Diet of *Paratriaenops auritus* (Chiroptera: Rhinonycteridae) in the Andrafiamena-Andavakoera protected area, northern Madagascar

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Abstract

Details on the foods taken by insectivorous bats of Madagascar is poorly known, particularly in the northern portion of the island. A study was conducted from 21 November to 6 December 2023, a period coinciding with the end of the dry season, on the diet of a regional endemic species, *Paratriaenops auritus*, in Andrafiamena-Andavakoera. Bats were captured at three sites in the protected area using Japanese mist-nets and a harp trap. Fecal samples were collected and stored separately for subsequent analysis that involved using a binocular scope and, for each animal, five fecal pellets were employed. Individual bats were measured, weighed, and sexed based on external genitalia; females were separated in two classes (pregnant and non-pregnant). The fecal analysis resulted in the identification of five orders of insects (Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, and Diptera). The investigation revealed variation in the diet of the three sex classes of *P. auritus*. Males and non-pregnant females mainly consumed Coleoptera followed by Lepidoptera. In contrast, the diet of the pregnant females was mainly composed of Lepidoptera.

Keywords: *Paratriaenops auritus*, diet, sexual difference, Andrafiamena-Andavakoera

Résumé détaillé

Il est connu que peu d'information est disponible sur les habitudes alimentaires des chauves-souris insectivores de Madagascar, particulièrement dans la partie nord de l'île. Une étude a été menée du 21 novembre au 6 décembre 2023, à la fin de la saison sèche, sur le régime alimentaire d'une des espèces de chauves-souris insectivores endémiques du Nord de Madagascar, *Paratriaenops auritus*, de l'aire protégée Andrafiamena-Andavakoera.

L'étude a été réalisée dans trois sites au sein de l'aire protégée : 1) la forêt de Binara (13°6'3.6''S, 49°14'24''E) située à 5,4 km à l'est d'Ankatsaka, près de la rivière Ambaratra, 2) la Grotte d'Antsahabe (12°53'39.1''S, 49°17'43.1''E) à 2,52 km au nord-ouest d'Anjakely et 3) la forêt d'Anjakely (12°54'46.8''S, 49°19'40.8''E) à 1,34 km au sud-est du village d'Anjakely. Le complexe Andrafiamena-Andavakoera est l'une des rares zones du Nord de Madagascar où coexistent différents types de formation végétale, allant de la forêt sub-humide avec des pentes sur des sols sablonneux à la forêt sèche sur des « *tsingy* » karstiques. La zone protégée est caractérisée par le climat du Nord avec une pluviométrie annuelle moyenne d'environ 1654 mm, une variation de température journalière de 21,0 °C à 30,8 °C. Les chauves-souris ont été capturées pendant leurs activités nocturnes de recherche de nourriture à l'aide de piège harpe et de filets japonais. Les chauves-souris capturées ont été séparément placées dans des sacs propres faits en coton pour recueillir leurs excréments.

Au total, 48 individus de *P. auritus* ont été échantillonnés sur les trois sites lors des travaux sur le terrain. Quarante-un individus ont fourni au moins cinq pelotes : 10 mâles, 21 femelles non gestantes et 10 femelles gestantes. Cinq ordres d'insectes ont été identifiés dans les restes fécaux : Coleoptera, Hymenoptera, Lepidoptera, Hemiptera et Diptera. Les mâles et les femelles non gestantes consomment majoritairement les ordres des Coleoptera suivis de celui des Lepidoptera et des Hymenoptera, tandis que les femelles gestantes consomment plus de Lepidoptera par rapport aux autres ordres d'insectes. Ces données permettent de mieux comprendre le régime alimentaire de *P. auritus* pour lequel aucune

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information n'était disponible auparavant. Des recherches supplémentaires sont nécessaires pour comprendre pleinement la variation intraspécifique de l'espèce entre le régime alimentaire des adultes et celui des juvéniles, ainsi que sa variation alimentaire saisonnière.

