Diet of the Mascarene grass frog, *Ptychadena mascareniensis*, in Madagascar

Tolojanahary N. L. Fatroandrianjafinonjasolomiovazo[1], Noromalala R. Rasoamampionona[1], David R. Vieites[2] & Miguel Vences[3]

[1] Département de Biologie Animale, Faculté de Sciences, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar
E-mail: nandinanjakana@gmail.com, rsnoro@yahoo.fr

[2] Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), C/ José Gutierrez Abascal nº2, 28006, Madrid, Spain
E-mail: vieites@mncn.csic.es

[3] Zoological Institute, Division of Evolutionary Biology, Technical University of Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany
E-mail: m.vences@tu-bs.de

Abstract

Stomach contents from 190 specimens of the Malagasy grass frog, *Ptychadena mascareniensis*, from rice fields near Ranomafana National Park were obtained by stomach flushing. Contents comprised 404 identifiable prey items, mainly arthropods. This species is a generalist that feeds on a variety of prey. The most common prey were coleopterans and ants (16.2% each), orthopterans (13.4%), spiders (11.7%), insect larvae (7.5%), and hemipterans (5.4%). This study reveals the presence of one metamorphosing froglet among the prey, which might indicate cannibalism although it was not possible to identify to which species it belonged. Female *P. mascareniensis* are significantly larger than males but consume a similar number of prey. We observed a positive correlation between prey size and frog size, and a significant negative correlation between number and size of prey ingested.

Key words: Amphibia, Ptychadenidae, frog, *Ptychadena mascareniensis*, diet, Ranomafana, Madagascar

Résumé détaillé

Le régime alimentaire de *Ptychadena mascareniensis* a été étudié à partir des analyses des contenus stomacaux de 190 spécimens (76 individus mâles et 114 femelles) collectés dans les rizières de la zone périphérique du Parc National de Ranomafana. Les études ont été effectuées du 18 janvier au 15 février 2004 comprenant des travaux sur le terrain et au laboratoire. Les méthodes consistent à capturer les grenouilles adultes dans leurs habitats naturels, à mesurer les différents paramètres morphométriques et à prélever les contenus stomacaux par la technique de lavage stomacale. L'identification est effectuée à l'aide de microscope, en utilisant les clés de détermination de Delvare & Aberlenc (1989), Bolton (1994), Dippenaar-Schoeman & Jocqué (1997) et Moisan (2006).

L'analyse a permis d'identifier 404 proies formées principalement des arthropodes. *Ptychadena mascareniensis* est une espèce généraliste, qui se nourrit d'une large variété des proies au sein de leur habitat. Les coléoptères et les fourmis (16,2% pour chacun des proies dans tous les contenus stomacaux), les orthoptères (13,4%), les araignées (11,7%), les larves d'insectes (7,5%) et les hémiptères (5,4%) constituent leurs proies majeures. Une petite grenouille est observée dans l'estomac d'un individu.

Les femelles de *P. mascareniensis* sont significativement de plus grandes tailles que les mâles mais aucune différence sur la quantité de proies consommées n'a été observée. La taille des proies ingérées est proportionnelle à celle des individus de cette espèce, mais le nombre et la taille des proies consommées sont inversement proportionnels. Autrement dit, plus les proies sont de grande taille, moins sont les nombres comptés dans les contenus stomacaux. La taille de proies consommées augmente au fur et à mesure que la grenouille s'agrandit. L'analyse de la diversité des proies cumulées montre que 20 échantillons suffisent pour savoir la principale nourriture de cette espèce.

