Revealing secondary seed removers: results from camera trapping

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Abstract

This paper reports the results of the first study on secondary seed removal of seeds dispersed by Sykes' monkeys (*Cercopithecus albogularis*) using camera traps in Africa. Patterns of primary seed dispersal are often superimposed by secondary conveyance, emphasising the need to study these secondary processes carefully. As the agents and mechanisms of seed dispersal are often concealed, being carried out by cryptic or nocturnal animals in dense vegetation, camera trapping was deemed a viable means to investigate secondary removal of seeds disseminated by *C. albogularis* in the Western Soutpansberg, South Africa. Camera traps were established at preferred feeding trees of the focal Sykes' monkey group to identify animal species that remove seeds and fruits spat and dropped to the forest floor and seed removal observations were carried out. This method proved to be effective in identifying seed removers and also allowed to get indications about the quantities of seeds removed. Ten animal species were recorded visiting the trees, of which eight were observed removing seeds and fruits. Overall seed and fruit removal rates were high, indicating that the foraging behaviour of *C. albogularis* attracts many terrestrial frugivores.

Key words: camera trapping, *Cercopithecus albogularis*, frugivory, seed removal, seed spitting, South Africa

Résumé

Cet article donne les résultats de la première étude portant sur l'enlèvement secondaire des semences dispersées par les cercopithèques de Sykes (*Cercopithecus albogularis*), réalisée en Afrique avec des pièges photographiques. Des transferts secondaires se superposent souvent aux schémas de dispersion primaire, ce qui montre bien la nécessité d'étudier soigneusement ces processus secondaires. Comme les agents et les mécanismes de la dispersion des graines sont souvent cachés, étant le fait d'animaux cryptiques ou nocturnes qui agissent dans une végétation dense, on a estimé que les pièges photographiques étaient un moyen viable d'étudier le prélèvement secondaire des semences disséminées par *C. albogularis* dans le Western Soutpansberg, en Afrique du Sud. On a placé des pièges photos près des arbres où le groupe de cercopithèques de Sykes qui nous intéressait se nourrit de préférence, pour identifier les espèces animales qui enlèvent les graines et les fruits crachés et rejetés sur le sol de la forêt et on a ainsi pu réaliser cette étude. Cette méthode s'est avérée efficace pour identifier les espèces concernées et a aussi permis d'avoir des indications sur la quantité de graines emportées. On a pu enregistrer le passage de dix espèces animales près des arbres, dont huit furent observées en train de prélever des graines et des fruits. Le taux global de prélèvement des graines et des fruits était élevé, ce qui montre que le comportement alimentaire de *C. albogularis* attire de nombreux frugivores terrestres.

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Introduction

Research on seed dispersal has a long tradition (Beal, 1898; Ridley, 1930), none the less the exact mechanisms of animal-mediated seed dispersal and its effects on vegetation structure are still poorly understood. Recently, new methodologies such as stable isotope analysis and molecular genetic markers have opened up different possibilities for seed-dispersal research (Wang & Smith, 2002). Applying techniques used in other disciplines to this subject can significantly advance our understanding of the complex relationships involved.

Automatic camera traps are a highly efficient and comparatively non-invasive method in studies of large vertebrates. They have been used to estimate population densities of large mammals, especially carnivores (Karanth & Nichols, 1998; Carbone *et al.*, 2001; O'Brien, Kinnaird & Wibisono, 2003), for assessments of the diversity and abundance of mammals in tropical and temperate forests (Trolle, 2003; Yasuda, 2004; Srbek-Araujo & Chiarello, 2005) and for studying the activity patterns of animals (Van Schaik & Griffith, 1996). When compared to direct observation, the advantages of camera trapping include reduced disturbance to animals, the inclusion of nocturnal and cryptic species and continuous sampling through all weather conditions.