Mots-clés : *Paratriaenops auritus*, régime alimentaire, différence sexuelle, Andrafiamena-Andavakoera

Introduction

Paratriaenops auritus (Grandidier, 1912) is one of the four endemic species of the family Rhinonycteridae on Madagascar. It was formerly placed in the genus *Triaenops*, but, based on morphological and molecular analysis, has been transferred to the genus *Paratriaenops* (Benda & Vallo, 2009). This species is restricted to northern Madagascar where it is known from the Loky-Manambato, Analamerana, Montagne des Français, Ankarana, and Andavakoera-Andrafiamena protected areas, and occurs across an elevational range from 4 to 600 m (Goodman & Ramasindrazana, 2013). It occurs in semi-deciduous or deciduous dry forest associated with limestone outcrops or other sedimentary rocks (Goodman, 2011). It is classified on the IUCN Red List as a Vulnerable (Monadjem *et al.*, 2017). As other members of this family, it is presumed that this species feeds exclusively on arthropods, but no data on this aspect of its biology is currently available (Goodman, 2011). Bats consume a wide variety of resources (Patterson *et al.*, 2003). In different portions of the world, there are families that mainly feed on fruit and nectar, aiding in seed dispersal and forest regeneration (Lopez & Vaughan, 2004; Muscarella & Fleming, 2007), such as Pteropodidae on Madagascar (Long & Racey, 2007; Andrianaivoarivelo *et al.*, 2011). Further, other families feed on arthropods, almost exclusively at night, and they help to regulate populations of insects such as agricultural pests and vectors of different zoonotic diseases (Kalka *et al.*, 2008; Kunz *et al.*, 2011; Taylor *et al.*, 2013, 2017; Karp & Daily, 2014; Tuneu-Corral *et al.*, 2023). On Madagascar, studies on the dietary habits of insectivorous bats families are by no means comprehensive and in some cases conducted at the community level (Ramasindrazana *et al.*, 2012a, 2012b; Rakotodramanana *et al.*, 2015; Rasoanoro *et al.*, 2015; Ravelomanantsoa *et al.*, 2019). Dietary data have been published for several families of Malagasy bats, in particular the Molossidae, Myzopodidae, and Hipposideridae (Andrianaivoarivelo *et al.*, 2006; Rajemison & Goodman, 2007; Rakotoarivelo *et al.*, 2007, 2009; Ramasindrazana *et al.*, 2009, 2012b; Ralisata *et al.*, 2010). On the basis of these studies, information on the prey taken by certain bat species remains largely or incompletely known, including for *P. auritus*. The main objective of this study is to determine the types of arthropod prey consumed by this species and examine differences between the two sexes and comparison between non-pregnant and pregnant females.

Methodology

Study area

This study was conducted in the Andrafiamena-Andavakoera protected area located in the DIANA Région. For further details on the site see Tahinarivony and Goodman (2025, herein).

Capture of bats and measurements

Bats were sampled from 21 November to 6 December 2023 at three site within the Andrafiamena-Andavakoera protected area: Site 1 – Binara Forest, 5.4 km E of Ankatsaka near the Ambaratra River (13°6'3.6''S, 49°14'24''E); Site 2 – Antsahabe Cave, 2.52 km NW of Anjakely (12°53'39.1''S, 49°17'43.1''E); and Site 3 – Anjakely Forest, 1.34 km SE of Anjakely (12°54'46.8''S, 49°19'40.8''E).

Capture took place at night using Japanese mist nets, either 12 m or 6 m in length and a mesh size of 32 mm or 36 mm, and two-bank Austbat Harptrap, (Faunatech, Rydalmere, Australia) composed of a metal frame on four telescoping legs and with vertically placed nylon fishing line 2.5 cm apart, with a large collecting bag at the base (Kunz & Kurta, 1988). The harp trap was placed either at the entrance of caves or in bat flight pathways where they were actively flying and presumably foraging. In total, 48 individuals of *Paratriaenops auritus* were captured.

After capture, standard measurements: total length, tail length, hind foot (excluding the claws), ear length, forearm (in mm), and weight (in gm) were taken from each individual bat. All of linear measurements were made with a clear plastic ruler, and weight taken with a Pesola spring balance.

Sex determination

Sex determination and reproductive state for each individual were assessed through observation of the eternal genitalia (Hutson & Racey, 2004). Males were identified by the presence of a penis and a pair of testicles. Females were characterized by the presence of a pair of mammary glands and a genital orifice. Pregnant bats were identified by the presence of a mass in their lower abdomen and with finger palpitation. For those taken as voucher specimens, the occurrence of an embryo could be verified and when present the crown-rump length (in mm), taken from the vertex to the coccyx, was measured.

