

eral forms of environmental action events such as reforestation activities and lemur festivals. We can conclude that environmental education programs such as the one undertaken as part of this work have positive impacts on young people. Knowledge of lemurs and their natural habitat was improved in young people following the sessions. Further work should seek to involve more schools within the capital in order to maximize the impact of this initiative.

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Observations of fission-fusion dynamics in diademmed sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar

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Abstract

As with other primate clades, many lemur species form social groups and coordinate their activities and travel. However, some primate species exhibit 'fission-fusion dynamics', meaning that the larger social unit breaks into two or more subgroups for hours or days, and those subgroups travel and forage independently for hours or days. This behavior serves to alleviate the effects of within-group feeding competition while preserving the overall social organisation. This behavior had previously been reported in lemurs, but only within Lemuridae (genera *Varecia* and *Eulemur*). Here we report fission-fusion behaviors in diademmed sifaka (*Propithecus diadema*, Indriidae) at Tsinjoarivo. Three of four groups studied exhibited fission-fusion dynamics, splitting on more than 50% of days studied, with splits lasting up to 48 hours and subgroups reaching up to 690 meters apart (greater than half the home range diameter). Further research is needed, both to understand the factors causing this behavior at Tsinjoarivo, to determine if other Indriids also exhibit this behavior, and finally to examine its impacts on social behavior and fitness (for example, through facilitating extra-group paternities).

Résumé

Comme d'autres clades de primate, beaucoup d'espèces de lémuriens mènent une vie sociale en groupe et synchronisent leurs activités et leur déplacement. Cependant, certaines de ces espèces montrent la «dynamique de fission-fusion», définissant la division d'un large groupe en deux ou plusieurs sous-groupes qui se déplacent et recherchent de la nourriture indépendamment, durant des heures ou des jours. Ce comportement sert à alléger les effets de la compétition alimentaire intra-groupe, tout en préservant l'organisation sociale en général. Celui-ci avait été précédemment observé sur les lémuriens, mais seulement chez la famille des Lemuridae (genres *Varecia* et *Eulemur*). Ici nous rapportons le comportement de fission-fusion chez le sifaka à diadème (*Propithecus diadema*, Indriidae) à Tsinjoarivo. Trois des quatre groupes étudiés ont montré la dynamique de fission-fusion, se séparant plus de 50% des jours étudiés, avec des fissions qui durent 48 heures et des sous-groupes atteignant une distance de 690 mètres (plus grand que la moitié du diamètre du territoire). Compte tenu de ces faits, d'autres recherches sont nécessaires pour comprendre les origines de ces facteurs à Tsinjoarivo; pour déterminer si d'autres Indriidae le pratiquent également; et finalement, pour examiner leurs impacts sur le comportement social et l'état de santé (par exemple, en facilitant les paternités de groupe supplémentaire).

Introduction

Primates exhibit great inter- and intra-species variation in the size, composition and cohesiveness of social groups. The term 'fission-fusion dynamics' describes the extent of variation in cohesion (Aureli *et al.*, 2008; Carnes *et al.*, 2011). Groups with high fission-fusion dynamics exhibit high temporal variation in spatial size, spatial cohesion and party size while those with low fission-fusion dynamics exhibit low temporal variation in spatial size, spatial cohesion and party size (Aureli *et al.*, 2008). Fission-fusion dynamics can be adaptive when optimal group size varies over short time periods (Lehmann and Boesch, 2004) as well as regulating intragroup scramble competition by decreasing feeding competition (Leighton and Leighton, 1982; Chapman *et al.*,

1995; Stevenson *et al.*, 1998; Chapman and Chapman, 2000) and allowing greater efficiency in exploiting food resources that tend to be heterogeneously clumped within the landscape (Asensio *et al.*, 2009).