Camera trapping has great potential for analyzing secondary seed removal as part of revealing complex seed-dispersal systems. Despite this, not many studies have used this methodology in studies of seed dispersal. Miura, Yasuda & Ratnam (1997) were the first to use camera trapping to reveal the identity of ground-dwelling animals removing fruits from the forest floor in Malaysia. Subsequent studies on seed dispersal using camera traps have examined seed and fruit removal from the ground in Peru (Beck & Terborgh, 2002), Malaysia (Nakashima, Lagan & Kitayama, 2008) and Thailand (Kitamura *et al.*, 2004, 2006); fruit removal from the canopy in Japan (Otani, 2001) and Sri Lanka (Jayasekara *et al.*, 2003); and scatter-hoarding behaviour of rodents in Malaysia (Yasuda, Miura & Hussein, 2000).

In this paper, the results of the first study on secondary seed removal using camera traps in Africa are reported. Automatic cameras were used to reveal the secondary removers of seeds primarily dispersed intact by Sykes' monkeys (*Cercopithecus albogularis,* Sykes 1831).

Monkeys of the genus *Cercopithecus* (Order: Primates, Family: *Cercopithecidae*) are potentially important seed dispersers, due to characteristics including a largely frugivorous diet, a wide geographical distribution, the utilization of both arboreal and terrestrial habitats, comparatively long gut-retention times and long daily travel-distances (Kaplin & Lambert, 2002). *Cercopithecus* monkeys exhibit several modes of seed handling: they not only ingest seeds but also drop seeds, from which they have removed part or all of the fruit pulp, beneath the parent tree (Kaplin & Moermond, 1998; Lambert, 1999; Heikamp, 2008). The tendency to spit seeds is a characteristic that distinguishes Cercopithecinae from other non-human primates (Corlett & Lucas, 1990). They are specially adapted to this behaviour by fine oral fruit-processing abilities combined with cheek pouches (Lambert, 1999). The effect of this seed spitting behaviour on post dispersal processes has barely been analysed (Lambert, 2001; Balcomb & Chapman, 2003).

Material and methods

Study area and study species

The study spanned a period from the end of the dry season in September 2007 to the beginning of the rainy season in November 2007 and was conducted at the Lajuma Research Centre (29°26′E. 23°01′S). The Lajuma Research Centre is situated in the Western Soutpansberg mountain range of South Africa's Limpopo Province on a private property of approximately 430 ha with an altitudinal range of 1100–1747 m asl. The area belonging to the Lajuma Research Centre is covered in the higher parts by montane grassland while further down, within the home range of the focal Sykes' monkey group, there are mainly found two distinct types of forest: moist evergreen forest beneath ridges nurtured by mist precipitation, dominated by *Xymalos monospora* (Harvey) Baillon and *Pachystigma bowkeri* Robyns, and semi-deciduous woodland and thicket dominated by *Acacia ataxacantha* de Candolle and *Ziziphus mucronata* Willdenow (Heikamp, 2008).

The Sykes' monkey *C. albogularis* was long considered a subspecies of *Cercopithecus mitis*, but Dandelot (1974) separated it from *C. mitis*. In the majority of recent taxonomic schemes (e.g. Bronner *et al.*, 2003; Groves, 2005) it is considered a distinct species. The Sykes' monkey is a forest-dwelling guenon that is largely arboreal. Its diet is predominantly frugivorous (43%, Beeson, 1989; 73%, Heikamp, 2008) but displays substantial seasonal variation depending on fruit availability (Beeson, 1989). *C. albogularis* has a fragmented distribution over the eastern and southern parts of Africa, ranging from Ethiopia and Kenya to South Africa.

Monitored fruiting trees

Heikamp (2008) followed a well-habituated local troop of Sykes' monkeys on Lajuma over one season and identified 25 fruiting trees heavily utilised by the monkey group. Three of the tree species most frequented in the beginning of that study were chosen for this study, namely: *Ficus sur* Forsskål (Moraceae), *Chionanthus foveolatus* (E. Meyer) Stearn (Oleaceae), and *Syzygium legatii* Burtt Davy & Greenway (Myrtaceae).