Fecal samples collection and analysis

Each captured bat was individually placed immediately after capture in a clean cotton bag where it was kept for several hours until it produced scat samples, which were collected and preserved in tubes with 90% ethanol. Fecal analysis involved identifying undigested parts of consumed arthropods (appendage fragments, antennae, mouthparts or elytra) following standard methods (Whitaker, 1988; Shiel *et al*., 1997; Whitaker *et al*., 2009). Five fecal pellets per individual were examined under a binocular scope (Leica, USA) with magnification of 10-40x and dissected with fine needles to isolate identifiable parts. Determination of arthropods remains was at least to the taxonomic level of order and in some cases to family.

Comparison of percent volume

Percent volume for a given bat was calculated by totaling the identifiable unique number of fragments of each arthropod taxonomic group divided by the total number of identifiable fragments and then multiplied by 100. This measure provides the means to estimate relative abundance of different prey types consumed (Whitaker, 1988).

Comparison of minimum number of prey

Following Ramasindrazana (2008) and Rasoanoro *et al*. (2015), the minimum number of individuals (MNI) of prey consumed by each individual bat was estimated by counting the number of unique fragments of paired parts, separated between the left and the right sides of the bilaterally symmetrical prey insects. For example, within a sample, if an identified taxonomic group contained three mandibles, two of which are the same side, the MNI was calculated as two. This measure provided an estimate of the number of prey animals consumed by an individual bat.

Data analysis

The statistical software R version 4.4.0 was employed. The Kruskal-Wallis H test was used to determine intraspecific variation of *Paratriaenops auritus* in different dietary aspects. ANOVA followed by Post-hoc Scheffé Tests were applied to examine pairwise differences between sex and reproductive state. The level of statistical significance was set as a probability of 0.05 or less.

Results

In total, 48 individuals of *Paratriaenops auritus* were sampled, 41 included at least five pellets for analysis: 10 males, 21 females, and 10 pregnant females (Table 1, Table 2). From these samples, we were able to identify five orders (Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, and Diptera). More precise taxonomic identifications were made for Coleoptera (families Scarabeidae, Carabidae, and Staphylinidae), Hymenoptera (family Ichneumonidae), Hemiptera (Corixidae), and Diptera (families Anisopodidae and Tipulidae).

Comparison percent volume

On the basis of percent volume, Coleoptera was the most represented order in the samples of *Paratriaenops auritus* for males and non-pregnant females, accounting for 46.1% of consumed prey in males and 43.1% in non-pregnant females. The next most frequently consumed order of insects was Lepidoptera, represented by 32.1% for males and 29.5% for non-pregnant females. In contrast, pregnant females consume predominantly

Table 1. Results of the dietary analysis for different sexes of *Paratriaenops auritus* in the Andrafiamena-Andavakoera protected area reporting the mean percent volume and standard deviation, and the *P*-value associated with the Kruskal-Wallis test. Data are represented as mean percent volume followed by standard deviation. M: male, F: female, and PF: pregnant female.

Taxa	M (n = 10)	F (n = 21)	PF (n = 10)	Probability
Coleoptera	46.1 ± 4.43	43.1 ± 4.02	20.9 ± 0.73	$P < 0.05$
Hymenoptera	16.7 ± 2.31	21.9 ± 2.50	12.7 ± 1.50	$P = 0.25$
Lepidoptera	32.1 ± 2.46	29.5 ± 2.43	59.1 ± 1.42	$P < 0.05$
Hemiptera	1.3 ± 0.48	2.3 ± 1.16	1.5 ± 0.67	$P = 0.88$
Diptera	3.7 ± 1.03	3.1 ± 1.16	5.6 ± 1.10	$P = 0.14$