Studies on fission-fusion dynamics in primates have largely focused on chimpanzees (Goodall, 1968; Nishida, 1968; Sugiyama, 1968; Itoh and Nishida, 2007) and spider monkeys (Robbins *et al.*, 1991; Asensio *et al.*, 2009), but fission-fusion dynamics have been reported in several other monkey and ape species (van Schaik, 1999; Delgado and van Schaik, 2000; Ren *et al.*, 2002; Aureli *et al.*, 2008; Snaith and Chapman, 2008). Some species of strepsirrhines have also exhibited fission-fusion dynamics, including red ruffed lemurs (*Varecia rubra*: Vasey, 1997; Vasey, 2006; Vasey, 2007), black and white ruffed lemurs (*Varecia variegata*: Morland 1991a, Morland 1991b; Baden *et al.*, 2015; Holmes *et al.*, 2016), white-fronted brown lemurs (*Eulemur albifrons*: Toborowsky 2008), white-collared brown lemurs (*Eulemur cinereiceps*: Johnson, 2002), black lemurs (*Eulemur macaco*: Colquhoun, 1997), common brown lemurs (*Eulemur fulvus*: Tattersall, 1977), crowned lemurs (*Eulemur coronatus*: Freed, 1996) and red-fronted brown lemurs (*Eulemur rufifrons*: Overdorff *et al.*, 2003; Pyritz *et al.*, 2013).

Baden *et al.* (2015) found, unlike other groups that exhibit high fission-fusion dynamics, black and white ruffed lemurs appear to exhibit this type of social structure due to communal breeding; forming small and cohesive groups during early lactation and high infant dependency. Other factors impacting their fission-fusion dynamics included fruit availability and climate. This is similar to haplorhines, although, unlike haplorhines, they exhibited small subgroup sizes, lower rates of association and a more female-centered social organization (Baden *et al.*, 2015). According to Holmes *et al.* (2016), fission fusion dynamics of black and white ruffed lemurs were largely predicted by fruit availability, season and presence of infants. However, unlike other studies of fission-fusion dynamics, they exhibit smaller subgroup sizes during periods of site-wide fruit availability. This may be due to the impact of fragmentation on fruit abundance, diversity or predictability (Holmes *et al.*, 2016). Vasey (2006) reports similar findings concerning the fission-fusion dynamics of red ruffed lemurs. They were largely impacted by their reproductive biology and patchy fruit-based diet (Vasey, 2006). Within Lemuriformes, fission-fusion dynamics have only been described in *Eulemur sp.* and *Varecia sp.* Here we report the occurrence of fission-fusion dynamics in diademed sifakas (*Propithecus diadema*) in Tsinjoarivo, Madagascar.

Methods

Tsinjoarivo forest is located about 80km SSE of Antananarivo and 45km SE of Ambatolampy, in the region of Vakinankaratra, with an altitude of 1400–1650m. Data were collected at two sites: Mahatsinjo (19°40'56"S, 47°45'28"E, altitude 1475–1625m, 10km SE of Tsinjoarivo), and Ankadivory (19°42'59"S, 47°49'18"E, altitude 1350–1575m, 17km SE of Tsinjoarivo (Irwin *et al.*, 2015; Rakotomalala *et al.*, 2017). Ankadivory is a relatively continuous, intact forest, while Mahatsinjo has been subjected to considerably more tree extraction and has fewer trees >5cm DBH per hectare, less basal area per hectare and a shorter, more discontinuous canopy (Irwin and Raharison, in press). These sites belong to the future protected area of Tsinjoarivo-Ambalaomby, which includes several forest blocks from Mahatsinjo to Ambalaomby along the Onive river.

The diademed sifaka is the largest lemur at Tsinjoarivo and classified as critically endangered (Andriaholinirina *et al.*, 2014). They live in small groups (2–10 individuals) including

a dominant female (sometimes accompanied by a second breeding female), a single adult male and offspring (Mittermeier *et al.*, 2014). Their diet is composed primarily of foliage (53% of feeding time), fruit, seeds and flowers (Irwin, 2008). Four groups were followed: CONT4 and CONT5 at Ankadivory and FRAG4 and FRAG5 at Mahatsinjo with seven, six, seven and three individuals, respectively (excluding infants born during the study; Tab. 1). All individuals in the group were collared during the study except 1-year-olds; all were identifiable.

