

Feeding ecology of the bokiboky, *Mungotictis decemlineata* (family Eupleridae)

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Abstract

The members of the order Carnivora display a variety of dietary patterns that appear to be linked to body size and activity. Small-bodied members of the family Herpestidae are known to specialize on an insectivorous diet and to be opportunistic generalists. However, the feeding ecology of the Malagasy mongoose-like carnivorans of the family Eupleridae remains poorly known. To fill this gap, we provide detailed observations on the feeding ecology of the forest-dwelling bokiboky (*Mungotictis decemlineata*). We investigated variation in their seasonal diet and foraging patterns in the Kirindy Forest/CNFEREF, a dry deciduous forest in central western Madagascar. Data from dry and rainy seasons were collected using a combination of fecal analysis and behavioral observations. A total of 420 food items from 22 different taxa were detected in 63 fecal samples. The present study revealed that *M. decemlineata* has a broad dietary preference, but is predominantly insectivorous. Furthermore, *M. decemlineata* responds to seasonal variation in prey abundance. Its inclination to insectivory may be a factor facilitating the formation of female groups.

Key words: diet composition, seasonality, insectivorous, *Mungotictis decemlineata*

Résumé détaillé

Le régime et le comportement alimentaire peuvent varier selon la taille corporelle et l'activité journalière au sein de l'ordre des carnivores. En particulier, les membres de la famille des Herpestidae sont connus pour se spécialiser pour le régime insectivore et comme étant des espèces généralistes et opportunistes. Cependant, concernant la famille des Eupleridae, l'écologie alimentaire reste encore peu investie. Afin de combler ce manque d'information, l'objectif de cette étude est d'examiner la composition du régime alimentaire et le comportement alimentaire de bokiboky, *Mungotictis decemlineata*, selon les saisons. Pour cela, la présente étude a été menée dans la forêt de Kirindy/CNFEREF (20°2'50"-20°4'57"S, 44°38'57"-44°41'33"E), située dans la partie centre-ouest de Madagascar pendant les saisons sèche et humide, du mois de mai à août 2013 et du mois de janvier à mars 2015.

La détermination du régime alimentaire a été basée sur l'analyse des fèces, alors que le comportement alimentaire a été étudié à partir des observations comportementales. Plusieurs méthodes ont été combinées afin d'identifier et d'estimer quantitativement les types de proies consommés par *M. decemlineata* pendant les deux saisons : le nombre minimum d'individus et la fréquence d'occurrence. En outre, des estimations de la richesse spécifique et de l'abondance des invertébrés terrestres dans les sites d'étude ont été faites pour connaître si *M. decemlineata* est sélective vis-à-vis du type de proies ou non. Au total, 420 proies appartenant à 22 taxa ont été identifiées à partir de 63 échantillons fécaux collectés. En outre, 37 individus focaux ont été suivis afin d'analyser leurs préférences en substrats lors de la recherche de nourriture et de connaître les proies pouvant être consommées par l'espèce mais qui ne pourront pas être détectées à partir des échantillons fécaux due aux processus de digestion.

Les résultats obtenus montrent que le régime et le comportement alimentaires de *M. decemlineata* sont influencés par l'abondance et la disponibilité des proies dans le milieu pendant les saisons sèche et humide. Cependant, même si les proies vertébrées et invertébrées sont présentes dans la

composition alimentaire de *M. decemlineata*, les arthropodes ont représenté une grande majorité des proies consommées que ce soit qualitativement ou quantitativement tout au long de l'année. Par ailleurs, l'utilisation des différentes strates par l'espèce durant la recherche alimentaire diffère suivant les saisons. Il a été noté que *M. decemlineata* concentre ses recherches dans les strates où la rencontre de proies est la plus probable, tels que la litière pour la saison sèche et les bois morts durant la saison des pluies. De plus, *M. decemlineata* ingère les mêmes taxons d'arthropodes pendant les deux saisons, mais ajuste son régime alimentaire selon l'abondance et la disponibilité saisonnière des différents types de proies.