Mots clés : Amphibiens, Ptychadenidae*, Ptychadena mascareniensis,* régime alimentaire, Ranomafana, Madagascar

Introduction

The native anuran fauna of Madagascar consists of five endemic clades, each the result of an independent colonization event (Glaw & Vences, 2007). Malagasy frogs comprise over 260 described species, with many more yet to be named (Vieites *et al*., 2009). Two of the endemic clades, the mantellids and the

Fatroandrianjafinonjasolomiovazo, T. N. L., Rasoamampionona, N. R., Vieites, D. R. & Vences, V. 2011. Diet of the Mascarene grass frog, *Ptychadena mascareniensis*, in Madagascar. *Malagasy Nature*, 5: 68-74.

scaphiophrynine + cophyline microhylids, are the most species-rich, with about 175 and 60 described species, respectively (Glaw & Vences, 2007). The three other clades are less diverse: the hyperoliid genus *Heterixalus* with 11 species, the microhylid subfamily Dyscophinae with three species, and the genus *Ptychadena* (family Ptychadenidae) with a single species, *P. mascareniensis*. This species was thought to be conspecific with *Ptychadena* populations from Africa, but recent molecular studies have revealed that the African populations are genetically divergent from the Malagasy ones. The ancestors of *P. mascareniensis sensu stricto* colonized Madagascar by overseas rafting, and subsequently it was introduced to the Mascarenes and Seychelles islands (Vences *et al*., 2004; Measey *et al*., 2007).

Ptychadena mascareniensis is the most common and widespread frog species in Madagascar, living close to shallow and non-flowing waters, as well as in marshes and swamps. It occurs from the sea level to over 2000 m above sea level, and frequents the arid regions of the southwest as well as the humid rain forest along the east coast. It is not a forest dwelling species, but lives in secondary rainforests, and is extremely common in open landscapes, including anthropogenic habitats such as grassland, savannah, and rice fields (Glaw & Vences, 2007).

Despite the considerable research activity on Malagasy frogs in the last decade (see Vences & Köhler, 2008), the ecology and biology of these animals is in general still poorly known. A few basic trophic ecological data are only available for certain species (Vences & Kniel, 1998; Vences *et al*., 1999; Clark *et al*., 2005; Woodhead *et al*., 2007). Some species of Malagasy frogs are microphagous, such as the genus *Mantella*, often consuming high percentages of mites and ants (Vences & Kniel, 1998; Clark *et al*., 2005; Woodhead *et al*., 2007). Other genera, such as *Aglyptodactylus, Boophis, Laliostoma*, and *Mantidactylus*, appear to be generalists, feeding on different groups of invertebrates, mainly arthropods. To date, no information is available on the geographic variation in the prey composition of any Malagasy amphibian.

The diet of *Ptychadena mascareniensis* was previously studied by McIntyre & Ramanamanjato (1999) in southeastern Madagascar. They observed adults of this species consuming a smaller conspecific frog and one individual of another frog species that they assigned to *Mantidactylus wittei* (now *Blommersia wittei*), ingested with other prey. In the present paper, we provide new information on the diet of *P. mascareniensis* based on stomach content analysis of 190 specimens from a mid-altitude site in the southern central east of Madagascar.

Materials and methods

Fieldwork was carried out near the Ranomafana National Park. The study site was a rice field directly adjacent to the village of Ranomafana, at 620 m above sea level (21°15’42”S, 47°27’34’’E). This rice field occupied about 7000 m^2, close to a secondary degraded forest and bordering Ranomafana village on one side and the hotel Manja on the other. Four species of frogs were common in the rice field during the study period: *Ptychadena mascareniensis*, *Boophis tephraeomystax*, *Mantidactylus betsileanus*, and *Heterixalus alboguttatus. Boophis tephraeomystax* and *H. alboguttatus* are arboreal species living in open areas and breeding in lentic water bodies, typically occurring in secondary habitats, such as rice fields, if some suitable shelter is available for adults (such as banana or *Typhonodorum* plants). *Mantidactylus betsileanus* is a species normally found in intact to highly degraded rainforests, usually breeding in slow-moving streams and colonizing rice fields when in close proximity to forest habitat.