Tab. 1: Composition of Tsinjoarivo diademed sifaka (*Propithecus diadema*) study groups, sampling time, and prevalence of fission-fusion behaviors.

Group	Composition (immatures' age in years) ¹	# Data Collection Days	# Days with	% Time in
				Fission-Fusion Activity
CONT4	2 Adult Female (RAD, GB) 1 Adult Male (RG) 4 immatures: PR (3), BP (2), JUVI (1), JUVI (1)	11 (2-7 July, 24-28 July)	10 (91%)	74%
CONT5	2 Adult Females (RAD, PS) 1 Adult Male (BR) 3 immatures: BG (approx. 4), TO (approx. 3), JUV (approx. 1)	11 (26-30 June, 30 July-4 Aug)	7 (64%)	52%
FRAG4	2 Adult Females (RAD, PB) 1 Adult Male (BG) 4 immatures: GS (5), PO (4), BR (3), JUV (1)	11 (11-16 June, 10-14 July)	8 (73%)	42%
FRAG5	1 Adult Female (RAD) 1 Adult Male (BP) 1 immature: JUV (1)	11 (18-23 June, 16-21 July)	0 (0%)	0%
Total		44	25 (57%)	42%

¹CONT5: RAD, CONT5:PS and FRAG4:PB gave birth during the study but these infants are not recorded in the table.

Data were collected between 11 June and 04 August 2018; each group was subjected to all-day focal animal follows for 11 days. Data were collected on one adult female and one adult male simultaneously; for three groups with two adult females each, observations were focused on the dominant, older adult female (CONT4: RAD, CONT5: RAD, FRAG4: RAD, Tab. 1) rather than the younger breeding adult female. Activity data (feeding, traveling, resting, social) were collected using instantaneous sampling with a 5-minute inter-scan interval for each focal animal. Additionally, a team of 2-3 research assistants monitored the position of all group members and estimated distances between each pair of animals (distances above 20 meters were recorded as ">20"). With few exceptions, the focal animals were followed daily from their waking until their dormitory tree.

A 'fission event' was defined as when subgroups became >250 meters from each other and a 'fusion event' was defined as when subgroups converged into visual and vocal contact (usually <20 meters). Thus, subgroups were sometimes considered as fissioned when less than 250 meters apart (when they had previously been >250 meters apart). Additionally, it was noted when the group stayed in a fissioned state, but the composition of subgroups changed. GPS points were recorded on all data collection days; when the group was cohesive, a single GPS unit was used, but a second GPS unit was deployed during certain days with fission-fusion events so that both the adult male and adult female's paths were recorded. Points were recorded at

5-minute intervals throughout the day (except if the animal had not moved during the last 5 minutes).

Data collected from GPS waypoints were mapped in ArcGIS Version 10.6 (ESRI, Redlands, California, USA) and used to measure selected distances between subgroups. Using times of fission and fusion events, cumulative times spent in fission situations were calculated and expressed this as a proportion of total observation time. This calculation included time passing overnight between consecutive days of data collection (this population almost never moved at night).

Results

Three of the four study groups exhibited fission-fusion dynamics (Tab. 1 - 4). Among those three groups, 64-73% of days sampled exhibited fission-fusion dynamics and 42-74% of overall time sampled was in a state of fission.

Tab. 2: Fission-fusion events for diademed sifaka (*Propithecus diadema*) study group CONT4.

