ECOLOGY OF THE GERMAIN'S LANGUR *Trachypithecus germaini* IN A PRE-RELEASE ENVIRONMENT AND THE IMPLICATIONS FOR ITS CONSERVATION

Brenda de Groot^{1,2*} and Anna Nekaris²

¹ Lange Brugstraat 44C2, 4811 WS, Breda, The Netherlands. E-mail: groot.de.brenda@gmail.com ² Anthropology Centre for Conservation Environment and Development, Oxford Brookes University, Oxford OX3 0BP, UK. E-mail: anekaris@brookes.ac.uk * Corresponding author

ABSTRACT

2

We studied the behaviour of captive Germain's Langur *Trachypithecus germaini* (Milne-Edwards) housed in a 3,000 m² naturalistic enclosure near Siem Reap, Cambodia. We studied a group of five individuals from May to July 2014, yielding 186 hours of data. We used instantaneous focal sampling to collect data on activities, social proximity, forest strata use and weather. The langurs were resting in 47.2% of scans, feeding in 43.6% of scans, traveling in 5.0% of scans, and grooming in 4.2% of scans. They spent 18.2% of their time in social proximity and varied in their time spent in different forest strata: the canopy (17.0%), understorey (53.7%) and forest floor (29.2%). The daily activity pattern showed three stages, feeding – resting – feeding. Feeding was inversely related to resting and grooming. More time was spent in the canopy and less on the floor during rain, while the opposite applied to sunny weather. Langurs were more often in social proximity during sunny weather. We additionally observed mycophagy and geophagy. The findings conform to the ecology of other *Trachypithecus* species and differences were likely due to the captive environment. An optimal pre-release environment should comprise a sufficient size, high-quality vegetation and appropriate feeding times, which may adjust the activity budget and pattern to fit a wild environment.

Keywords: activity pattern, geophagy, langur, mycophagy, translocation, time budget, weather

INTRODUCTION

Trachypithecus spp. are folivorous monkeys distributed across Southeast Asia. The genus Trachypithecus belongs to the group of Asian Colobines, along with the two other langur genera, Semnopithecus spp. and Presbytis spp. Within the genus Trachypithecus, 20 species are acknowledged (Roos et al., 2014). The IUCN (2014) recognised 14 species as threatened with extinction; however, this number recently increased to 16 at the November 2015 IUCN Red List of Threatened Species List assessment workshop for Asian primates (Ramesh Boonratana, pers. comm.). Like most primates, the main threats to these langur populations are habitat loss, hunting and live capture (Chapman & Peres, 2001). One species that is particularly threatened is the Germain's Langur T. germaini (Milne-Edwards), sometimes known as Indochinese Silvered Langur. The species is found in Lao PDR, Vietnam, Thailand, Myanmar and Cambodia (Roos et al., 2014),

of which Cambodia holds the highest numbers of T. germaini (Moody et al., 2011; Timmins et al., 2013). The total population declined more than 50% over the past 36 years, or three generations, the period influencing the IUCN's threat status classification (Nadler et al., 2008). Although data on the impact of hunting on these primates are scarce, their near or complete absence in some highly suitable habitats signifies that they may have been hunted out (Moody et al., 2011; Timmins et al., 2013). Despite their Endangered status (Nadler et al., 2008), the species has received little conservation attention (Moody et al., 2011) and until now, no ecological or behavioural studies have been conducted on these langurs (Coudrat et al., 2011). The absence of baseline ecological data hampers suitable conservation action and management strategies for the dwindling populations of *T. germaini* (Moody et al., 2011; Phan & Stevens, 2012). It is therefore of critical

importance to increase our knowledge of the species.

Activity budgets and patterns provide this basic ecological information, which contributes to both ongoing and successive conservation efforts such as conservation translocation (Phan & Stevens, 2012). Conservation translocation (hereafter referred to as translocation) is defined as the international movement and release of a living organism where the primary objective is a conservation benefit (IUCN SSC, 2013). Before translocating animals into the wild, the IUCN urges that baseline data of the species' natural activity have been collected (IUCN SSC, 2013). Decent pre- and postrelease studies are however scarce and both the quality and quantity of these studies should be enhanced (Mathews et al., 2005). Studies on activity budgets and patterns can include information on forest strata use (Bernstein, 1972; Schneider et al., 2010; Ampeng & Md-Zain, 2012; Workman & Schmitt, 2012) and examine ecological responses to external variables such as the weather (Bernstein, 1972; Altmann, 1974; Stelzner & Hausfater, 1986; Bronikowski & Altmann, 1996; Janmaat et al., 2006), which will not only enhance the quality of pre-release studies but also facilitate postrelease monitoring.

The activity budgets of different species of wild Trachypithecus do not vary substantially; however, activity budgets between captive and wild langurs can differ significantly (e.g. Phan & Stevens, 2012). For conservation purposes, the pre-release activity budget should closely approximate that of wild conspecifics, since more 'natural' behaviours in pre-release primates are found to be an indicator for successful translocation (Soorae, 2008). To overcome or prevent a discrepancy in pre- and post-release activity budgets, one could provide a pre-release environment that closely represents the post-release environment. This will cause the primates to adapt to the new situation quicker, which increases their chance of survival and reproductive success (Kleiman et al., 1989; Mathews et al., 2005). It is therefore important to understand what parameters should be taken into account when constructing prerelease environments. In this study, we present prerelease ecological information of captive T. germaini. We analysed their daily activity budget, activity pattern and relationships between weather type and activity budget. We discuss the ecological correspondence with wild Trachypithecus species and implications for pre-release environments.