Frogs were collected by hand between 19.00 and 20.30 hours from 18 January to 15 February 2004, which corresponds to the period when this species is active on a daily basis. Stomach contents were obtained by flushing (Fraser, 1976; Legler & Sullivan, 1979; Opatrny, 1980), a method that is non-lethal (Durtsche, 1995). A syringe with a catheter and filled with water was used to flush the stomach contents into a fine-grid net, from which the contents were recovered with forceps, and preserved in 70% alcohol. Frogs were then released at the capture site. Identification of the prey remains was performed with a microscope, using the determination keys of Delvare & Aberlenc (1989), Bolton (1994), Dippenaar-Schoeman & Jocqué (1997), and Moisan (2006). Orthopteran and coleopteran individuals were determined to family level, and for ants to the genus level. Unidentifiable samples were classified as “other prey”.

We consider “occurrence” as the number of stomachs that contained one type of prey and “frequency” of the different prey categories as the percentage of stomachs containing a particular type of prey.

Snout-vent length and mouth width of the frogs were measured using a dial calipers to the nearest of 0.1 mm. Mensuration of total prey length was performed with a dial calipers and for the smallest specimens with lined paper delineated in millimeters. The size of each fragmented prey was estimated by direct comparison with those of entire specimens of the same prey type. Weights of frogs were recorded using a Pesola balance to the nearest 0.1 g. Dry weights of prey were measured with a digital balance to the nearest 0.01 g after being dried overnight. Correlations between frog size, prey number, and category values, as well as rank correlations, were calculated with the software SPSS version 10.00. The minimum sample size to get adequate sampling of stomach contents per species and sexes was estimated from cumulative diet diversity curves using the Shannon-Wiener index (Shannon, 1948) and the formula:

$$H' = -\sum_{i=1}^{n} \frac{n_i}{N} \log \frac{n_i}{N}$$

where n_i = number of prey in each category of prey i; N = number of prey in all categories.

Results

Females of *Ptychadena mascareniensis* are bigger than males; significant differences were found in snout-vent length, head width and weight: $P < 0.001$ with Mann-Whitney U-test. The SVL ranges from 30.7 to 43.3 mm in males and 32.8 to 53.3 mm in females (Table 1).

Table 1. Data on body size of *Ptychadena mascareniensis* at Ranomafana. These data show the mean, with standard deviation in parentheses and the range: minimum – maximum. The snout vent length (SVL) and the mouth width (MW) are in mm; the weight (W) is in g.

	Males	Females
SVL	36.84 (2.54)	43.52 (3.53)
range	30.7 – 43.3	32.8 – 53.3
MW	10.60 (1.03)	12.26 (1.20)
range	8.5 – 15.1	9.0 – 15.5
W	4.64 (1.12)	7.23 (1.92)
range	2.9 – 9.6	2.4 – 12.7
N	76	114

Stomach contents were obtained from 76 males and 114 females of *P. mascareniensis*. A total of 404 prey items (169 in males and 235 in females) were identified and other 22 items remained unidentified. The main categories of prey (Table 2, Figure 1) included beetles (16.2%), ants (15.7%), orthopterans (13.4%), spiders (11.7%), insect larvae (7.5%), and hemipterans (5.4%). A small proportion was recorded for the prey types amphipods (3.5%), snails (2.8%), dipterans (2.8%), dermapterans (2.4%), lepidopterans (2.1%), dictyopterans (0.9%), and hymenopterans other than ants (0.9%). A single case of a vertebrate (metamorphosing froglet) eaten by a frog male was also observed among the prey (Figure 2). Representatives of five genera of ants were found exclusively in female stomach contents, *Aphaenogaster*, *Camponotus*, *Pachycondyla*, *Paratrechina*, and *Strumigenys*; one genus exclusively in males, *Crematogaster*; and two genera, *Tetramorium* and *Pheidole*, both in males and females (Table 3). With respect to the frequencies of occurrence, ants, coleopterans, and orthopterans are the principal groups consumed by *Ptychadena mascareniensis*, followed by spiders, while the frequency of other groups is notably lower (Table 2). The number of prey items identified is shown in detail in Table 4; diversity of coleopterans, ants, and orthopterans found in the stomach contents are shown in Tables 3 and 5.

Table 2. Category of prey in the diet of *Ptychadena mascareniensis*: N, number of one prey type found in analyzed stomachs; % N, percentage of one type of prey identified in all stomach contents; O, occurrence; % O, frequency of occurrence.