Date/Time	Fission/Fusion Event	No. of Subgroups	Notes
2 July, 07:25	Start Data Collection: RAD, GB, RG, PR, BP, JUV1, JUV2	1	
2 July, 8:15	Fission: RAD, PR/GB, RG, BP, JUV1, JUV2	2	
2 July, 10:15	Fission: RAD, PR/GB, RG, BP, JUV1/JUV2	3	
2 July, 13:00	Fusion: RAD, GB, RG, PR, BP, JUV1/JUV2	2	
4 July, 12:30	Fission: RAD, GB, BP, JUV1/RG, PR/JUV2	3	
5 July, 10:50	Fusion: RAD, GB, RG, PR, BP, JUV1/JUV2	2	
7 July, 16:00	End Data Collection: RAD, GB, RG, PR, BP, JUV1/JUV2	2	JUV2 was seen by a plant collection team, roughly 500 m from the group (7 July, 13:24)
24 July, 06:45	Start Data Collection: RAD, PR, BP, JUV/GB, RG, JUV	2	
24 July, 8:15	Fusion: RAD, BG, RG, PR, BP, JUV1, JUV2	1	
26 July, 14:45	Fission: RAD, GB, BP, JUV1, JUV2/RG, PR	2	
27 July, 12:10	Subgroup composition change: RAD, BP, JUV1, JUV2/GB, RG, PR	2	
28 July, 11:08	Fusion: RAD, GB, RG, PR, BP, JUV1, JUV2	1	
28 July, 16:05	End Data Collection	1	

Tab. 3: Fission-fusion events for diademed sifaka (*Propithecus diadema*) study group CONT5.

Date/Time	Fission/Fusion Event	No. of Subgroups	Notes
26 June, 08:00	Start Data Collection: RAD, PS, TO, JUV, BR, BG	1	
26 June, 13:40	Fission: RAD, PS, TO, JUV/BR, BG	2	BR, BG lost until next fusion
27 June, 09:40	Fission: RAD, PS / TO, JUV/BR, BG	3	
27 June, 10:35	Fusion: RAD, PS, TO, JUV/BR, BG	2	

Date/Time	Fission/Fusion Event	No. of Subgroups	Notes
28 June, 12:45	Fission: RAD, JUV / PS, TO/BR, BG	3	
28 June, 13:50	Fusion: RAD, PS, TO, JUV, BR, BG	1	BR, BG relocated by research team at time of fusion
28 June, 14:40	Fission: RAD, PS, TO, JUV/BR, BG	2	
30 June, 13:12	Fusion: RAD, BR, BG, PS, TO, JUV	1	BR+BG had been stationary for 1h40 minutes when another subgroup arrived
30 June, 15:06	Fission: RAD, PS, TO, JUV/BR, BG	2	
30 June, 17:45	End of Data Collection Cycle: RAD, PS, TO, JUV/BR, BG	2	
30 July, 07:30	Start Data Collection: RAD, PS, TO, JUV, BR, BG	1	
3 August, 16:20	Fission: RAD, PS, TO, JUV/BR, BG	2	
4 August, 08:15	Fission: RAD, PS/BR, TO, BG/JUV	3	
4 August, 08:50	Fusion: RAD, PS/BR, TO, BG, JUV	2	
4 August, 16:35	End of Data Collection Cycle: RAD, PS/ BR, TO, BG, JUV	2	

Tab. 4: Fission-fusion events for diademed sifaka (*Propithecus diadema*) study group FRAG4.

Date/Time	Fission/Fusion Event	No. of Subgroups	Notes
11 June, 7:40	Start of Data Collection: RAD, BG, GS, JUV/PB, PO, BR	2	PB, PO, BR missing but not within 250 m
12 June, 14:50	Fusion: RAD, BG, PB, PO, GS, BR, JUV	1	PB, PO, BR relocated at time of fusion
14 June, 13:05	Fission: RAD, BG, GS, PO/PB, JUV, BR	2	
15 June, 13:10	Fusion: RAD, BG, PB, PO, GS, BR, JUV	1	
16 June, 16:20	End of Data Collection: RAD, BG, PB, PO, GS, BR, JUV	1	
10 July, 08:35	Start of Data Collection: RAD, BG, PB, JUV/GS, PO, BR	2	GS, PO, BR missing but not within 250 m
11 July, 11:15	Subgroup Composition Change: RAD, PB, PO, GS, BR, JUV/BG	2	BG falls behind while remainder of group joins
11 July, 15:30	Fusion: RAD, BG, PB, PO, GS, BR, JUV	1	
12 July, 7:50	Fission: RAD, BG, GS, JUV/PB, TO, BR in rear	2	
12 July, 15:20	Fusion: RAD, BG, PB, PO, GS, BR, JUV	1	
14 July, 12:55	Fission: RAD, PB, PO, GS, BR, JUV/BG	2	
14 July, 16:00	End of Data Collection: RAD, PB, PO, GS, BR, JUV/BG	2	