METHODS Study area

The research was conducted at the Angkor Centre for Conservation of Biodiversity (ACCB), established in 2008 by Munster Zoo and the Zoological Society for the Conservation of Species and Populations (ZGAP) (Westfälischer Zoologischer Garten Münster AG, 2013). The centre is situated at the protected site of Kbal Spean, adjacent to Phnom Kulen National Park and located in Cambodia's north-western Siem Reap Province. ACCB is not open to the public but provides guided tours from Mondays to Saturdays at 9:00 h and 13:00 h.

Study animals

At the start of this study, ACCB housed five *T. germaini* individuals, of which three had been rescued from the illegal wildlife trade and two were born at the centre. ACCB aims to translocate the group of langurs when a suitable habitat is found.

The study group included one adult and three subadult females and one adult male. It was unknown whether the subadult females were related to either of the adults because reports on the animals were absent or incomplete. The langurs were situated in a naturalistic open enclosure measuring approximately 3,000 m² (Fig. 1-3). They could cross the entire enclosure through the canopy. One side bordered the enclosure of three female Pileated Gibbons Hylobates pileatus Gray. A satellite cage used for food provisioning was situated at the rear of the enclosure. Keepers entered the cage each day at 13:00 h to scatter vegetables (Chinese long beans, Thai eggplant, pumpkin, carrot, beetroot and turnip, cut in pieces of 5-10 cm) and monitor the langurs' condition. Visitors had little interaction with the animals: guided tours only passed the lower right corner of the enclosure and were separated 2 m from its border by a second fence. Additionally, the enclosure's dense vegetation prevented tour visitors from viewing the langurs during feeding time.

Data collection

I (the first author) observed the langurs from outside the enclosure from May to July 2014 on five randomised days per month, which were chosen by using an online random calendar date generator. I followed the primates from dawn to dusk (6:00 h–18:25 h), and collected 186 hours of observation data. I applied the instantaneous focal sampling method (Martin and Bateson, 1993) using 20-minute samples with 5-minute intervals. After each sample there were 5 minutes to search for the next individual. I used a stopwatch to 4

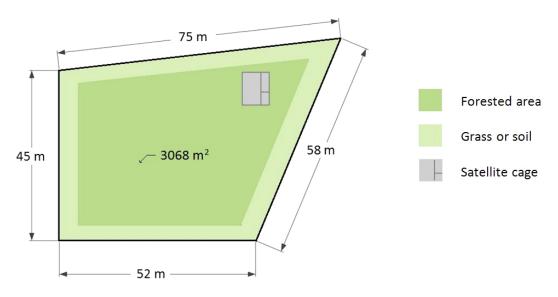


Fig. 1. Top view of the naturalistic open enclosure of *T. germaini* at Angkor Centre for Conservation of Biodiversity, Cambodia.



Fig 2. Illustration of the enclosure of *T. germaini* at Angkor Centre for Conservation of Biodiversity, including vegetation strata (1: canopy, >6m; 2: understorey, 1-6m; 3: floor <1m). Illustration by B. de Groot.

keep track of time, which signalled sampling instants through vibrations. Each individual was observed six times in a predetermined randomised sequence, of which the order was obtained through an online random sequence generator, adding up to 30 samples per day. I used Celestron Nature DX 8x42 binoculars when behaviours were too ambiguous to determine with the naked eye. The oldest subadult female died from pneumonia and colitis after the 11th day of observation; hence I observed each individual seven or eight times on days 12–15. I calculated inter-observer reliability from a synchronised observation session of eight samples, with the help of the second observer, Gabrielle Nussbaum (the Assistant Project Manager of ACCB). Following the method of Caro et al. (1979), with a sample size of five observations x five individuals (=25 observation samples), inter-observer agreement proved to be 95%.

I collected data on activities, social proximity, forest strata use and weather (Altmann, 1974) and refer to the first three categories together as the activity budget. Activities included feeding, resting, locomotion, grooming, playing, agonistic behaviour and other behaviour. If the individual was not visible, it was scored 'out of sight'. A sample was excluded from analysis when the focal animal was out of sight for more than one recording (>20%), which did not happen during this study: I was able to keep all individuals within sight as all areas in the enclosure were visually accessible from a certain place around the fence. This was facilitated by the way the trees in the enclosure formed parallel rows (Fig. 2). I additionally collected data on social proximity ('social', i.e. within one arm's reach of another individual; 'nonsocial'), forest strata use (floor; understorey; canopy) and weather (sunny; cloudy; raining).