Category of prey	N	% N	O	% O
Coleoptera	69	16.20	51	26.84
Araneae	50	11.74	43	22.63
Insect larvae	32	7.51	24	12.63
Ants	67	15.73	54	28.42
Hymenoptera	4	0.94	4	2.10
Orthoptera	57	13.38	51	26.84
Lepidoptera	9	2.11	9	4.74
Hemiptera	23	5.40	21	11.05
Diptera	12	2.82	8	4.21
Dermaptera	10	2.35	10	5.26
Amphipods	15	3.52	12	6.32
Gasteropods	12	2.82	8	4.21
Dictyoptera	4	0.94	3	1.58
Other prey	62	14.55	28	14.74

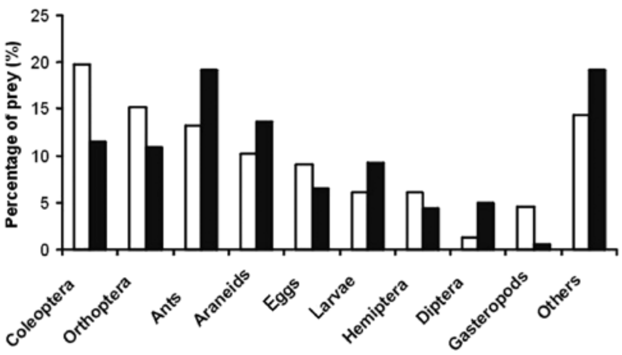

Figure 1. Prey categories consumed by *Ptychadena mascareniensis*.