La consommation d'une grande variété de proies a permis de classer *M. decemlineata* parmi les prédateurs généralistes, au surplus elle est largement opportuniste et fortement insectivore. Cette adaptation aux variations saisonnières à l'abondance et à la disponibilité des proies permet à l'espèce d'optimiser le taux d'énergies obtenues ; mais aussi le régime insectivore peut être une des facteurs facilitant la mise en place de la vie en groupe surtout chez les femelles adultes, qui peut être caractérisée par l'absence de compétition alimentaire directe chez les groupes de femelles durant les observations comportementales. Ainsi on peut conclure que l'écologie alimentaire de *M. decemlineata* présente beaucoup de similitudes à celle de *Galidictis fasciata grandidieri* dans le Sud de Madagascar mais aussi à celle des petites espèces d'Herpestides diurnes.

Mots clés : régime alimentaire, comparaison saisonnière, insectivore, *Mungotictis decemlineata*

Introduction

The different families of the order Carnivora exhibit considerable size-related variation in diet and activity. Small carnivores, including most members of the families Herpestidae and Eupleridae, the latter endemic to Madagascar, generally feed on small prey items, such as invertebrates and small vertebrates (Gittleman, 1985; Carbone *et al.*, 1999; Andriantsimetry *et al.*, 2009; Goodman, 2012). Several studies revealed that African and Malagasy species have an insectivorous diet and are known to be opportunistic generalists (Herpestidae: *Galerella nigrata*: Rathbun *et al.*, 2005; Eupleridae: *Galidictis grandidieri*: Andriantsimetry *et al.*, 2009). This specialization is presumably due to an adaptation

of their energy budget to balance hunting costs and energy gain (Carbone *et al.*, 2007).

According to optimal foraging theory, maximization of the net rate of energy intake is shaped by the abundance and availability of resources (Bond, 1980; Pyke, 1984; Sano, 1993; Tinker *et al.*, 2008; Balestrieri *et al.*, 2009). One major factor that may influence food availability and its abundance in many habitats is seasonality. For instance, arthropod abundance is related with seasonal variation in rainfall (Wolda, 1988). However, ground-dwelling arthropods exhibit less seasonal patterns in variation of their abundance than flying species (Dammhahn & Kappeler, 2008). Diet composition was indeed found to be more diversified due to greater abundance and prey availability during the rainy season compared to the corresponding lean season in several species of carnivores (Herpestidae: *Suricata suricatta*: Doolan & MacDonald, 1996; Eupleridae: *Cryptoprocta ferox*: Hawkins & Racey, 2008).

Food availability and abundance are also primary ecological factors affecting mammalian social systems as they may facilitate the maintenance of stable groups by reducing intra-specific competition associated with food abundance (Palomares & Delibes, 1993; Kappeler *et al.*, 2013). For species with an insectivorous diet, the availability and renewability of invertebrate food are known to decrease the intensity of feeding competition (Rood, 1986; Palomares & Delibes, 1993; Veron *et al.*, 2004; Le Roux *et al.*, 2009). Thus, an insectivorous diet is not only an adaptation to high insect availability (Cavallini & Nel, 1995), but also one of the conditions promoting group living in some carnivores (Rood, 1986; Baker, 1989; Palomares & Delibes, 1993; Doolan & MacDonald, 1996). In the Herpestidae, in particular, a combination of an insectivorous diet, diurnal activity and small body size are thought to promote group living (Cavallini & Nel, 1995; Veron *et al.*, 2004).

In contrast to the Herpestidae, the feeding ecology of their Malagasy sister group, the Eupleridae (Yoder *et al.*, 2003), has not been studied in detail. Only a few studies on the behavioral ecology of euplerids have been conducted (Albignac, 1976; Rasoloarison *et al.*, 1995; Hawkins & Racey, 2008; Andriantsimetry *et al.*, 2009; Lühns & Kappeler, 2013, 2014; Lühns *et al.*, 2013; Schneider & Kappeler, 2016; Schneider *et al.*, 2016), and their feeding ecology remains poorly known. We therefore conducted a study of the feeding ecology of the euplerid *Mungotictis decemlineata*, known by the vernacular name bokiboky.