During fission events, the number of subgroups varied between two and three for groups CONT4 and CONT5, but only reached two for group FRAG4. The composition of subgroups varied (Tab. 2 - 4). Among the three adults in CONT4, 'fissioning' involved either the older adult female (RAD) separating from the other two (younger female GB and adult male RG) or the adult male separating from both adult females. Further variations in subgroup composition were caused by different arrangements of the immature animals. In CONT5, the most common arrangement was the adult male (BR) and an older immature (BG) separat-

ing from the remaining four animals, but those four animals would also fission into two subgroups of two individuals each. At the end of the second data collection cycle, the older and younger adult females (RAD and PS) were together, with the adult male (BR) with the three immatures (except for a short time when JUV was alone). In FRAG4, the most common 'fissioning' involved the younger adult female PB (who was born in this group in 2012 and reproduced for the first time in 2018) splitting from the older adult female (RAD) and adult male (BG). PB often had some immatures accompanying her. On another occasion, three immatures separated from the group, and on two occasions the adult male (BG) separated from the group alone.

Subgroups often remained separated for extended periods, including overnights (using separate, distant sleep trees). The longest consecutive time spent in fission (including overnight time) was >127.75h (CONT4: 2-7 July), which included the separation of JUV2 (a 1-year-old) from the remainder of group CONT4 for >125.75h. The next longest consecutive time spent in fission (including overnight time) was 48.2h (CONT5: 26-28 June), followed closely by 46.5h (CONT5: 28-30 June) and 44.4h (CONT4: 26-28 July).

The distances among subgroups were considerable (Fig. 1). CONT5's subgroups on 28 June were 690m apart at 16:50 and slept 580m apart. On 29 June, the subgroups were 490m apart at 10:40 and slept 190m apart. On 30 June, they slept 265m apart. For reference, CONT5's home range is 62.9ha and measures roughly 1230m north to south and 1030m west to east (Irwin and Raharison, in press). CONT4's subgroups were 340m apart at the beginning of the day on 28 July. For reference, CONT4's home range is 90.2ha and measures roughly 945m north to south and 1630m west to east (Irwin and Raharison, in press).

Discussion

Our observations show an extremely high prevalence of fission-fusion behavior in diademed sifakas, at least during this short study during the lean season. The fact that three of four groups exhibited the behavior means it is not an idiosyncrasy of a single group, and further, the fact that it was observed in two groups in relatively intact forest (CONT4 and CONT5) and another group in more degraded forest (FRAG4) suggests that this behavior is not expressed only in more degraded habitat, as was suggested for spider monkeys (Rodrigues, 2017). It is notable that the two CONT groups exhibited higher percentages of time in fission (52-74%), and a higher number of simultaneous subgroups (2-3) relative to FRAG4 (42% and 2, respectively). This may be due to the CONT habitat's larger groups and larger home ranges, or the nature of the food resources (Irwin, 2008; Irwin and Raha-

ison, in press). The lack of fission-fusion in FRAG5 may be due to its small group size (3). However, the observed differences may also be artifacts of the relatively small sample size.

Although this is the first published report, fission-fusion behavior has been observed previously (but not quantified) by research teams studying this diademed sifaka population. In particular, in FRAG4, the adult male BG has been seen for several years now to separate from groupmates, often with one or more immatures. In CONT4, similar splits between the three adults were observed in 2016-17. Thus, this behaviour is not a rare occurrence driven by an unusual year in terms of resource availability.