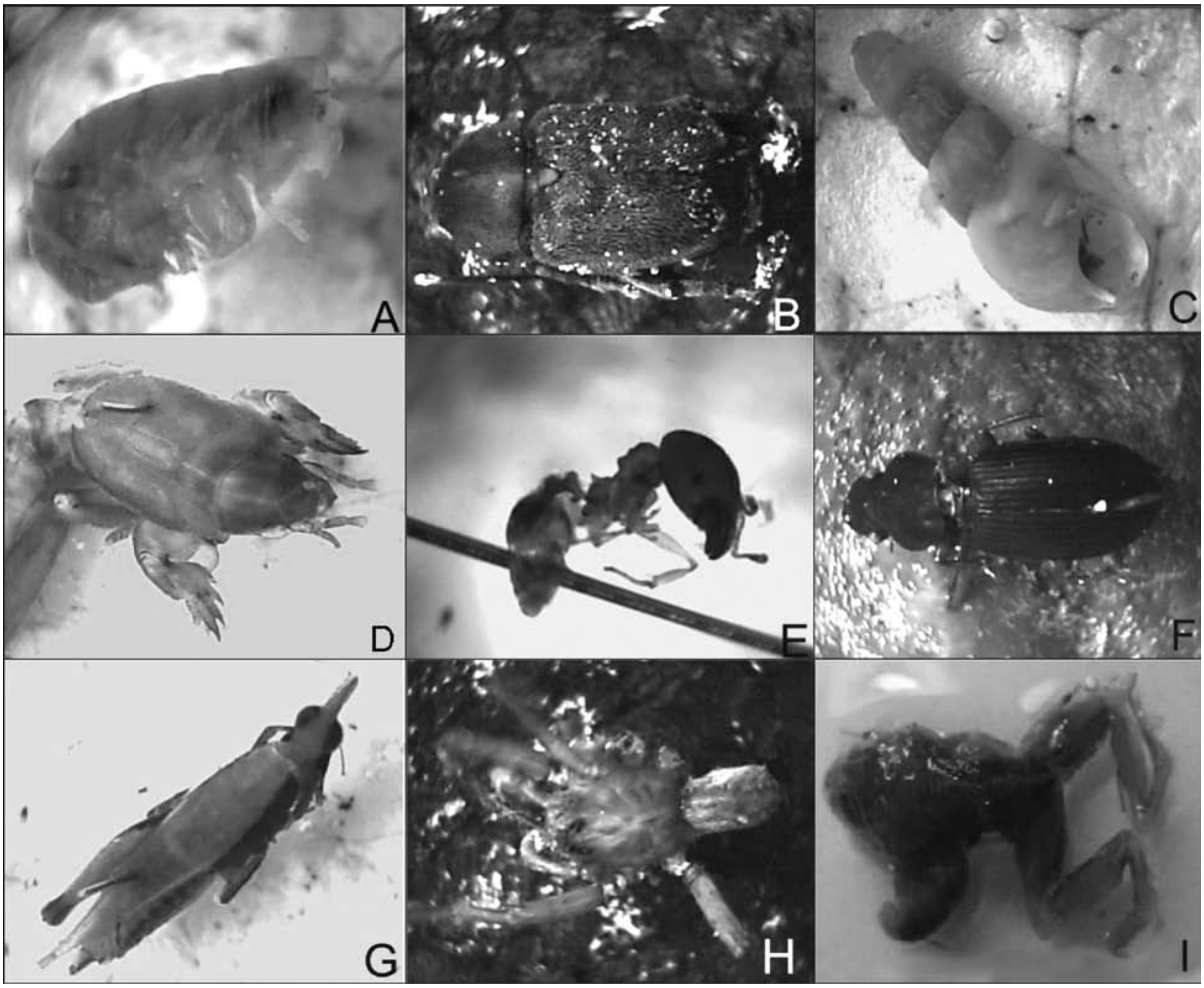

Figure 2. Prey eaten by *Ptychadena mascareniensis* (A: amphipod, B: Coleoptera (Scarabaeidae), C: gastropod, D: Orthoptera (Gryllotalpidae), E: ant (Formicidae: *Pheidole*), F: Coleoptera (Carabidae), G: Orthoptera (Tetrigidae), H: Aranea (Zodariidae); I: metamorphosing froglet).

Table 3. Family-level diversity of Coleoptera and genus-level diversity of Formicidae found in male and female *Ptychadena mascareniensis* stomach contents.

	Males	Females
Coleoptera		
Anobidae	1	
Apionidae		3
Bostrichidae	2	
Buprestidae	1	
Carabidae	3	2
Cerambycidae		1
Coccinellidae		1
Dermestidae		2
Elateridae		2
Hydrophilidae	3	1
Lucanidae	1	3
Platypodidae		1
Scarabaeidae	3	18
Staphylinidae	1	3
Tenebrionidae		1
Unidentified family	6	10
Number of families	9	13
Formicidae		
Aphaenogaster		2
Camponotus		2
Crematogaster	1	
Pachycondyla		2
Paratrechina		1
Pheidole	6	3
Strumigenys		1
Tetramorium	19	14
Unidentified genus	9	7
Number of genera	4	8

Based on unfragmented prey (UP), in cases when size could be unambiguously measured, males and females of *P. mascareniensis* consumed a similar number of prey (Mann-Whitney U-test, $P = 0.889$), with a tendency of females eating larger prey (UP: Mann-Whitney U-test, $P = 0.053$). However, with unfragmented + fragmented preys (UFP), where size could only be roughly estimated, not difference was found between males and females (UFP: Mann-Whitney U-test, P = 0.384). A negative correlation was detected between number and size of prey ingested (UP: R^2 = -0.211, $P < 0.05$; UFP: R^2 = -0.328, $P < 0.001$). Hence, animals that feed on large prey consume fewer prey items.

Table 4. Number of prey items identified in stomach contents of 76 male and 114 female *Ptychadena mascareniensis*.

Prey category	Males	Females
MOLLUSCA		
Gastropoda	1	11
CRUSTACEA		
Amphipoda	6	9
HEXAPODA		
Coleoptera	21	48
Hymenoptera: Formicidae	35	32
Other Hymenoptera	3	1
Orthoptera	20	37
Lepidoptera	5	4
Hemiptera	8	15
Diptera	9	3
Dermaptera	5	5
Dictyoptera	1	4
Phasmoptera		1
Insect larvae	17	15
MYRIAPODA	0	2
ARACHNIDA		
Araneae	25	25
Acari		1
Invertebrate eggs	12	22
Unidentified	14	8
VERTEBRATA		
Anura (metamorphosing froglet)	1	
Total prey items	183	243

Table 5. Family-level diversity of Orthoptera found in male and female *Ptychadena mascareniensis* stomach contents.