Mungotictis decemlineata is one of the eight native species of Eupleridae, and is restricted to the dry deciduous forests of western Madagascar (Veron *et al.*, 2017). *Mungotictis decemlineata* exhibits a rare mammalian social organization, with females and males living in small same-sex units (Schneider *et al.*, 2016); little is known on the dietary correlates of this type of social organization. According to Albignac (1976), *M. decemlineata* has a specialized diet during the dry season that mainly consists of insect larvae, whereas during the rainy season its dietary choice becomes more variable and includes more reptiles and other small vertebrates due to higher abundance and availability of these prey types. Because Albignac's report is based on qualitative observations, the current study aims to document the seasonal composition of the diet of a habituated population of individually marked individual *M. decemlineata*. Specifically, we asked the following questions concerning *M. decemlineata*: 1) what is the dietary composition during the different seasons, 2) do they selectively feed on certain prey, and 3) does resource use vary according to prey availability between seasons?

Material and methods

To investigate the feeding ecology of *M. decemlineata* during different seasons, we radio-tracked and observed individuals from a marked population in Kirindy Forest/CNFEREF and collected their fecal samples during one dry season and one rainy season. We described diet composition based on direct observations and scat analyses, and examined whether study animals had any foraging sphere preferences and prey selectivity based on estimates of species richness and abundance of ground-dwelling arthropods in the study area.

Study sites and study periods

This study was conducted from May to August 2013 (dry season) and from January to March 2015 (wet season) in Kirindy Forest/CNFEREF, central western Madagascar (20°2'50"-20°4'57"S, 44°38'57"-44°41'33"E). The Kirindy Forest is a dry deciduous forest with a climate characterized by strong seasonality: hot wet season from December to March and dry season from April to November (Kappeler & Fichtel, 2012). *Mungotictis decemlineata* was studied at two local forest blocks, locally known as N5 and CS7.

Behavioral observations

During both study periods, 37 marked individuals, including 16 males and 21 females, were followed for 30 min units of focal animal sampling (Altmann, 1974). Radio-collared animals were searched by radio-tracking before conducting observations. Behavioral observations were conducted on seven female groups and on nine solitary males. Focal observations were rotated among social units and balanced between 07:00 and 17:00 h. Instantaneous focal sampling was used to collect behavioral data every 10 min during 30 min of focal animal sampling (Altmann, 1974). The method was used to record the frequency of strata used by *M. decemlineata* during foraging activities. A total of 204 observation hours were recorded for both dry and rainy seasons.

Foraging strata use

Stratum use was recorded in order to determine any potential preference during foraging activities. These data may also indicate the presence of some prey that are impossible to detect in scat analysis, such as insect larvae, which Albignac (1976) suggested to comprise the preponderant prey type during the dry season. For this study, we distinguished among four foraging strata: soil, litter, fallen rotten wood, and fallen trees resting on the ground level.

Arthropod sampling

Ground-dwelling arthropods were collected using pitfall traps. During both study periods, three sessions of arthropod sampling per season were carried out. For each session, 36 pitfall traps were placed randomly within the home ranges of six female groups, i.e. six pitfall traps per group. The traps were standardized by using the basal portions of plastic bottles with an aperture diameter of 95 mm, a base diameter of 82 mm, and a depth of 100 mm. The top of the trap was placed flush with the soil, filled at a one-third level with 70% ethanol, and covered with leaves. For every session, arthropods were collected every 72 h and when pitfall traps were refilled with 70% ethanol.

Scat collection and analysis

A total of 63 scat samples were collected during animal trapping or behavioral observations and used for determining diet composition. All scats could be unambiguously assigned to an individual. After collection, each scat was air-dried, and then oven-

dried to ensure the absence of humidity. Scat samples were kept in silica gel until analysis to ensure their conservation. Subsequently, each scat was soaked in 70% ethanol and broken into small pieces. Arthropod fragments, bones, hairs, feathers, and other types of remains (e.g. reptile egg membranes) were removed from fecal material with fine dissecting needles.

For determining prey items, invertebrate remains were identified to the level of order, using specimens collected from the pitfall traps as reference material. The different isolated prey remains recovered from the scats were identified under a dissecting scope to the most precise taxonomic levels feasible.