The implications of fission-fusion behaviour on daily life are potentially meaningful. In terms of feeding competition, it could be crucial in alleviating within-group feeding competition and maximizing foraging efficiency. However, it is curious that this behaviour would be expressed in the lean season. This season sees a switch to lower-quality fall-back foods, greatly reduced feeding times and lower aggression rates compared to other seasons, suggesting an 'energy minimizer' strategy, during which feeding competi-

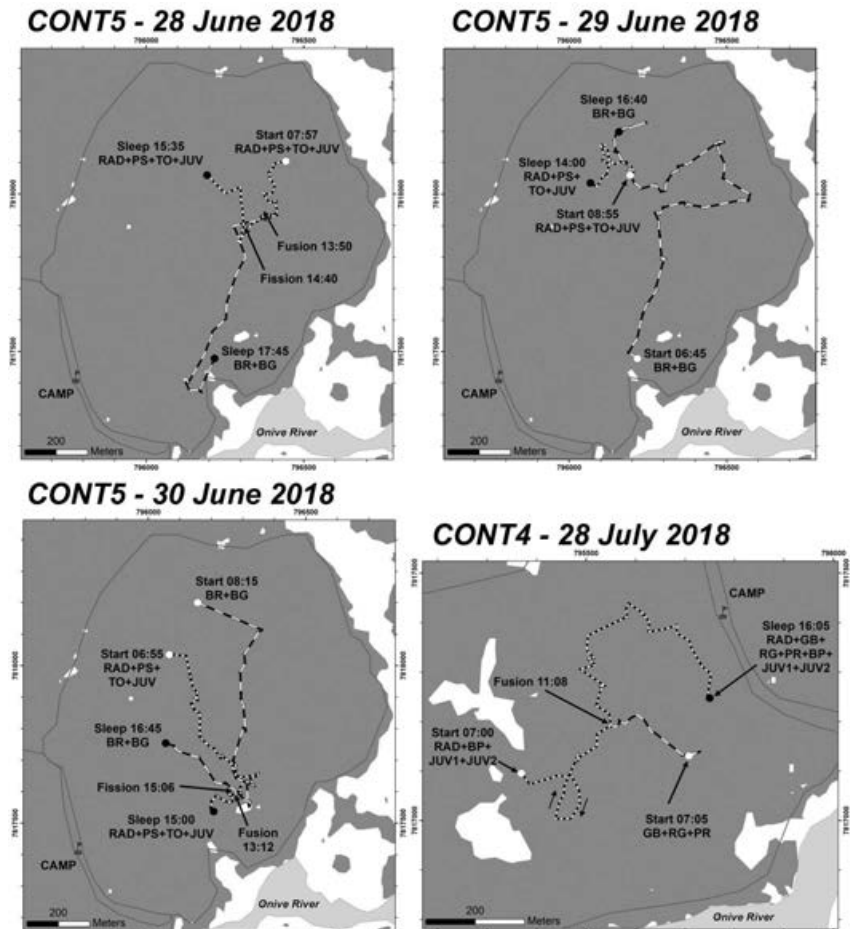


Fig. 1: Daily paths of subgroups during fission-fusion events of diademed sifaka (*Propithecus diadema*) at Tsinjoarivo. White dots indicate starting points (waking up); black dots indicate ending points (sleep trees). Lines with short dashes represent the subgroups containing the adult female(s) or the whole group; lines with long dashes represent the subgroups containing the adult male. The first three panels are three consecutive days of fission-fusion events in CONT5; on the first day BR+BG were not located until fusion at 13:50 (their early morning path is therefore not shown); on the second day the subgroups never joined up, and on the third day they joined and then split again. Group CONT4 on 28 July (fourth panel) woke up in two subgroups but joined and slept together.

tion should be lessened (Irwin, 2006; Irwin *et al.*, 2015; Irwin and Raharison, *in press*). Further study is needed to quantify seasonal variation in the tendency to fission-fusion and to explore links between this behavior and feeding competition. If conducted across multiple groups, the linkages with habitat disturbance could also be explored.