Ficus sur is a medium to large semi-deciduous tree occurring in forest and bushveld. Figs of *F. sur* grow in large (up to 1 m long), leafless clusters of branchlets on the trunk or on main branches (Van Wyk & Van Wyk, 1997). They are on average 36 mm long and 34 mm wide, containing numerous seeds of less than 2 mm (Heikamp, 2008). *Ficus sur* is distributed throughout the Sykes' monkey's home range and is not discernibly related to either the evergreen or the semi-deciduous forest (Heikamp, 2008).

Chionanthus foveolatus is a small to medium-sized evergreen tree occurring in forest and wooded ravines (Van Wyk & Van Wyk, 1997). Fruits of *C. foveolatus* are dark purple when ripe and are on average 22 mm long and 14 mm wide one-seeded drupes, with the seeds being on average 20 mm long and 12 mm wide with a hard, lignified endocarp (Linden, pers. obs.). *Chionanthus foveolatus* was observed as an element of the semi-deciduous forest in the study area (Heikamp, 2008).

Syzygium legatii is a medium-large evergreen tree with a dense crown (Van Wyk & Van Wyk, 1997). Its rotund drupes, pink to purple when ripe, are on average 20 mm wide and 19 mm long, with one or occasionally two seeds, on average 16 mm wide and 12 mm long (Heikamp, 2008) and a relatively thin and soft endocarp (Seufert, per. obs.). *Syzygium legatii* was identified by Heikamp (2008) as a typical element of the evergreen forest in the study area, becoming a dominant tree species on more exposed ridges.

The fruits of *F. sur* were either dropped by the monkeys whole or half-eaten, whereas the drupes of *S. legatii* and *C. foveolatus* were either dropped intact or half-eaten, or their seeds spat to the ground once cleaned of fruit pulp.

Camera trapping

Four individual trees of both *S. legatii and F. sur* visited regularly by the monkey troop, beneath which many dropped seeds and fruits could be found, were monitored. For *C. foveolatus* only two individual trees remained, as the Sykes' monkeys stopped their visits to this species during the course of the study period when the remaining fruits on these trees became scarce. In total therefore, 10 trees spread over an area of ca. 700 × 900 m were monitored and used as sites for camera trapping.

Three automatic cameras (Wildview Xtreme 2) were used intermittently between the various camera-trap sites. One camera was used per individual tree and mounted at about 1 m height on a trunk next to the monitored fruiting tree. Individual trees were monitored for approximately six days in order to obtain at least 25 days of monitoring for each species.

The camera automatically recorded date and time for each photograph taken. Once an animal appeared within range of the camera trap and the motion detector of the camera was activated, the camera took three images in succession, with an interval of 3–8 s between each picture. A sequence of three photographs with intervals of less than 10 s between them was considered a single record. Because of the many consecutive records of the same species, independent visits by different individuals were difficult to separate. Independent visits were therefore defined following O'Brien *et al.* (2003) as (i) consecutive records of individuals of different species, (ii) non-consecutive records of individuals of the same species, (iii) consecutive records of individuals of the same species taken more than 30 min apart. The sampling effort was defined as the number of trap days and the sampling success as the number of visits recorded per 100 trap days. The duration of each independent visit was defined as the difference between the times of the first and the last photograph of the visit. Taxonomic nomenclature for the visiting animal species follows Wilson & Reeder (2005).

Seed removal

Because of climatic and logistical constraints, the cameras could not always be checked on a daily basis, but were monitored at intervals of 1–3 days. To determine to what extent the visiting animals were feeding on seeds of the different tree species primarily dispersed by the monkeys, a pile of bare seeds the monkeys had spat and a pile of intact or half-eaten fruits they had dropped beneath the parent tree were separately assembled in front of each camera. For *F. sur* no seeds were laid out as the monkeys did not spit fig seeds.