For prey quantification, two methods were used. The minimum number of individuals (MNI) is defined as a measure of the minimum number of prey ingested. For arthropod remains, in the case of MNI prey items, Orthoptera were identified and counted based on heads and mandibles, Coleoptera based on tarsi and elytra, Araneae based on chelicera and tarsi, centipedes based on tarsi, and Scorpionidae based on telsons. Bilateral tarsi and mandible elements were counted with the MNI being the largest number from either the left or right side. In cases when several scales were presented for one identified taxon, the most pertinent fragment was considered as representative, such as head or mandibles (Shiel *et al.*, 1997). When it was not possible to determine the MNI of prey items per taxon, but the remains could be identified, it was counted as a single individual. For mammal hairs and bird feathers, the MNI was assumed to equal a single individual per taxon.

We also recorded the percentage frequency (%F), which is expressed as the number of occurrences of the category (i.e. the number of scats containing the item in question) divided by the total occurrences for all categories, multiplied by 100 (Shiel *et al.*, 1997). The sum of percentage frequencies adds up to 100% and provides an estimate of the relative importance of each food type.

Statistical analyses

Prey remains from scats were analyzed qualitatively and quantitatively. In the qualitative part, similarities between the prey diversity consumed during the two seasons were calculated with Jaccard's Index J for each study period. In this context, each prey taxon was recorded as either being present or absent during each season. Quantitatively, we analyzed differences in the diets of *M. decemlineata* across seasons via χ^2 tests, using MNI data of prey remains obtained from the scat analysis. MNI as a conservative method

was used to represent net abundance of each prey type found in the fecal samples in order to avoid estimation bias.

For all statistical analyses, we used the software R 3.1.2. (R Core Team, 2014). We calculated proportion of use of each type of foraging stratum from observations of followed individuals. Influences of season and sex on the use of foraging spheres were analyzed by using pairwise analyses of variance per permutation with the package RVAideMemoire. A pairwise t-test with Bonferroni correction for P -value adjustment was used as *post-hoc* test to compare foraging spheres use between seasons. Abundance of arthropods obtained by trapping were estimated by using the Shannon-Wiener Index H (Shannon, 1948) and compared between seasons. Species richness differences were investigated by comparing Jaccard's Index J from both seasons (Jaccard, 1980). In order to investigate whether *M. decemlineata* consumes different prey according to their abundance, we calculated the correlation between prey abundances in scats and traps.

Results

Diet composition

We found that *Mungotictis decemlineata* consume a wide variety of food items, including invertebrates and vertebrates. A total of 420 food items of 22 different taxa were detected in 63 fecal samples (number of scats during dry season = 26; number of scats during rainy season = 37) (Table 1). Invertebrate remains occurred in 100% of the samples in both seasons, while vertebrates were found in 38.5% and 43.2% of the scats collected during the dry and rainy seasons, respectively.

Invertebrates were the most important prey characterizing the diet of *M. decemlineata* during both seasons, both in frequency of occurrence and MNI (dry season: %F = 85.4, MNI = 159; rainy season: %F = 87.2, MNI = 212), whereas vertebrates made up a smaller portion of the diet (dry season: %F = 14.3, MNI = 25; rainy season: %F = 12.8, MNI = 24) (Table 1). No significant difference was found between the amount of items at the group level consumed by *M. decemlineata* between both season (Chi-squared test: $X^2 = 3.92$, $df = 3$, $P > 0.05$; Figure 1).

Prey selectivity

Jaccard's index was calculated as $J = 1$, indicating that the same categories of arthropods were consumed by *M. decemlineata* during both seasons. However,

the quantity of each arthropod order eaten by *M. decemlineata* differed between the two seasons (Chi-squared test: $X^2 = 106.71$, $df = 8$, $P < 0.01$; Figure

Table 1. Taxonomic composition of prey taken by *Mungotictis decemlineata* during dry and rainy seasons in Kirindy Forest, as determined by scat analysis (total number of scats during both seasons: $N = 63$; number of scats during the dry season: $N_{dry} = 26$; number of scats during the rainy season: $N_{rainy} = 37$) (MNI: minimum number individual; %F: frequency of occurrence).