If occurring during the mating season, fission-fusion could affect mating access and mate choice and may facilitate extra-group paternities (which have not yet been detected in this population). We do not have evidence that this has occurred, but it is interesting to note that PB in FRAG4 gave birth during our study, despite being a natal female (born in FRAG4 in 2012) and her presumed father (BG) being the sole resident male since at least 2006. Although it is possible she bred with her father, it is also possible that PB's infant was sired by an extra-group male, or that she herself was sired by an extra-group male rather than by BG. Further paternity sampling would be necessary to explore this possibility.

Finally, we were surprised by the long separation of a 1-year-old (CONT4: JUV2) from its group (2-7 July; Tab. 2). 1-year-olds are noticeably smaller than adults (approximately 2.9 vs 5.0 kg), meaning they should be more vulnerable to predation, and typically maintain closer distances to adults (particularly their mother) during both resting and active times (Irwin, *unpublished data*). It is possible this was an unintentional separation.

Conclusion

In sum, fission-fusion dynamics in lemurs do not seem to be restricted to two genera (*Eulemur* and *Varecia*) within a single family (Lemuridae). This report is the first we are aware of outside the Lemurids. It is possible that the true occurrence in nature is even more widespread; further research efforts should seek to document this behavior, and explore its causes, in this population and in lemurs more broadly.

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Utilisation verticale de l'habitat par *Hapalemur griseus griseus* dans la forêt tropicale humide de Maromizaha (Andasibe)

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Résumé

Lorsqu'on parle de l'espèce *Hapalemur griseus*, c'est le Parc National de Ranomafana qui est considéré comme un site de référence. L'étude sur l'utilisation verticale de l'habitat par *Hapalemur g. griseus* a été effectuée dans la forêt humide tropicale de Maromizaha pendant la saison humide et sèche en 2016. *Hapalemur g. griseus*, un lémurien folivore, se trouve dans cette forêt mais les informations scientifiques sur ce taxon restent méconnues, notamment sur cette utilisation verticale et les facteurs qui peuvent l'influencer, voire les enjeux environnementaux qui peuvent également modifier l'habitat de l'animal. A cet effet, la présente étude a fait l'objet d'identifier les facteurs bioécologiques dans l'utilisation verticale de l'habitat d'*Hapalemur g. griseus*. Des données sur cette utilisation ont été obtenues par la méthode de l'observation focal. En effet, *Hapalemur g. griseus* occupe toutes les strates forestières disponibles de son habitat (basses, moyennes et supérieures), mais avec différentes fréquences. Quand l'animal occupe la strate basse (0.1-3m), il récupère les pousses, les jeunes feuilles de bambou et les jeunes feuilles d'autres plantes ainsi qu'il se repose dans un endroit sécurisé. Pour les autres strates, l'animal l'utilise pour surveiller leur environnement. Dans cette utilisation de l'habitat verticale, la hauteur d'*Hapalemur g. griseus*, dépend de la hauteur des arbres utilisés comme support ($R_s=0.712$; $P<0.0001$). En outre, *Hapalemur g. griseus* exploite les supports de deux façons pour récupérer les aliments. Pour la première méthode, il se nourrit sur un support, l'animal récupère les feuilles du bambou sur cette même plante (*Cephalostachyum* sp), il exploite les fruits de *Canthium* sp les feuilles et les fruits de *Ficus sorocoides* et de *Ficus reflexa* sur ce même arbre. Pour la deuxième méthode, l'animal collecte son aliment en s'appuyant sur un autre support. Dans l'organisation sociale d'*Hapalemur g. griseus*, l'animal se regroupe pendant leur activité et parfois il se disperse. Il y a une distance du voisin moyenne minimale et maximale par rapport à l'animal focal qui est respectivement $1.3m \pm 0.0m$ et