A removal event was recorded every time seeds or fruits had been removed from the piles at each site inspection and the number of seeds and fruits removed in each removal event was noted. Freshly dropped fruits and/or freshly spat seeds were added to the piles, depending on the abundance of seeds and fruits lying beneath the fruiting tree.

An attempt was made to assign removal events to visits captured by camera traps in which the visiting animals were observed feeding from the laid out seed and fruit piles. When more than one visit in which animals were observed feeding from the piles occurred between two site inspections, the removal event was not assigned to a single visit but to the number of such visits that occurred in the interval between site inspections (e.g. if two different species were recorded removing fruits or seeds from piles between two site inspections, the removal event was assigned to both species). As in such cases it was not possible to determine the extent to which the different visitors contributed to the removal event, only the removal event per se, not the associated number of seeds or fruits removed, was assigned to the visitors.

Results

Camera trapping

The total sampling effort of the camera trapping consisted of 1920 h, or 80 days. Ten mammal species belonging to five different mammalian orders visited the monitored fruiting trees (Table 1). These were recorded in 118 photographic records of which 53 were determined to be independent visits (Table 2). The hyrax was the only visitor that could not be identified to species level because of the insufficient quality of the pictures. It could be either *Procavia capensis* (rock hyrax) or *Heterohyrax brucei* (yellow-spotted rock hyrax). The bushpig (*Potamochoerus larvatus*) was by far the most frequent visitor, accounting for 56.6% of all visits and for 57.1% of the assigned seed and fruit removal events (Table 1). The majority of all visits to the fruiting trees (n = 37) occurred at night (i.e. between sunset and sunrise). Five animal species were nocturnal visitors while the other five species visited the trees during daytime (Table 3).

In 49.1% (n = 26) of the visits the animals were observed feeding on those seeds or fruits naturally fallen or dropped by the monkeys to the ground and in 38.0% (n = 20) of the visits they were observed feeding on the laid out seed and fruit piles. The carnivorous leopard (*Panthera pardus*) and the frugivorous galago (*Otolemur crassicaudatus*) were the only two animal species which were not observed feeding on fruits or seeds from the ground.

Seed removal

Out of a total of 53 recorded visits, *S. legatii* was frequented 39 times, followed by eleven visits to *F. sur* and three to *C. fovoelatus* (Table 2). The fruit removal ratio (Table 2) was

Table 1 Number of independent visits of each animal species captured by automatic cameras at the different tree species and number of seed and fruit removal events assigned to visits at the Lajuma Research Centre, South Africa

		Visits to fruiting trees (n)				Assigned
Order/species		*Ficus sur*	*Chionanthus foveolatus*	*Syzygium legatii*	Total	removal events (n)
Hyracoidea						
Hyrax sp.		–	–	1	1	1
Primates						
Cercopithecus albogularis (Sykes, 1831)	Sykes' monkey	4	–	1	5	1
Chlorocebus pygerythrus (F. Cuvier, 1821)	Vervet monkey	1	–	–	1	1
Otolemur crassicaudatus (E. Geoffroy, 1812)	Greater galago	–	1	–	1	–
Papio ursinus (Kerr, 1792)	Chacma baboon	2	–	2	4	2
Rodentia						
Cricetomys gambianus (Waterhouse, 1840)	Gambian giant rat	2	1	1	4	2
Hystrix africaeaustralis (Peters, 1852)	Cape porcupine	–	–	4	4	1
Carnivora						
Panthera pardus (Linnaeus, 1758)	Leopard	–	–	1	1	–
Artiodactyla						
Cephalophus natalensis (A. Smith, 1834)	Red duiker	2	–	–	2	1
Potamochoerus larvatus (F. Cuvier, 1822)	Bushpig	–	1	29	30	8

The hyrax could not be identified to species level; it could be either *Procavia capensis* (rock hyrax, Pallas, 1766) or *Heterohyrax brucei* (yellow-spotted rock hyrax, Gray, 1868).