Food remains	Dry season		Rainy season	
	MNI	%F	MNI	%F
Invertebrates				
Araneae	37	26	13	7.7
Scorpionidae	1	1	6	3.8
Chilopoda	1	1	17	9.6
Diplopoda	1	1	2	1.3
Blattodea	77	27	35	21.2
Orthoptera	9	9.5	78	19.2
Coleoptera	21	15	49	20.5
Hymenoptera	11	4.2	11	3.2
Lepidoptera	-	-	1	0.7
Gastropoda	1	1	-	-
Subtotal	159	85.7	212	87.2
Vertebrates				
Lemuridae	1	1	-	-
<i>Microcebus</i> sp.	1	1	-	-
Rodentia	-	-	6	3.8
<i>Rattus rattus</i>	2	1	2	1.3
<i>Mus musculus</i>	1	1	-	-
<i>Eliurus myoxinus</i>	1	1	3	1.9
Birds	2	2.1	-	-
Amphibia	-	-	4	1.9
Serpentes	1	1	2	1.3
<i>Oplurus</i> sp.	1	1	5	1.3
Gecko	4	4.2	2	1.3
Chameleon	8	1	-	-
Subtotal	25	14.3	24	12.8
Total	184	100	236	100

2). Analyses of the pitfall trapping results revealed that species richness during the two seasons was similar at 46% ($J = 0.46$). In addition, both seasons had a similar abundance diversity of arthropods (Shannon Wiener: $H_{rainy} = 1.57$, $H_{dry} = 1.21$) (Table 2). Even if the abundances of arthropods between the two seasons showed no statistical differences, the rainy season appeared to be characterized by greater arthropod diversity, particularly for groups such as Orthoptera (Figure 3). The relation between arthropod abundance from the pit-fall traps and those identified from the scat remains was not significant (dry season: Spearman's $r = 0.23$, $n = 7$, $P > 0.05$; rainy season: $r = 0.28$; $n = 22$, $P > 0.05$). These results indicate that *M. decemlineata* is not selective in term of prey types and consumes different items according to their abundance and availability.

Table 2. Number of individuals of each order of arthropod captured with pitfall traps from the dry and rainy seasons; Jaccard Index J calculation between both seasons and Shannon Wiener Index H respectively.

Arthropods at order level (n)	Dry season	Rainy season
Araneae	43	15
Coleoptera	195	120
Diptera	15	5
Hymenoptera	314	139
Lepidoptera	3	4
Orthoptera	45	72
Blattodea	0	4
Hemiptera	0	5
Diplopoda	0	18
Jaccard Index J	1	
Shannon Wiener Index H	1.21	1.57

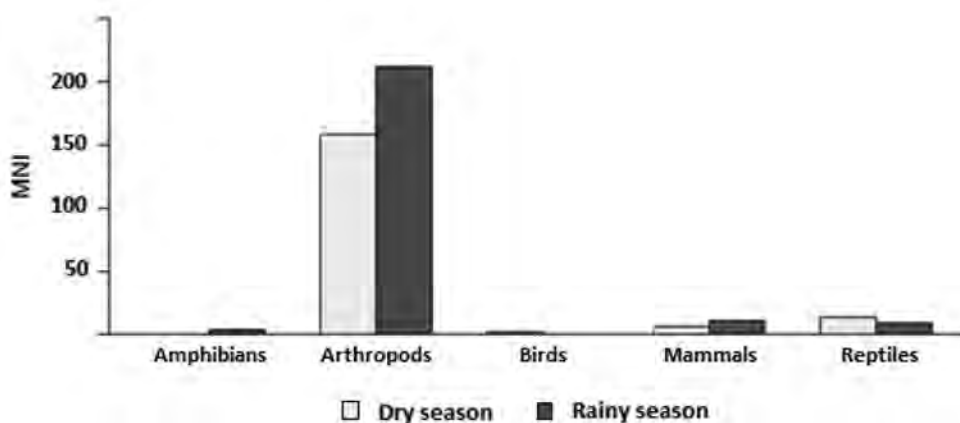


Figure 1. Composition of prey types at higher taxonomic levels in the diet composition of *Mungotictis decemlineata* in Kirindy Forest during the dry and rainy seasons (MNI: minimum number individual).