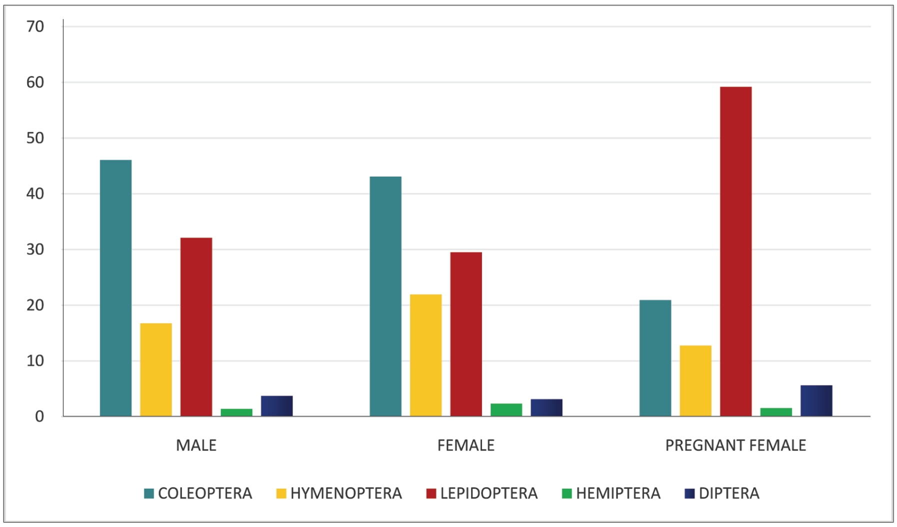

Figure 1. Percentage volume of prey consumed in the feces of *Paratriaenops auritus* in the Andrafiamena-Andavakoera protected area.

Lepidoptera, presenting 59.1% of the diet, followed by Coleoptera making up 20.9% (Figure 1, Table 1).

No significant difference in the percent volume was found for the consumption by males, non-pregnant females, and pregnant females for Hymenoptera (H = 2.78, df = 2, P = 0.25), Hemiptera (H = 0.25, df = 2, P = 0.88), and Diptera (H = 3.96, df = 2, P = 0.14). However, significant differences were found between these three different sex classes in percent volume for Coleoptera (H = 12.14, df = 2, P = 0.002) and Lepidoptera (H = 21.56, df = 2, P < 0.0001). In the case of pregnant females, they consumed more Lepidoptera as compared to non-pregnant females (X^2 = 8.42, df = 1, P < 0.0001).

Minimum number of individuals consumed

As presented in the Table 2, on average, a male *Paratriaenops auritus* was estimated to consume a minimum of 7 Coleoptera, 3 Hymenoptera, and 5 Lepidoptera in a single foraging bout and for non-pregnant female, 6 Coleoptera, 3 Hymenoptera, and 4 Lepidoptera. In the case of a pregnant female, a minimum of 2 Coleoptera, 2 Hymenoptera, and 8 Lepidoptera can be preyed upon in a foraging bout (Table 2). Based on our analysis, members of the orders Hemiptera and Diptera were rarely taken by the different sex classes of *P. auritus.*

No statistically significant difference was found in the number of individual insects consumed by males, non-pregnant females, and pregnant females for Hymenoptera (H = 4.84, df = 2, P = 0.09), Hemiptera (H = 1.12, df = 2, P = 0.6), and Diptera (H = 2.88, df = 2, P = 0.24). In contrast, a significant difference was found in the consumption of Coleoptera (H = 20.33, df = 2, P < 0.0001) and Lepidoptera (H = 23.23, df = 2, P < 0.0001). Pregnant females consume more Lepidoptera than non-pregnant females (X^2 = 5.23, df = 1, P < 0.0001).

Discussion

Previous dietary studies on stomach contents and fecal pellets have provided insight into prey taken by certain Malagasy bats species belonging to the family of Rhinonycteridae, including *Paratriaenops furculus* and *Triaenops menamena* in the dry deciduous forest areas of the west (Razakarivony *et al*., 2005; Rakotoarivelo *et al*., 2007, 2009) and southwest (Bambini *et al*., 2011; Ramasindrazana *et al*., 2012b);

Table 2. Results of MNI analysis for different sexes of *Paratriaenops auritus* in the Andrafiamena-Andavakoera protected area and statistics comparing the mean number of individuals of each prey order consumed, and the P-value associated with the Kruskal-Wallis test. Data are presented as mean number of individuals of each prey consumed followed by the standard deviation. M: male, F: female and PF: pregnant female.

Taxa	M (n = 10)	F (n = 21)	PF (n = 10)	Probability
Coleoptera	7.6 ± 2.95	5.7 ± 2.84	2.5 ± 0.52	P < 0.05
Hymenoptera	2.9 ± 1.28	3.5 ± 2.20	1.9 ± 1.19	P = 0.09
Lepidoptera	4.8 ± 1.39	4.1 ± 1.48	8.1 ± 0.73	P < 0.05
Hemiptera	0.3 ± 0.48	0.3 ± 0.97	0.1 ± 0.31	P = 0.06
Diptera	0.5 ± 0.70	0.4 ± 0.98	0.9 ± 0.99	P = 0.24

these sites are at the very least about 850 km southwest of Andrafiamena-Andavakoera protected area and the fecal samples not necessarily collected during the same season. For *P*. *auritus*, found in the extreme north, no information was previously available on its diet and the current study fills that gap.