Table 2 Tree species monitored with an automatic camera system, sampling effort, sampling success, number of records (i.e. sequence of three pictures with intervals of less than 10 s), number of independent visits (i.e. records with intervals of ≥ 30 min between pictures), mean duration of stay per visit of the visiting animal species, number of removal events and mean seed and fruit removal ratios (with ± SE in parentheses) for the three monitored tree species at the Lajuma Research Centre, South Africa

Tree species	Sampling effort (days)	Sampling success (visits per 100 days)	Records (n)	Visits (n)	Mean duration of stay (min)	Removal events (n)	Removal ratio (%)	
							Seeds	Fruits
Chionanthus foveolatus	26	11.5	3	3	< 1	5	35.4 (± 13)	10.7 (± 6)
Ficus sur	25	44	19	11	5.5	10		9.6 (± 6)
Syzygium legatii	29	134.5	96	39	9.8	11	71.1 (± 11)	61.8 (± 13)
Total	80	66.3	118	53	/	26		

Table 3 Ecology of the visiting animal species: foraging guild (C, carnivore; F, frugivore; Fo, folivore; Gm, graminivore; Gn, granivore; R, roots, bulbs, tubers; S, scavenger), effect on seeds (D, disperser; P, predator), habit (t, terrestrial; a, arboreal), habitat, activity period (d, diurnal; n, nocturnal) and body mass

Order/Species	Foraging guild[a]	Effect on seeds	Habit	Habitat[a]	Activity period	Body mass[a]
Hyracoidea						
Hyrax sp.	Gm, Fo, F	?	t, a	Rock outcrops	d	1.8–5.5 kg
Primates						
Cercopithecus albogularis	F, Fo	D[b]	a, t	Evergreen forests	d	3.5–12 kg
Chlorocebus pygerythrus	Gn, F,	D[c]	a	Woodland	d	3.5–8 kg
Otolemur crassicaudatus	Gn, F, C	D[d]	a	Dense vegetation in Miombo, coastal and montane areas	n	0.5–2 kg
Papio ursinus	R, F, Gn, C	D[e]	t, a	Most habitats	d	12–45 kg
Rodentia						
Cricetomys gambianus	F, Gn, Fo	P	t	most habitats	n	1–1.4 kg
Hystrix africaeaustralis	R, S	?	t	most habitats	n	10–24 kg
Carnivora						
Panthera pardus	C	-	t	most habitats	n	28–90 kg
Artiodactyla						
Cephalophus natalensis	F, Fo	?	t	coastal, riverine and montane forests	d	12–14 kg
Potamochoerus larvatus	R, F, Gm, C, S	?	t	forests, woodland	n	45–150 kg

[a]Data from Kingdon (1997).
[b]Heikamp (2008).
[c]Foord *et al.* (1994).
[d]Ejidike & Okosodo (2007).
[e]Van den Bremer *et al.* (2005).

highest in *S. legatii* (61.8% ± 13) and varied significantly between different tree species (Kruskal-Wallis test, H = 7.66, $P = 0.02$). The seed removal ratio was higher than the fruit removal ratio in both *C. foveolatus* and *S. legatii* but this difference was not significant in either case (Wilcoxon signed-rank test, $z = 1.83$, $P = 0.07$ and $z = 1.75$, $P = 0.08$, respectively).

The seed and fruit removal events that could be assigned to visits captured by camera traps were fourteen out of 26; the remaining twelve removal events were not recorded as the cameras failed to release or did not capture the animal in the frame. Therefore, the assignment of a particular removal event to a particular visit captured by the cameras must be seen as a presumption. In four cases, more than one visit occurred between site inspections and the removal events were assigned to all visits that had occurred since the previous site inspection.

Discussion

Camera trapping

When applying the method of camera trapping – which is above all used in studies of carnivores and other larger vertebrates – to a study of seed removal, it has to be adapted to the desired use. For example, the required zone of detection of the camera trap is considerably smaller compared with camera traps set to monitor a game trail as the camera has only to monitor a relatively small area surrounding the seed and fruit piles. The trigger speed of the camera equipment used in this study (up to 15 s with full batteries, according to the technical data sheet of the camera equipment) was relatively slow and probably the primary reason for the failure of the camera traps to capture the visiting animals in twelve out of the 26 removal events.