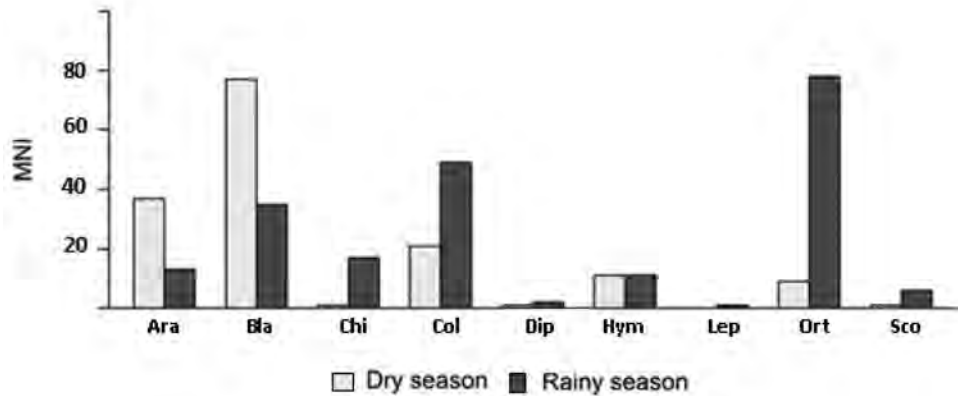


Figure 2. Arthropod remains categories in the diet of *Mungotictis decemlineata* during the dry and rainy seasons in Kirindy Forest (MNI: minimum number individual; Ara: Araneae; Bla: Blattodea; Chi: Chilopoda; Col: Coleoptera; Dip: Diplopoda; Hym: Hymenoptera; Lep: Lepidoptera; Ort: Orthoptera; Sco: Scorpionidae).

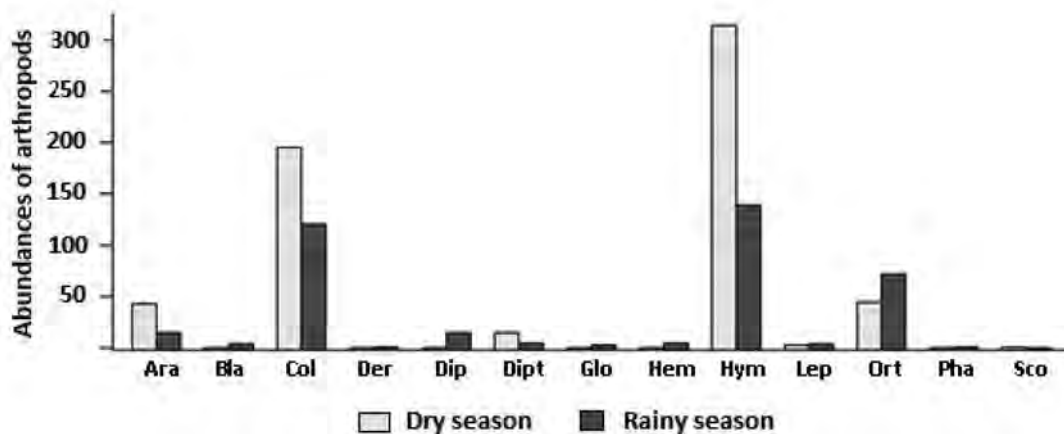


Figure 3. Species richness and abundance of arthropods from pitfall trappings during dry and rainy seasons in Kirindy Forest (Ara: Araneae; Bla: Blattodea; Col: Coleoptera; Der: Dermaptera; Dip: Diplopoda; Dipt: Diptera; Glo: Glomerida; Hem: Hemiptera; Hym: Hymenoptera; Lep: Lepidoptera; Ort: Orthoptera; Pha: Phasmida; Sco: Scorpionidae).

Foraging strata use

Mungotictis decemlineata was observed to use four strata types while foraging. The use of foraging strata by this species was examined to identify the presence of prey items that cannot be identified in the scat analysis, such as arthropods larvae. Diet composition was found to be identical for males and females based on the scat analysis (Wilcoxon test: $W = 8$, $P > 0.05$). Analysis of the use of foraging strata showed seasonal differences (pairwise ANOVA per permutation: $P < 0.001$, number of permutation = 999); but not influenced by sex (pairwise ANOVA per permutation: $P > 0.05$, number of permutation = 999). Post-hoc comparisons using the t-test with Bonferroni correction indicated that the uses of fallen rotten wood, fallen tree, and litter by *M. decemlineata* were

significantly different from each other during both seasons ($P < 0.001$). However, the use of fallen rotten wood did not significantly differ from the use of soil in both seasons ($P > 0.05$) (Figure 4).