Data analysis

We pooled the raw data into thirteen hourly timeintervals from 06:00 (5:30–6:30) h to 18:00 (17:30– 18:30) h for each day (N=195). We calculated the proportion of records that the langurs spent (a) feeding, resting, locomoting or grooming; (b) in social proximity or not; (c) on the floor, understorey or canopy; (d) in sunny, cloudy or rainy weather, and (e) out of sight, as percentages of the total count of (1) activities; (2) social proximity; (3) forest strata use; (4) weather; and (5) visibility respectively. We used a Kruskal-Wallis test to analyse variation in activities over the hours of the day and applied a Spearman's rank correlation to explore associations between activities. Finally, we applied Spearman's rank correlation to explore the relationship between the three weather variables and nine activity budget components ('non-social' excluded; 'out of sight' included). The significance level was 0.005 after a Bonferroni correction. Since this correction decreased the test's statistical power, we present all correlational findings and consider their effect sizes (García, 2004; Nakagawa, 2004). Although the percentages reported in the following findings represent proportions of instantaneous recordings (Altmann, 1974), we refer to them as 'percentages of time' to facilitate comprehension.

RESULTS Activity budget

The langurs spent most of their daily time resting (47.2%) and feeding (43.6%), while locomotion (5.0%) and grooming (4.2%) were scored less frequently (Fig. 4). Non-provisioned feeding objects included young



Fig 3. Three individuals resting in the understorey. Photo taken from the shortest side of the enclosure, by B. de Groot.

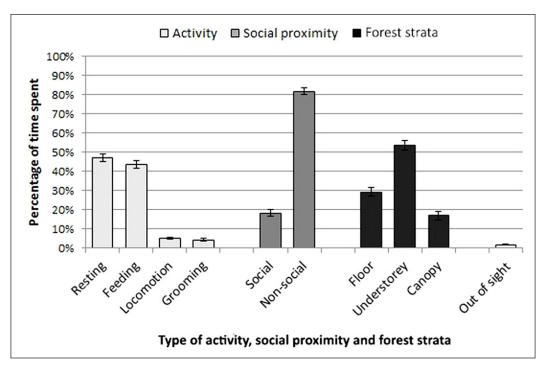


Fig. 4. Activity budget (mean± SE) of T. germaini, including time spent out of sight. Most time was spent resting and feeding, in a non-social context and in the understorey of the vegetation.

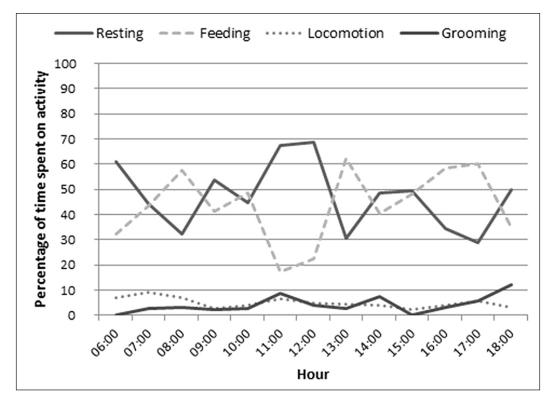


Fig. 5. Activity pattern of *T. germaini*. A peak in resting can be observed around noon; a peak in feeding around 13:00 h indicates time of food provisioning. Lines serve solely illustrative purposes since hours represent discrete data points.

	Weather								
Total Activity Budget	Sunny			Cloudy			Raining		
	%	r _s	р	%	r _s	р	%	r _s	р
Behaviour									
Resting	47%	-0.06		46%	-0.01		59%	0.18	0.014
Feeding	44%	-0.02		45%	0.04		39%	-0.07	
Locomotion	5%	0.12		4%	-0.04		2%	-0.15	0.032
Grooming	5%	0.14		4%	-0.06		0%	-0.19	0.008
Social proximity ^a									
Social	94%	0.20	0.004*	84%	-0.18		80%	-0.18	0.013
Forest strata									
Floor	38%	0.32	0.000*	25%	-0.14	0.045	1%	-0.36	0.000*
Understorey	53%	-0.02		59%	0.12		39%	-0.03	
Canopy	10%	0.29	0.000*	16%	0.08		61%	0.28	0.000*

Table 1. Percentage (%) of time spent on activities, in social proximity and in forest strata, under different weather conditions. Relationships between activity budget variables (N=195) and weather type are measured in correlations (Spearman's rho, r_). P-values of significant correlations (p<0.05) are given.

^aNon-social was left out of the analysis since it was mutually exclusive with Social.

Note. Significant correlations after Bonferroni correction (p<0.005) are indicated with an asterisk (*).

and mature leaves of *Xylia xylocarpa* (Roxb.) Taub., *Dipterocarpus alatus* Roxb. ex. G.Don., and *D. intricatus* Dyer, buds, bark, mushrooms and soil. On three days near the end of June for at least three consecutive hours we observed *T. germaini* feeding on mushrooms, a food source that until now was unknown to be included in their diet (e.g. Zinner et al., 2013). We never observed play behaviour, and agonistic behaviours were rare and did not occur on sampling instants. The animals were in social proximity to another individual for 18.2% of the time. They spent more than half of their time in the understorey (53.7%), followed by the forest floor (29.3%) and canopy (17.0%). The langurs were out of sight for 1.8% of the time.

Activity pattern

Resting and feeding were significantly related to time of day (Kruskal-Wallis test: H [12]=43.78, p<0.001; H [12]=51.41, p<0.001 respectively). The langurs fed most often on non-provisioned food in the early morning (8:00 h) and late afternoon (15:00 h–17:00 h), when on average feeding comprised more than 50% of their activities (Fig. 5). Resting increased around noon, but the peak in feeding at 13:00 h marks the time of food provisioning. As shown by the Spearman's rank correlation, there was a strong significant inverse relation between feeding and resting r_s = -0.87, p<0.01, and, less strong, between feeding and grooming, r_s =-0.23, p<0.01. This indicates that grooming and resting occurred more frequently at times when feeding occurred less. Locomotion was fairly evenly distributed over the day and did not account for more than 10% of daily activities on any hour.