On the other hand the many advantages of camera trapping became apparent in the present study. The camera traps revealed numerous visitors and seed removers at the monitored fruiting trees and the majority of them were captured at night. Several of the visitors were shy animals, which are difficult or even impossible to observe directly (e.g. *Cricetomys gambianus*, *Hystrix africaeaustralis*). Direct observation would most likely have scared off shy animals, underestimated nocturnal visitors and would have required a much greater effort to collect the 1920 h of observation achieved with the cameras.

Seed removal

The piling of seeds and fruits in front of the cameras probably influenced the behaviour of seed removers, attracting them to an artificial concentration of food resources. At one *S. legatii* camera trap site all seeds and fruits laid out were removed by *P. larvatus* over four consecutive days (the sites having been checked daily in this instance). This observation gave the impression of animals returning deliberately to the trap site in search of the seed and fruit piles. Possibly, the high sampling success rate of 118 records over 80 days can be attributed to the attraction of the seed and fruit piles.

Nevertheless, the method of piling seeds and fruits was deemed appropriate as the aim of the study was not the quantification of seed removal but rather a qualitative analysis of the seed remover community. The main purpose of the piles was to attract seed removers in order to identify the animals visiting the trees with camera traps. The gathering of seeds and fruits in piles used in this study was not appropriate for a quantitative analysis of seed removal. For an exact quantification of seed removal, more detailed removal observations and experiments would have had to be conducted.

Arboreal resources for terrestrial animals

Arboreal primates like the Sykes' monkey often handle fruits wastefully and drop numerous fruits uneaten to the ground beneath the parent tree (Howe, 1980). In this study, the method used did not allow to distinguish between ripe fruits fallen to the ground without interference by frugivores and intact fruits dropped by the monkeys. Handling by the monkeys could only be ascertained in the case of half-eaten fruits which the monkeys had bitten and in the case of bare seeds cleaned of fruit pulp by the monkeys and then spat out. The proportion of fruits falling to the ground naturally without the aid of frugivores varies between different tree species. Some fruits, especially large ones, remain attached to the tree and eventually decay if they are not handled by frugivores (e.g. *Monodora myristica*, Balcomb & Chapman, 2003). In other tree species that produce fruits in great abundance, large proportions of the fruits drop ripe and intact without being handled by frugivores (e.g. 59% of the figs of *Ficus tiliifolia* on Madagascar, Goodman, Ganzhorn & Wilmé, 1997). The exact proportion of intact fruits on the ground attributed to monkey activity could not be quantified in this study.

Fruits represent important food resources for many ground-dwelling animals (e.g. duikers, Wilson, 2005). Of the visiting animal species in this study, three are strictly terrestrial (*Cephalophus natalensis*, *P. larvatus*, *H. africaeaustralis*), two (*C. gambianus*, Hyrax sp.) are largely terrestrial and all of these were observed feeding on seeds and fruits dropped by the monkeys. Judging from the numerous visits to the fruiting trees during the relatively short study period, arboreal primates can make valuable food resources available to non-arboreal animals. At the *S. legatii* trees in particular, the visiting animals spent much time (approximately 10 min per visit on average,

Table 2) and many of the animals removed all of the laid out fruits and seeds, indicating a thorough search of the ground for food resources. During the study period, a red duiker (*C. natalensis*) was observed following the focal monkey group for several hours on at least three occasions, taking advantage of the many fruits dropped by the foraging monkeys.

Ecology of seed removers

Lambert (2001) found that the process of seed spitting by *Cercopithecus ascanius* in Uganda not only increased germination rates (also found for *C. albogularis* in this study, unpubl. data) but also reduced the amount of seed removal (which she interpreted as seed predation by rodents) when compared to intact fruits fallen from the fruiting tree. However, in this study the visiting animals removed more bare seeds of *S. legatii* and *C. fovoelatus*, which had been spat by the monkeys, than intact fruits. This difference was not significant but the statistical analysis has to be interpreted with caution because of the small sample size (n = 13 in *S. legatii*; n = 8 in *C. fovoelatus*).