Discussion

The present study revealed that *Mungotictis decemlineata* feeds on a variety of prey items, including invertebrates and vertebrates. However, arthropods and insect larvae dominated their diet. During both seasons, arthropods were consumed and represented the majority of the diet, both in occurrence and in MNI from scat analysis. This species fed on a similar variety of arthropods during both seasons, including Blattodea (especially Blaberidae), Coleoptera, and Araneae. However, quantitatively,

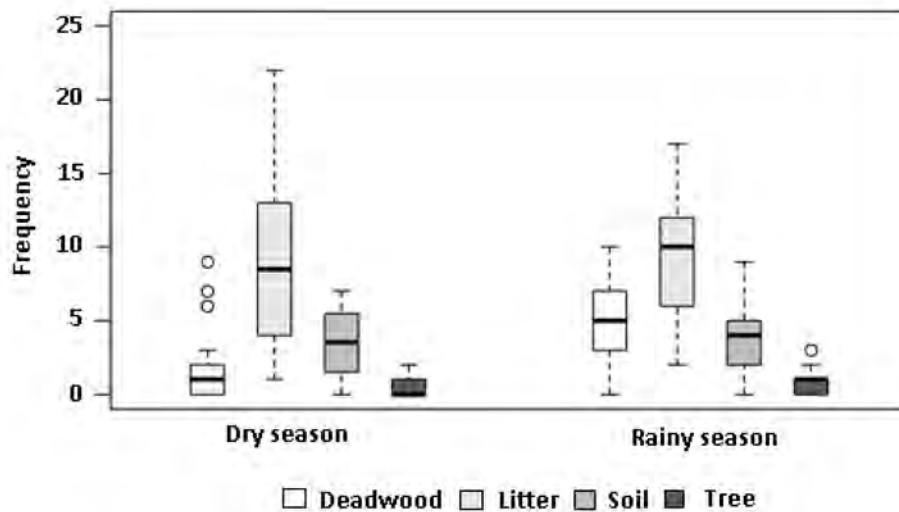


Figure 4. Comparison of the use of foraging strata exploited by *Mungotictis decemlineata* during dry and rainy seasons at Kirindy Forest.

each type of arthropod was consumed in different proportions during the dry and wet seasons. Ground-dwelling arthropods in Kirindy Forest do not exhibit pronounced seasonal variation in abundance (Dammhahn & Kappeler, 2008). The high proportion of Blaberidae in the diet is not unexpected, though this taxon was not the most abundant prey obtained in the pit-fall traps at both sites during the two seasons. Moreover, direct behavioral observations revealed that *M. decemlineata* frequently consumed the large cockroach *Gromphadorhina portentosa*. Hence, the pit-fall traps were probably not efficient to assess all prey types available for this carnivoran. Furthermore, the absence of difference between food composition and pitfall results is probably because the sample of pit-fall traps used was not representative of the overall food availability in the study sites during both study periods.

The use of different foraging strata differed across seasons. *Mungotictis decemlineata* primarily exploited the litter and soil during their foraging activities, suggesting that they generally forage by searching through the ground litter and by digging into the top soil. Nonetheless, they sometimes foraged on fallen trees or in fallen rotten wood, illustrating that they rely on a variety of substrates. However, during the wet season, *M. decemlineata* foraged more on fallen rotten wood and more on litter compared to the dry season. Thus, this species may concentrate its foraging activities on strata with the highest seasonal profitability. The study of foraging strata across seasons also revealed the presence of important prey items, such as insect larvae, which were impossible to detect in scat. This tendency to prey upon insect

larvae may be explained by their high energetic value, which may help *M. decemlineata* to cope with the dry season (Albignac, 1976). Insect larvae are also abundant and relatively easily available, contributing to a positive energy balance while foraging for this prey item.