	Males	Females
Gryllidae	1	3
Gryllotalpidae	7	14
Tetrigidae		1
Unidentified family	12	19
Number of families	3	4

The average length of the prey recovered from male stomachs of *Ptychadena* was 6.34 mm, with a minimum length of 1.2 mm, and a maximum length of 20.9 mm (variance = 15.8 mm and standard deviation = 4.0 mm). For females, the average length of prey items is 8.6 mm, with a minimum length of 0.9 mm, and a maximum length of 45.6 mm (variance = 58.9 mm and standard deviation = 7.7 mm). Comparison between the size of prey and relative frogmouth width revealed no clear correlation (R^2 = 0.000, P > 0.05). There was a tendency for a positive correlation, although not significant, between prey size and frog SVL (R^2 = 0.186, P = 0.052), indicating that larger frogs consume larger prey (Figure 3).

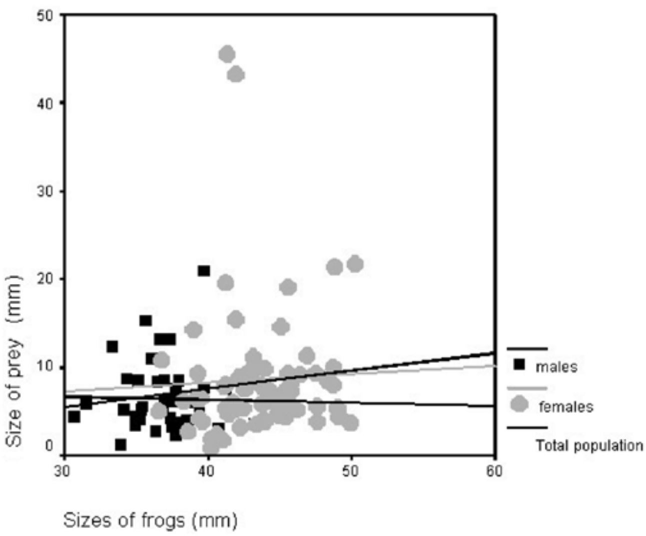

Figure 3. Correlation between size of prey and size (SVL) of *Ptychadena mascareniensis*.

Discussion

Our results suggest that *Ptychadena mascareniensis* is a generalist species that feeds mainly on beetles, grasshoppers, and ants, as well as other invertebrates commonly found in rice fields. Although we have no data about prey availability at our rice field study sites, the variety of prey consumed suggests that the species is a generalist that will eat a wide variety of invertebrates and the prey size depends upon that of the individual frog. Although the occurrence of this frog is closely linked to stagnant water, it is usually found in terrestrial environments, close to water. Consequently, we assume *Ptychadena* feeds mainly outside of the water, and this is confirmed by the absence of strictly aquatic prey in the stomachs analyzed.

Vences *et al.* (2003) identified worms and small butterflies from the stomachs contents of a few individuals of *P. mascareniensis*. Further, McIntyre & Ramanamanjato (1999) reported from *Ptychadena* specimens collected in two sites in southeastern Madagascar, snails, small grasshoppers, grubs, one frog probably of the genus *Blommersia*, and one smaller conspecific frog. Our identification of a juvenile frog in one stomach of an adult male of *P. mascareniensis* confirms its predation upon smaller frogs, although we could not identify this prey and therefore cannot confirm whether it represents an instance of cannibalism.

It is interesting that even in this generalist species, ants constitute an important proportion of the prey (over 15% of prey items), although only a single mite specimen was detected. In other species of Malagasy frogs, such as *Mantella*, the proportions of mites and ants are much higher, ranging from 14 to 74% (Vences & Kniel, 1998; Clark *et al*., 2005; Woodhead *et al*., 2007), and these frogs are considered as microphagous specialists. Other frogs (e.g. *Pelophylax nigromaculatus*) that inhabit rice fields in other parts of the world are also generalists (Hirai & Matsui, 1999), with ants constituting a major component of their diet, followed by beetles and hemipterans.