Weather and activity budget

The activity budget varied under different weather conditions (Table 1). The Spearman's rank correlation depicted the following significant associations between weather and activity budget variables. Time spent on the floor was positively correlated with sunny weather (r_s=0.32) and negatively correlated with rain (r_s=-0.36). Time spent in the canopy was positively correlated with rain (r_s=0.28) while it was negatively correlated with sunny weather (r_s=-0.29). Thus, langurs were more often on the floor during sunny weather and less during rain, while the opposite was true for rainy weather. Social proximity too was positively related to sunny weather (r_s=0.20). We present all findings (Table 1), however, the relationships found when no Bonferroni correction would have been applied all fell below r_s=0.20, indicating only small effects (Field, 2009).

Table 2. Daily	/ activities in	percentages	(%)	for various	Trachypithecus	species.
I CADIO EI DOMI)		poroornagoo	(, 0)	ion vanoao	naonypiaiooao	0000000

		_				
Species	Resting	Feeding	Locomotion	Social	- Source	
Delacour's Langur¹ <i>T. delacouri</i> (Osgood)	45	29	13	13	Phan & Stevens, 2012	
Francois' Langur² <i>T. francoisi</i> (Pousargues)	45	32	14	9	Yang et al., 2007	
Francois' Langur² <i>T. francoisi</i> (Pousargues)	64	22	12	2	Yang et al., 2005	
Indochinese Silvered Langur ³ <i>T. germaini</i> (Milne-Edwards)	47	44	5	4	Current study	
Hatinh Langur¹ <i>T. hatinhensis</i> (Dao Van Tien)	57	17	19	7	Phan & Stevens, 2012	
Capped Langur² <i>Trachypithecus pileatus</i> (Blyth)	40	35	18	7	Stanford, 1991	
White-headed Langur ² <i>T. leucocephalus</i> Tan	50	13	18	19	Li & Rogers, 2004	
Cat Ba Langur² <i>T. poliocephalus</i> (Trouessart)	66	15	11	8	Schneider et al., 2010	
Dusky Leaf-monkey ² <i>T. obscurus</i> (Reid)	35	40	23	2	Md-Zain & Ch'ng, 2011	

¹ Captive individuals inhabiting semi-free ranging enclosures of 2–5 ha.

² Free-ranging individuals in a wild environment.

³ Captive individuals inhabiting a naturalistic open enclosure of 1/3 ha.

Note. We collapsed behaviours if studies had more than four behavioural categories. Social activities included grooming and playing; Resting included all other stationary behaviour such as autogrooming, vocalization, huddling and other non-moving behaviour.

DISCUSSION

Ecological correspondence with other Trachypithecus species

The activity budget of the *T. germaini* largely agrees with the overall pattern found in *Trachypithecus* species, with high percentages of feeding and resting, and low percentages of social behaviours (Table 2). Their folivorous diet requires obligatory resting time for the process of rumination (Korstjens et al., 2010), which restricts the time that can be spend on social activities. The low amount of locomotion may be a result of the higher abundance of leaves over fruit (Huang et al., 2003). We would like to note that the absence of information on the preferred food sources and feeding behaviour of *T. germaini* in the wild prevents a wellfounded explanation of their activity budget.

Kirkpatrick (2011) describes Asian colobines as rather unsocial primates, based on the percentage of their time spent grooming. Although being social is the least time-consuming activity of *Trachypithecus* species (Table 2), they show higher percentages of social time than the colobine species described in Kirkpatrick (2011), which were social for around 2% of their time. Although *T. germaini* groomed only 4.2% of their time, they were 18.2% of the day in close social proximity with another individual. Being in social proximity was not a matter of chance; the langurs actively searched for each other's company, would then sit down within each other's reach and rest together.

We did not observe play behaviour in *T. germaini*, presumably since all langurs were independent individuals. Agonistic behaviour seldom occurred. It has been argued that the generally low rate of intragroup agonistic behaviours in folivorous primates, as compared to frugivorous species, is a consequence of their diet (McKenna, 1979; Isbell, 1991; Sterck & Steenbeek, 1997). Fruits are fairly scarce and clumped (Janson & Chapman, 1999) and therefore easier to monopo-

lise than a more abundant and dispersed food source such as leaves (Wrangham, 1980; Whitten, 1983; Harcourt, 1987; Cowlishaw & Dunbar, 2000). The group composition (age and sex classes of the individuals) may form an additional explanation of the absence of play and agonistic behaviours.