Based on fecal analysis, which provides identifications to the level of order and sometimes family, *P*. *auritus* appears to be a generalist and foraging on different prey types, including Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, and Diptera. In our samples, Coleoptera and Lepidoptera comprised more than the majority if its diet.

Using Malaise traps placed in different western dry forests of Madagascar, Faliarivola *et al*. (2022) conducted a study of arthropod diversity during the dry season at three sites, one being the Parc National d'Ankarafantsika in the northwest of Madagascar, which provides some reference information on arthropod diversity and potential available prey for bats in our study area. Based on their study, Coleoptera was the most represented among the order of arthropods collected in the Malaise traps, represented by 24 families, followed by Diptera, Hymenoptera, and Lepidoptera. Based on a broad extrapolation, the proportion of different arthropod orders at Ankarafantsika, coincided with the dietary composition of *P*. *auritus* in the Andrafiamena-Andavakoera Protected area, which included mostly Coleoptera and Lepidoptera followed by Hymenoptera. At least at the ordinal level, these comparisons suggest that the diet of this species is related to prey availability and there is no clear sign of specialization, with the exception of pregnant females (see below).

Similar conclusions can be made with respect to the diet of the two other species of Malagasy Rhinonycteridae, *P*. *furculus* and *Triaenops menamena.* On the basis of the work of Ramasindrazana *et al*. (2012b) and Rakotoarivelo *et al*. (2007), the diet of these two species is, also, related to food abundance and these species feed extensively on Coleoptera and Lepidoptera. In the extreme southwest, specifically in the Parc National de Tsimanampesotse, with spiny bush vegetation, the two species consume mostly Coleoptera during the dry season when they are the most abundant prey type. However, during the rainy season, Lepidoptera increase in abundance and *P*. *furculus* and *T*. *menamena* switch their diet and consume primarily this order the most (Ramasindrazana *et al*., 2012b). In the central west, in the Parc National de Bemaraha, characterized by dry deciduous forest, the diet of *P*. *furculus* and *T*. *menamena* is mainly composed of Lepidoptera during both the dry and rainy seasons. Given that Diptera followed by Lepidoptera were the most abundant arthropods captured with Malaise traps during both summer (November) and austral winter (July) (Rakotoarivelo *et al*., 2007), these results seem to indicate some form of differential prey selection (but see immediately below).

Although Diptera were found to be abundant in the dry deciduous forest of Madagascar throughout different seasons (Rakotoarivelo *et al*., 2007; Faliarivola *et al*., 2022), the ratio of Diptera observed in the feces of *P*. *furculus* and *T*. *menamena* (Ramasindrazana *et al*., 2012b), as well as for *P*. *auritus*, was notably lower as compared to the other orders consumed. This difference can be explained by Diptera are smaller and softer than the insects from other orders (Lease & Wolf, 2010). Soft-bodied insects may be partly or wholly digested, rendered the fragment unidentifiable and would bias the results (Kunz & Whitaker, 1983), or based on size are preferentially less taken than larger insects.

Pregnant bats have notably higher energetic requirements associated with greater body mass and embryonic development (Aldridge & Brigham, 1988) and the mass of a well-advanced embryo can add something on the order of 30% to the body weight of a pregnant *P*. *auritus* (Goodman *et al*., 2025, herein). Males and non-reproductive females of this species feed mostly on Coleoptera, whereas pregnant females feed predominantly on Lepidoptera (59.1%). Preying on Coleoptera might result for pregnant females in intraspecific competition with males and non-pregnant females. Perhaps more importantly, given what is presumed to be a lower maneuverability and higher energetic costs for flight in pregnant females, and not exceeding the critical balance of output and input (Rydell, 1989), these individuals seem to adopt a different hunting strategy and prey mostly on Lepidoptera. Furthermore, many species of Lepidoptera possess auditory organs that enable them to hear bat echolocation calls (Pavey & Burwell, 1998) and in return certain bat species adapt with specialized foraging techniques associated with moth wing beats (Sierro & Arlettaz, 1997). Finally, according to Haarsma *et al*. (2023), within the same species pregnant bats often forage in different areas than males and take lighter prey, which further helps to explain our results.

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