G. developed the methodology and performed the analyses. L.M., A.C., C.D.G., L.V. performed the fieldwork. L.M, M.G., J.R., I.N., V.T., O.F., and C.G. contributed to developing the methods, interpreting the results, and provided editorial advice. L.M., M.G., I.N., V.T, C.D.G., and C.G. wrote the manuscript.

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Data Availability The data sets analyzed during this study are available from the corresponding author or downloadable from https://github.com/sciabolajIOP_MIARETSOA_OCT21.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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Authors and Affiliations

Longondraza Miaretsoa¹ · Andrea Cascella¹ · Luigi Vadàla¹ · Daria Valente^{1,2} · Chiara De Gregorio¹ · Valeria Torti¹ · Ivan Norscia¹ · Jonah Ratsimbazafy³ · Olivier Friard¹ · Cristina Giacoma¹ · Marco Gamba¹ 

✉ Marco Gamba
marco.gamba@unito.it

- ¹ Department of Life Sciences and System Biology, University of Turin, Via Accademia Albertina 13, Turin, Italy
- ² Equipe de Neuro-Ethologie Sensorielle (ENES), Centre de Recherche en Neurosciences de Lyon (CRNL), CNRS, INSERM, University of Lyon / Saint-Étienne, Saint-Étienne, France
- ³ GERP (Groupe d'Etude Et de Recherche Sur Les Primates de Madagascar), Antananarivo, Madagascar