Weather and activity budget

We found that T. germaini spent more time in the canopy and less time on the floor during rain, while the reverse was true for sunny weather. Sitting in the canopy during rain likely protected the langurs from the heavy showers that fell down from water-saturated leaves, while during sunny weather they may have preferred the shade of lower forest strata. The langurs never came down to the floor during or soon after rain, presumably since the ground was wet and muddy. Although Southern Pig-tailed Macagues Macaca nemestrina (Linnaeus) did not spend less time on the floor during rain, perhaps due to the discrepancy in their behavioural ecology compared to langurs, the macaques did show less social behaviours such as grooming and playing (Bernstein, 1972). In line with this finding, T. germaini never groomed in rainy weather, which without the applied Bonferroni correction would have led to a significant negative relationship between the two variables. Rain may make grooming less enjoyable for the receiving individual, as the water may reach the skin which most likely is an unpleasant experience. This may also explain why T. germaini spent more time in social proximity during sunny weather.

Ecological inconsistencies with other Trachypithecus species

T. germaini shows the highest percentage of feeding and lowest percentage of locomotion compared to the other *Trachypithecus* species (Table 2). This inconsistency was likely due to their captive environment, relating to (1) the relatively small size of the enclosure; (2) the low quality of the vegetation; and (3) food provisioning.

Firstly, the majority of the *Trachypithecus* species described in Table 2 were wild, and the semi-free ranging Hatinh Langur *T. hatinhensis* (Dao Van Tien) and Delacour's Langur *T. delacouri* (Osgood) had significantly larger enclosures than *T. germaini* (5 ha; 2 ha and 1/3 ha respectively). Indeed, caged *T. hatinhensis* and *T. delacouri* in 10 m x 5 m x 3 m enclosures spent more time feeding and less time locomoting than their semi-free ranging conspecifics (Phan & Stevens, 2012). Langurs in larger enclosures may benefit from traveling farther distances since this would lead them to new food sources. Traveling equally long distances

in smaller enclosures implies visiting the same areas over again, which would cost energy without gaining any benefits. As the limited size of the enclosure may have significantly affected the observed behaviours, extrapolation of the findings to the wild must be treated with caution.

Secondly, the low quality of the vegetation in the enclosure could have caused T. germaini to spend more time feeding to gain enough nutrients (c.f. Li & Rogers, 2004; Zhou et al., 2007). Apart from two trees, the langurs' enclosure solely contained trees of the species D. alatus, and leaves of dipterocarp trees are generally not favoured by colobines as they have a low protein to fibre ratio and contain high levels of terpenes (Bennett & Davies, 1994; Gupta & Chivers, 1999). Fibre delays the passage of food in the stomach of foregut fermenters like Trachypithecus (Janson & Chapman, 1999); secondary compounds like terpenes have been negatively related to primate feeding behaviour (Glander, 1982). The langurs fed often on more digestible vegetation like grass and young leaves on shrubs, which contain more protein and less fibre (Davies et al., 1988). This is reflected by the large amount of time that the langurs spent on the floor (29.3%) compared to other Asian colobines (e.g. Nilgiri Langur T. johnii [Fischer]: <14%, Poirier, 1969; Northern Plains Gray Langur Semnopithecus entellus [Dufresne]: <1.2%, Oppenheimer, 1976; Gee's Golden Langur T. geei Khajuria: 0%, Mukherjee, 1978). Colobine feeding behaviour is subject to seasonal influences (Stanford, 1991; Li et al., 2010; Kirkpatrick, 2011) and since some dipterocarp trees shed their leaves annually during the dry season, it might be worthwhile to investigate how the activity budget of T. germaini and forest strata use may be affected by the sprouting of young leaves, which are known to be a preferred food item of many colobines (Kirkpatrick, 2011).

The low quality of the vegetation may additionally have led to the consumption of other forest-floor food items such as mushrooms (Fig. 6) and soil, which are suggested to supplement dietary deficiencies (Krishnamani & Mahaney, 2000; Hanson et al., 2003 respectively). For most fungi-consuming primates, mycophagy only occurs at low rates of around 5% of the daily feeding time (Hanson et al., 2003). *Trachypithecus germaini* however would spend the entire afternoon feeding time foraging on mushrooms (Fig 6). The langurs would move quickly through dense undergrowth to collect the mushrooms (c.f. Hanson et al., 2003) and then ascend to higher forest strata to consume them while seated in a typically crouched position (Fig. 6bd). Mushrooms provide little energy for most animals 10

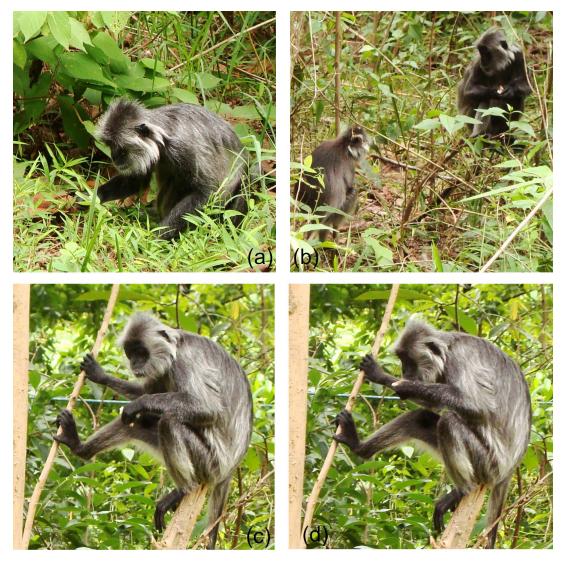


Fig. 6. Mycophaghy in *T. germaini*, including 'hunting' (a) and ingesting mushrooms (b-d). Photos were taken on 16 June 2014 (a-b) and 24 June 2014 (c-d) by B. de Groot.

since they are difficult to digest (Claridge et al., 1999). Yet foregut fermenters are able to extract most of the mushrooms' protein, as is the case in marsupials (e.g. Claridge & Cork, 1994; McIlwee & Johnson, 1998). This finding might also apply to the foregut-fermenting *T. germaini*.