Behavioral observations revealed also the presence of gastropods (land snails) in the overall diet of *M. decemlineata*. Especially during the rainy season, individuals were observed to prey frequently on gastropods, which are abundant in the litter during that season. *Mungotictis decemlineata* was occasionally seen removing litter or digging in the soil and inspecting the inside of shells. When a non-empty shell was located, it was broken by throwing it up in the air or bumping it against a tree, as described by Razafimanantsoa (2003); or putting the shell into sun that the prey was forced to come out to escape the heat.

In contrast to Albignac (1976), who suggested that *M. decemlineata* consumes invertebrates only during the dry season, we found them to be insectivorous during the two seasons of this study. Thus, the most abundant and available prey appears to be taken preferentially, a strategy also known from other non-Malagasy small-bodied carnivores feeding on small prey (Rood, 1986; Carbone et al., 1999, 2007). Yet, other sympatric mammals at Kirindy are more opportunistic and consume prey according to their availability and abundance across seasons. For instance, the notably larger bodied euplerid *Cryptoprocta ferox* feeds more on tenrecs during the wet season and more on lemurs during the dry season (Hawkins & Racey, 2008).

Prey abundance is also considered as an important factor influencing the diet composition of other Malagasy euplerids (Andriatsimetry *et al.*, 2009). Inhabiting a distinctly drier and seasonally harsh zone, *Galidictis fasciata grandidieri* feeds mainly on invertebrates, especially the large cockroach *Gromphadorhina portentosa* that is abundant year-round, whereas vertebrate consumption peaks during the wet season (Andriatsimetry *et al.*, 2009). Reliance on the most abundant and available prey types also characterizes the feeding ecology of herpestids, qualifying them as opportunistic predators (*Herpestes sanguineus*: Rood & Wasser, 1978; *Cynictis penicillata* and *Galerella pulverulenta*: Hiscock & Perrin, 1991; *Cynictis penicillata*: Cavallini & Nel, 1995; *Suricata suricatta*: Doolan & MacDonald, 1996).

The diet and foraging behavior of *M. decemlineata* are similar to those of African herpestids living in seasonal habitats. Here, insectivory is also found in small, diurnal, and social mongooses (Rood, 1986). For instance, *S. suricatta* consumes mostly insect larvae and beetles whose availability shows seasonal variation. Reptiles are the most frequently eaten vertebrates all year round with a peak during the warmer months. Thus, *S. suricatta* also feeds on the most seasonally abundant prey, which is thought to contribute to a more positive energy balance (Doolan & MacDonald, 1996). Likewise, *C. penicillata* is an opportunistic predator feeding mainly on insects, which exhibit high availability in its habitat (Cavallini & Nel, 1995). *Galerella pulverulenta*, which is more solitary, feeds largely on small mammals, as they are more abundant and available in its habitat (Cavallini & Nel, 1995). In addition, the solitary and nocturnal, *Atilax paludinosus*, with a flexible diet feeds on the more abundant prey ranging from crabs and insects to small mammals (Baker, 1989).

Invertebrates are known to be an important abundant food resource and a factor facilitating group formation in mongooses due to their availability and high reproduction (Rood, 1986; Palomares & Delibes, 1993; Doolan & MacDonald, 1996; Veron *et al.*, 2004). Furthermore, no difference in the diet of male and female *M. decemlineata* was found during both seasons; a pattern also observed in *S. suricatta* (Doolan & MacDonald, 1996). During our behavioral observations, direct feeding competition was not observed between female group members, which is probably due to the abundance and availability of arthropods during the two seasonal periods of this study. Such small food items that are distributed

unpredictably in space and time generally do not promote within-group contest competition (Goldberg *et al.*, 2000; Johnson *et al.*, 2002; Overington *et al.*, 2008), and this effect has been used to argue for a facilitation of group living in mongooses (Rood, 1986; Schneider & Kappeler, 2014).

In conclusion, the combination of scat analyses and behavioral observations indicate that *M. decemlineata* is a generalist and opportunist forager. Its reliance on a wide variety of food items, many of which are available and abundant year-round contributes to reduced foraging costs. They respond adaptively to seasonal variation in prey abundance, and the nature of their most common prey may facilitate the formation of female groups. This Malagasy euplerid therefore exhibits convergences in foraging ecology with other small diurnal African herpestids.

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