We observed a positive correlation between prey size and frog size, and a significant negative correlation between the number of prey consumed and size of prey ingested. This suggests that bigger frogs are able to feed on bigger prey in comparison to smaller frogs that may be limited by their size. Small frogs (SVL = 30.7 mm) ate prey having average body size of 4.3 mm, while for large frogs the average body size was 9.9 mm (size estimated) to 21.7 mm (real size), although the largest prey size recorded (45.6 mm) were found in medium size frogs (SVL between 41 and 42 mm). This suggests that in general, larger frogs are able to feed on the largest prey in comparison to smaller frogs that may be limited by their size and eat smaller prey. Although, large prey may not always be available, quantities of small prey are consumed to cover the energetic requirements of the frogs independently of their size.

The accumulated prey diversity in males and females indicates saturation after the analysis of about 20 stomachs (Figure 4). Hence, for future studies a sample size of ca. 50 stomach contents for analysis may be sufficient to obtain a representative overview of the prey diversity in *Ptychadena mascareniensis*, although larger sample sizes would be needed to understand relationships between prey size and prey numbers, and dietary differences between frog size classes and sexes.

One potential problem with the quantification stomach contents is differential digestibility of different prey types. Hard invertebrate prey, such as adult beetles, are harder to digest and may be disproportionately better represented in stomach contents as compared to softer items (e.g. larvae). Sampling during the period the frogs were feeding helped to minimize this bias. The small number of unidentified prey corresponds mainly to prey that were rapidly digested.

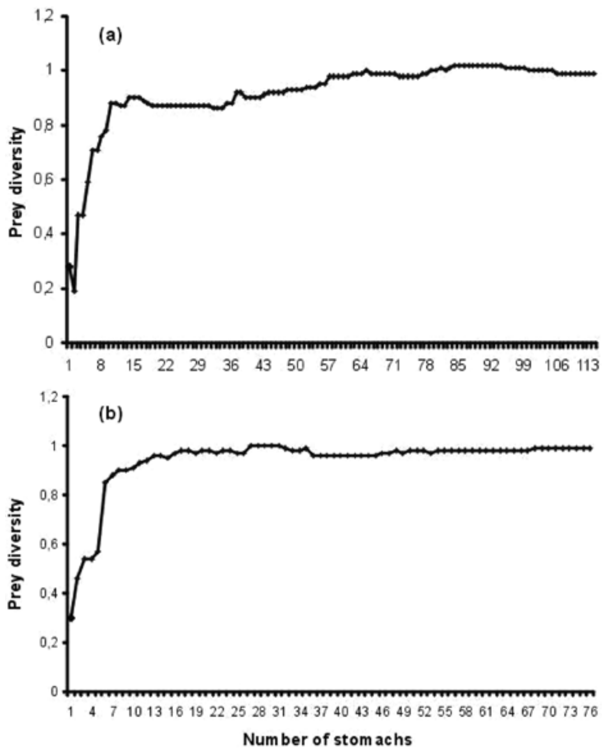

Figure 4. Accumulated prey diversity as a function of the number of stomachs examined for *Ptychadena mascareniensis* females (a), males (b).

The current study provides new data on the trophic ecology of *P. mascareniensis*, and the method adopted can be duplicated for similar studies of other frog species. Apart from few cases (e.g. *Mantella*), no information is available for most species of Malagasy frogs and further research is needed to better understand the ecological requirements and trophic position of most Malagasy frogs.

Acknowledgements

We are grateful to Jeanne Rasamy Razanabolana for permission to use a digital balance from the Laboratoire de Biologie des Populations Parasitaires, Département de Biologie Animale, to Valery Rakotomalala for her help and training in arthropod identification, and to the Ministry of Environment and Forest for delivering research permits to conduct this project. Thanks also to Edouard Randriamitso and Cindy Woodhead for field companionship. Achille Raselimanana and Steve Goodman provided useful comments on an earlier version of this article.