The langurs additionally fed on soil on four occasions. They would dig up moist soil and kneaded the sand before ingesting it. Geophagy is frequently observed in other primates as well and is performed mainly for mineral supplementation, adsorption of toxins, to control diarrhoea or to adjust the pH of the gut (Krishnamani & Mahaney, 2000). Geophagy may play an important role in the diet of wild *T. germaini* as well. Phayre's Langur *T. phayrei* ssp. *phayrei* (Blyth) travel further, faster and with fewer stops on days they visit salt licks (Lloyd & Suarez, 2005), indicating the dietary value of soil consumption for this langur species. Although camera traps recorded wild *T. germaini* near salt licks (Rawson & Bach, 2011; Edwards et al., 2012), the act of geophagy was until now not yet directly reported for the species (but see Zinner et al., 2013).

Thirdly, food provisioning could also have had an influence on the amount of time the langurs spent feeding and locomoting. In contrast to the findings of this study, the provisioning of food generally leads to less feeding and more resting in food-provisioned primates compared to non-provisioned primates (e.g. Yellow Ba-

boon Papio cynocephalus [Linneaus]: Altmann & Muruthi, 1988; Olive Baboon Papio anubis [Lesson]: Elev et al., 1989; Barbary Macaque M. sylvanus [Linneaus]: El Alami et al., 2012). The timing of food provisioning could explain the present study's paradoxical finding. In addition to the two peaks in feeding behaviour in the morning and afternoon, food provisioning at 13:00 h caused a third peak at midday, thereby replacing resting time with feeding time. Since the provisioned food was most likely more nutritious than what the enclosure provided, T. germaini fed at midday even though Asian colobines normally rest at this time (e.g. Whiteheaded Langur T. poliocephalus ssp. leucocephalus Tan: Huang et al., 2003; Black Snub-nosed Monkey Rhinopithecus bieti [Milne-Edwards]: Ding & Zhao, 2004; Francois Langur T. francoisi [Pousargues]: Zhou et al., 2007; Cat Ba Langur T.p. ssp. poliocephalus [Pousargues]: Schneider et al., 2010). The decrease in locomotion may be caused by the clumped nature of the provisioned food, which did not require much locomotion to obtain.

Implications for captive care and reintroduction

We have shown that the pre-release environment affects the ecology of T. germaini in such a way that their activity budget and activity pattern deviates from wild Trachypithecus species, which could have consequences for successive captive management and reintroduction efforts. To overcome potentially harmful dissimilarities between the pre- and post-release environment, first the enclosure should be of sufficient size so that there is enough vegetation to satisfy their dietary needs. Secondly, the foliage in the enclosure should represent the vegetation they would forage on in the wild. For organisations that lack the capacity to facilitate these conditions, we recommend to transfer langurs to a pre-release environment that does suit the conditions, before reintroducing them into the wild. Thirdly, appropriate feeding times, such as in the early morning and late afternoon instead of noon, will likely make their daily activity pattern similar to that of wild conspecifics, which will increase the probability of a successful translocation. Considering the high level of interspecies ecological correspondence, these findings might be generalised to other Trachypithecus species as well. Similar studies could shed light on other primates' ecology and pre-release requirements, which would likewise aid in their conservation. For T. germaini, it is of vital importance that baseline data on their behaviour and ecology in the wild is gathered. Only then, we can determine their species-specific needs and facilitate a successful release.

ACKNOWLEDGEMENTS

We would like to thank Dr G. Donati, Prof. V. Nijman, Prof. S. Bearder, Dr S. Cheyne and Prof. C. Hill, for sharing their knowledge and experience, which enabled the successful implementation of this research. Our gratitude further goes to Angkor Centre for Conservation of Biodiversity, which provided the opportunity to study their T. germaini group, to D. Roper-Jones, for his statistical advice and logistical help and to Y. Poeu and P. Chhunheang for the identification of vegetation. A pilot study was made possible thanks to G. Kranendonk and Burger's Zoo, The Netherlands. This work was undertaken with the support of The Mohamed bin Zayed Species Conservation Fund, project no.14058504, and the Conservation Fund of the Primate Society of Great Britain and Born Free Foundation. Finally, we would like to thank the two anonymous reviewers, and Drs John Fellowes and Ramesh Boonratana for their constructive criticism of the manuscript.

REFERENCES

- Altmann, J. 1974. Observational study of behavior: sample methods. *Behaviour* **49**: 227–267.
- Altmann, J. and Muruthi, P. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology* **15**: 213– 221.
- Ampeng, A. and Md-Zain, B.M. 2012. Ranging patterns of critically endangered colobine *Presbytis chrysomelas chrysomelas. The Scientific World Journal* 2012: 1–7.
- Bennett, E.L. and Davies, A.G. 1994. The ecology of Asian colobines. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution, A.G. Davies and J.F. Oates (eds.), pp. 129–171. Cambridge University Press, New York, USA.
- Bernstein, I.S. 1972. Daily activity cycles and weather influences on a pigtail monkey group. *Folia Primatologica* **18**: 390–415.
- Bronikowski, A.M. and Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology* **39**: 11–25.
- Caro, T.M., Roper, R., Young, M. and Dank, G.R. 1979. Inter-observer reliability. *Behaviour* **69**: 303–315.
- Chapman, C.A. and Peres, C.A. 2001. Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology* **10**: 16–33.