Fruit removal ratios were relatively high in *S. legatii* (61.8%, Table 2) but low in *F. sur* (9.6%) and *C. foveolatus* (10.7%). Seed removal ratios instead were high in *S. legatii* (71.1%) and intermediate in *C. fovoelatus* (35.4%). High seed removal could be an indication of high seed predation. Yet without further studies on the fate of removed seeds, seed removal should not necessarily be equated with seed predation (Vander Wall, Kuhn & Beck, 2005). The Gambian giant rat (*C. gambianus*) was the only animal observed predating on seeds, removing the endosperm of seeds of *S. legatii* and *C. foveolatus*, leaving the seed coat and fruit pulp behind. By exposing the seed through their seed spitting behaviour, the monkeys could provide a useful service for animals like *C. gambianus* which feed on the nutrient rich endosperm. Thereby, seed-spitting could potentially attract such seed predators.

Bushpig (*P. larvatus*) removed seeds and fruits of *S. legatii* without leaving any remnants behind, this being an indication that these animals ingested every part of the seeds and fruits. Data are not available on whether this species is capable of dispersing large seeds of >10 mm size or if it mainly acts as a seed predator. Concerning the other animal species, no conclusions about seed handling could be drawn, neither from the state of the seeds and fruits left behind, nor from the photographs taken. While there have been numerous seed dispersal studies conducted on primates (e.g. Foord, Van Aarde & Ferreira, 1994 for *Chlorocebus pygerythrus*; Ejidike & Okosodo, 2007 for *Otolemur crassicaudatus*; Van den Bremer, Heitkönig & Gaigher, 2005 for *Papio ursinus*), the role of terrestrial vertebrates as seed dispersers or seed predators is not as well-studied (Table 3).

With its relatively large and soft seeds, *S. legatii* could be prone to seed predation. The seeds of *C. foveolatus* are of similar size but they are protected by a hard, lignified endocarp. In the case of *F. sur*, the small size of *Ficus* seeds (<2 mm) increases their likelihood of remaining undamaged through ingestion and gut passage (Lambert, 1999), and thus the likelihood of their dispersal by animals (Gautier-Hion *et al.*, 1985). Still, to make more grounded statements about the role of seed removers as seed dispersers or seed predators for the different tree species, faecal analysis and germination experiments need to be conducted.

The composition of the seed remover community and the number of visits varied between tree species. This implies varying attraction to the different tree species of seed removers. As most visiting animal species were generalists with a more or less omnivorous diet (Table 3), no indication as to the reason for the preference for certain tree species could be found.

Conclusions

The present study shows that the role of *C. albogularis* as a seed disperser cannot be assessed simply by observations of the primate itself, but that secondary processes through secondary seed removers have to be considered. The foraging and feeding behaviour of the Sykes' monkeys attracts frugivorous animals who remove the fruits and seeds dropped and spat by the monkeys and who can potentially act as seed dispersers or seed predators. These secondary seed removers thus overlay the primary seed deposition patterns of *C. albogularis*.

The agents and mechanisms of seed dispersal are often concealed as they are carried out by cryptic or nocturnal animals in dense vegetation, unable to be revealed through direct observations. The camera trapping method combined with seed-removal observations used in this study proved to be very effective in identifying seed removers and in analysing seed removal at different tree species. When checking the cameras and the laid out seed and fruit piles regularly, seed removal events can to a certain degree be assigned to individual visiting animals. When checked on a daily basis, the contribution of the different animal species to seed removal could possibly be quantified. Moreover, when combined with faecal analysis of the removing animal species and subsequent germination experiments the method is a promising tool to assess the role of seed removers in the dispersal network.

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