References

Bolton, B. 1994. *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge, Massachusetts.

Clark, V. C., Raxworthy, C. J., Rakotomalala, V., Sierwald, P. & Fisher, B. L. 2005. Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the Neotropics. *Proceedings of the National Academy of Sciences of the USA*, 102: 11617-11622.

Delvare, G. & Aberlenc, H. 1989. *Les insectes d'Afrique et d'Amérique tropicale*. *Clés pour la reconnaissance des familles*. CIRAD-PRIFAS, Montpellier.

Dippenaar-Schoeman, A. & Jocqué, R. 1997. *African spiders, an identification manual*. Handbook number 9. Biosystematics Division, ARC-Plant Protection Research Institute, Pretoria.

Durtsche, R. D. 1995. Foraging ecology of the fringe-toed lizard, *Uma inornata,* during periods of high and low food abundance. *Copeia*, 1995: 915-926.

Fraser, H. 1976. The pathology of natural and experimental scrapie. In *Slow virus diseases of animals and man*, ed. R. H. Kimberlin, pp. 267-305. Elsevier, Amsterdam.

Glaw, F. & Vences, M. 2007. *A field guide to the amphibians and reptiles of Madagascar*, 3rd edition. Vences & Glaw Verlag, Cologne.

Hirai, T. & Matsui, M. 1999. Feeding habits of the pond frog, *Rana nigromaculata,* inhabiting rice-fields in Kyoto, Japan. *Copeia*, 1999: 940-947.

Legler, J. M. & Sullivan, L. J. 1979. The application of stomach flushing to lizards and anurans. *Herpetologica*, 35: 107-110.

McIntyre, P. & Ramanamanjato, J.-B. 1999. *Ptychadena mascareniensis mascareniensis* diet. *Herpetological Review*, 30: 223.

Measey, G. J., Vences, M., Drewes, R. C., Chiari, Y., Melo, M. & Bourles, B. 2007. Freshwater paths across the ocean: molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. *Journal of Biogeography*, 34: 7-20.

Moisan, J. 2006, *Guide d'identification des principaux macroinvertébrés benthiques d'eau douce du Québec. Surveillance volontaire des cours d'eau peu profonds*. Direction du suivi de l'état de l'environnement. Ministère du Développement durable, de l'Environnement et des Parcs, Québec.

Opatrnỳ, E., 1980. Food sampling in live amphibians. *Vestnik Ceskoslovenske spolecnosti zoologicke*, 44: 268-271.

Shannon, C. E. 1948. A mathematical theory of communication. *The Bell System Technical Journal*, 27: 379–423, 623–656.

Vences, M. & Kniel, C. 1998. Mikrophage und myrmecophage Ernährungsspezialisierung bei madagassischen Giftfröschen der Gattung *Mantella*. *Salamandra*, 34 (3): 245-254.

Vences, M. & Köhler, J. 2008. Global diversity of amphibians (Amphibia) in freshwater. *Hydrobiologia,* **595**: 569-580.

Vences, M., Glaw, F. & Zapp, C. 1999. Stomach content analyses in Malagasy frogs of the genera *Tomopterna*, *Aglyptodactylus*, *Boophis* and *Mantidactylus* (Anura: Ranidae). *Herpetozoa*, 11: 109-116.

Vences, M., Glaw, F. & Raselimanana, A. P. 2003. *Ptychadena*, Mascarene grass frog. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 927-933. The University of Chicago Press, Chicago.

Vences, M., Kosuch, J. M., Rödel, O., Lötters, S., Channing, A., Glaw, F. & Böhme, W. 2004. Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *Journal of Biogeography*, 31: 593-601.

Vieites, D. R., Wollenberg, K. C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the USA*, 106: 8267-8272.

Woodhead, C., Vences, M., Vieites, D. R., Gamboni, I., Fisher, B. L. & Griffiths, R. A. 2007. Specialist or generalist? Feeding ecology of the Malagasy poison frog *Mantella aurantiaca*. *Herpetological Journal,* 17: 225-236.