- Claridge, A.W. and Cork, S.J. 1994. Nutritional-value of hypogeal fungal sporocarps for the long-nosed potoroo (*Potorous tridactylus*), a forest-dwelling mycophagous marsupial. *Australian Journal of Zoology* **42**: 701–710.
- Claridge, A.W., Trappe, J.M., Cork, S.J. and Claridge, D.L. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. *Journal of Comparative Physiology B* **169**: 172–178.
- Coudrat, C.N.Z., Rogers, L.D. and Nekaris, K.A.I. 2011. Abundance of primates reveals Samkos Wildlife Sanctuary, Cardamom Mountains, Cambodia as a priority area for conservation. *Oryx* **45**: 427–434.
- Cowlishaw, G. and Dunbar, R.I. 2000. *Primate Conservation Biology*. University of Chicago Press, London, UK.
- Davies, A., Bennett, E.L. and Waterman, P.G. 1988. Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **34**: 33–56.
- Ding, W. and Zhao, Q.K. 2004. *Rhinopithecus bieti* at Tacheng, Yunnan: diet and daytime activities. *International Journal of Primatology* **25**: 583–598.
- Edwards, S., Allison, J. and Cheetham, S. 2012. Recent mammal records from the Oddar Meanchey portion of the Kulen-Promtep Wildlife Sanctuary, Northern Cambodia. *Cambodian Journal of Natural History* **1**: 8–12.
- El Alami, A., Van Lavieren, E., Rachida, A. and Chait, A. 2012. Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the Endangered Barbary macaque (*Macaca sylvanus*) in the Central High Atlas Mountains, Morocco. *American Journal of Primatology* **74**: 210–216.
- Eley, R.M., Strum, S.C., Muchemi, G. and Reid, G.D.F. 1989. Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *American Journal of Primatology* **18**: 209–219.
- Field, A. 2009. *Discovering Statistics Using SPSS*. SAGE Publications Ltd., London, UK.
- García, L.V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**: 657–663.

- Glander, K.E. 1982. The impact of plant secondary compounds on primate feeding behaviour. *American Journal of Physical Anthropology* **25**: 1–18.
- Gupta, A.K. and Chivers, D.J. 1999. Biomass and use of resources in South and South-East Asian primate communities. In: *Primate Communities*, J.G. Fleagle, C. Janson and K. E. Reed (eds.) pp. 38–54. Cambridge University Press, Cambridge, UK.
- Hanson, A.M., Hodge, K.T. and Porter, L.M. 2003. Mycophagy among primates. Mycologist *Mycologist* **17**: 6–10.
- Harcourt, A.H. 1987. Dominance and fertility among female primates. *Journal of Zoology* **213**: 471–487.
- Huang, C., Wei, F., Li, M., Li, Y. and Sun, R. 2003. Sleeping cave selection, activity pattern and time budget of white-headed langurs. *International Journal of Primatology* 24: 813–824.
- Isbell, L.A. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology* **2**: 143–155.
- IUCN 2014. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 April 2015.
- IUCN SSC. 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.
- Janmaat, K.R., Byrne, R.W. and Zuberbühler, K. 2006. Primates take weather into account when searching for fruits. *Current Biology* **16**: 1232–1237.
- Janson, C. and Chapman, C.A. 1999. Resources and primate community structure. In: *Primate Communities*, J.G. Fleagle, C. Janson and K.E. Reed (eds.), pp. 237–267. Cambridge University Press, Cambridge, UK.
- Kirkpatrick, R.C. 2011. The Asian colobines: diversity among leaf-eating monkeys. In: *Primates in Perspective*, C.J. Campbell, A. Fuentes, K.C. MacKinnon and M. Panger (eds.), pp. 189–202. Oxford University Press, Oxford, UK.
- Korstjens, A.H., Lehmann, J. and Dunbar, R.I.M. 2010. Resting time as an ecological constraint on primate biogeography. *Animal Behaviour* **79**: 361–374.
- Krishnamani, R. and Mahaney, W.C. 2000. Geophagy among primates: adaptive significance and ecological consequences. *Animal behaviour* **59**: 899–915.

- Li, Z. and Rogers, E. 2004. Habitat quality and activity budgets of white-headed langurs in Fusui, China. *International Journal of Primatology* **25**: 41–54.
- Lloyd, E. and Suarez, S.A. 2005. The impact of geophagy on ranging behaviour in Phayre's leaf monkeys (*Trachypithecus phayrei*). *Folia Primatologica*, **76**: 342–346.
- Martin, P. and Bateson, P. 1993. *Measuring Behaviour: An Introductory Guide*. Cambridge University Press, Cambridge, UK.
- Mathews, F., Orros, M., McLaren, G., Gelling, M. and Foster, R. 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biological Conservation* **121**: 569–577.
- McIlwee, A.P. and Johnson, C.N. 1998. The contribution of fungus to the diets of three mycophagous marsupials in Eucalyptus forests, revealed by stable isotope analysis. *Functional Ecology* **12**: 223–231.
- McKenna, J.J. 1979. The evolution of allomothering behavior among colobine monkeys: function and opportunism in evolution. *American Anthropologist* 81: 818–840.
- Md-Zain, B.M. and Ch'ng, C.E. 2011. The activity patterns of a group of Cantor's dusky leaf monkeys (*Trachypithecus obscurus halonifer*). *International Journal of Zoological Research* **7**: 59–67.
- Moody, J.E., Dara, A., Coudrat, C.N., Evans, T., Gray, T., Maltby, M., Soriyun, M., Meng Hor, N., O'Kelly, H., Bunnat, P., Channa, P., Pollard, E., Rainey, H.J., Rawson, B.M., Vann, R., Chansocheat, S., Setha, T. and Sokha, T. 2011. A summary of the conservation status, taxonomic assignment, and distribution of the Indochinese silvered langur, *Trachypithecus germaini* (*sensu lato*) in Cambodia. *Asian Primates Journal* 2: 21–28.
- Mukherjee, R.P. 1978. Further observations on the golden langur (*Presbytis geei* Khajuria, 1956), with a note to capped langur (*Presbytis pileatus* Blyth, 1843) of Assam. *Primates* **19**: 737–747.
- Nadler, T., Timmins, R.J. and Richardson, M. 2008. *Trachypithecus germaini*. In: IUCN 2014. The IUCN Red List of Threatened Species. Version 2014.3. http://www.iucnredlist.org. Downloaded on 18 April 2015.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* **15**: 1044–1045.

- Oppenheimer, J.R. 1976. *Presbytis entellus*: birth in a free-ranging primate troop. *Primates* **17**: 541–542.
- Phan, J. and Stevens, N.J. 2012. A comparative study of activity budgets in captive and semi-free ranging Hatinh and Delacour's langurs (*Trachypithecus hatinhensis* and *T. delacouri*). *Vietnamese Journal of Primatology* **2**: 55–66.
- Poirier, F.E. 1969. The Nilgiri langur (*Presbytis joh-nii*) troop: its composition, structure, function and change. *Folia Primatologica* **10**: 20–47.
- Rawson, B.M. and Bach, L.T. 2011. Preliminary observations of geophagy amongst Cambodia's Colobinae. *Vietnamese Journal of Primatology* **1**: 41–46.
- Schneider, I., Tielen, I.H., Rode, J., Levelink, P. and Schrudde, D. 2010. Behavioral observations and notes on the vertical ranging pattern of the critically endangered Cat Ba langur (*Trachypithecus poliocephalus poliocephalus*) in Vietnam. *Primate Conservation* **25**: 111–117.
- Soorae, P.S. (ed.) 2008. *Global Re-introduction Perspectives: Re-introduction Case-studies From Around the Globe*, pp viii + 284. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE.
- Stanford, C.B. 1991. The capped langur in Bangladesh: behavioral ecology and reproductive tactics.
 In: Contributions to Primatology, Volume 26, F.S. Szalay (ed.), pp. 1–179. Karger Medical and Scientific Publishers, Basel, Switzerland.
- Stelzner, J.K. and Hausfater, G. 1986. Posture, microclimate, and thermoregulation in yellow baboons. *Primates* **27**: 449–463.
- Sterck, E.H. and Steenbeek, R. 1997. Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour* **134**: 749–774.
- Timmins, R.J., Steinmetz, R., Poulsen, M.K., Evans, T.D., Duckworth, J.W. and Boonratana, R. 2013. The Indochinese Silvered Leaf Monkey *Trachypithecus germaini* (*sensu lato*) in Lao PDR. *Primate Conservation* **26**: 1–12.
- Whitten, P.L. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology* **5**: 139–159.
- Workman, C. and Schmitt, D. 2012. Positional behavior of Delacour's langurs (*Trachypithecus delacouri*) in Northern Vietnam. *International Journal of Primatology* **33**: 19–37.

- Wrangham, R.W. 1980. An ecological model of femalebonded primate groups. *Behaviour* **75**: 262–300.
- Yang, L., Minghai, Z., Jianzhang, M., Ankang, W., Shuangxi, W. and Shusen, Z. 2005. Time budget of daily activity of Francois' langur (*Trachypithecus francoisi francoisi*) in Guizhou Province. *Acta Theriologica Sinica* 25: 156–162.
- Yang, L., Minghai, Z., Jianzhang, M., Ankang, W., Shuangxi, W. and Shusen, Z. 2007. Time budget of daily activity of Francois' langur (*Trachypithecus francoisi francoisi*) in disturbance habitat. *Acta Ecologica Sinica* 27: 1715–1722.
- Zinner, D., Fickenscher, G.H. and Roos, C. 2013. Family Cercopithecidae (Old World monkeys). In: Handbook of the Mammals of the World, Volume 3: Primates, R.A. Mittermeier, A.B. Rylands, and D.E. Wilson (eds), pp. 550–753. Lynx Edicions, Barcelona, Spain.
- Zhou, Q., Wei, F., Huang, C., Li, M., Ren, B. and Luo, B. 2007. Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *International Journal of Primatology* 28: 657–671.