SALAMANDRA	44	3	177-186	Rheinbach, 20 August 2008	ISSN 0036-3375

Prey composition of two syntopic *Phrynobatrachus* species in the swamp forest of Banco National Park, Ivory Coast

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Abstract. We studied the diet of two syntopic and morphologically very similar leaf litter frogs, *Phrynobatrachus ghanensis* and *P. phyllophilus*, in Banco National Park, south-eastern Ivory Coast. We determined the prey composition of females of both species to understand the potential avoidance of competition for food. Insects dominated (> 80%) the general diet of both species. We determined insect prey items down to the level of the order. At this level the diet of both species differed, however not significantly. Whereas *P. ghanensis* preyed mainly on hymenoptera (65.6%, mostly ants); *P. phyllophilus* mainly preyed on coleoptera (56.8%). With respect to seasons these differences were even larger, although again not statistically significant. Hence, there seem to be some differences in the food preference of the two species. However, the large overlap in prey can be taken as a hint that competition for food does not play a major role between these two frogs. The slightly different diets are more likely the result of so far undetected differences in habitat preferences and / or activity patterns.

Key words. Amphibia: Anura: Phrynobatrachidae: *Phrynobatrachus ghanensis*, *P. phyllophilus*, diet, swamp forest, syntopic occurrence, West Africa.

Résumé. Les régimes alimentaires de *Phrynobatrachus ghanensis* et *P. phyllophilus*, deux grenouilles de litière vivant en sympatrie et morphologiquement très proches ont été étudiés dans le Parc National du Banco, sud-est de la Côte d'Ivoire. Chez des individus femelles, les types de proies ont été déterminées afin de comprendre comment les deux espèces peuvent-elles éviter les effets de nuisance relatifs à la compétition pour la nourriture dans un même habitat. Les insectes dominent le régime alimentaire général de *P. ghanensis* et de *P. phyllophilus* (> 80%). Pour ce qui concerne les ordres des proies consommées, les deux espèces diffèrent. *P. ghanensis* se nourrit principalement d'hyménoptères (65,5%), en particulier de fourmis. En revanche, *P. phyllophilus* consomme principalement les coléoptères (56,8%). Cette différence observée entre espèces n'est cependant pas significative du point de vue statistique. Concernant les régimes saisonniers, les variations enregistrées au niveau des préférences alimentaires sont grandes, mais non significatives sur le plan statistique. Certes, il semble y avoir des préférences alimentaires chez ces deux espèces. Mais, un grand chevauchement trophique pourrait insinuer que la compétition pour la nourriture ne joue pas un rôle majeur entre les deux espèces de grenouilles. Les légères différences des régimes alimentaires sont plus vraisemblablement, de loin, le résultat de l'existence d'habitat et/ou d'activités non décelés.

Mots-clés. Amphibia: Anura: Phrynobatrachidae: *Phrynobatrachus ghanensis*, *P. phyllophilus*, régime alimentaire, forêt marécageuse, occurrence en sympatrie, Afrique de l'Ouest.

Introduction

The genus *Phrynobatrachus* is one of the most species rich African anuran genera (Poynton 1999). Currently approximate 72 valid species are known, occurring exclusively in Sub-Saharan Africa (Frost 2007). Species of this genus inhabit a huge variety of habitats, ranging from dry savanna to rainforests (Rödel 2000, Channing 2001, Channing & Howell 2006). With a few exceptions (Rödel & Ernst 2002a, b, Rödel et al. 2004), *Phrynobatrachus* species exhibit similar reproduction strategies and often occur in sympatry (Lamotte & Dzieduszycka 1958, Barbault & Trefaut Rodrigues 1978, 1979, Barbault & Pilorge 1980, Barbault 1984, Rödel 1998, 2000, De Sá & Channing 2003, Ernst et al. 2006). From West African forests up to 13 *Phrynobatrachus* species have been reported (Rödel & Ernst 2004). Although, some *Phrynobatrachus* species, together with members of the genus *Arthroleptis*, are among the most abundant leaf litter frogs in West Africa, there seem to be no or only minor competition for food between these species (Ernst & Rödel 2006). However, only a few studies have so far investigated the prey of *Phrynobatrachus* species (Inger & Marx 1961, Barbault 1974a, Rödel 1995). In Banco National Park two morphologically very similar and abundant *Phrynobatrachus* species, *Phrynobatrachus ghanensis* and *P. phyllophilus*, co-occur in the swampy parts of the primary forest (Assemian et al. 2006, N.G. Kouamé unpubl. data). In this paper we investigate what these two species prey upon and if their food composition is different or not.

Materials and methods

Study site

The Banco National Park (BNP, 5°21'-5°25' N; 4°01'-4°05' W) is a small (3000 ha) rain forest park, located in the middle of Abidjan, the economic capital of Ivory Coast. The mean annual temperature in Banco is 26-27°C. The mean annual precipitation ranges from 1600-2500 mm. A longer major dry season extends from December to March, and is followed by the period with highest precipitation in March to July. A minor rainy season lasts from October to November. Assemian et al. (2006) provide an overview about the climate, vegetation and especially the anuran fauna of this park.

Target species

Phrynobatrachus ghanensis Schiøtz, 1964 was described from rainforests in southern Ghana (Schiøtz 1964, Perret 1988) and was only recently rediscovered (Rödel et al. 2005). In Banco National Park, this species seems to reach its westernmost distribution limit (Assemian et al. 2006). *Phrynobatrachus phyllophilus* Rödel & Ernst, 2002 was described from western Ivory Coast and has its easternmost distribution limit in Banco (Assemian et al. 2006). Both species are small leaf litter frogs of similar morphology and size that prefer swampy parts of primary rainforests. The Banco National Park is the only site where both species are known to occur in sympatry and even syntopy.

Prey composition

Within a general amphibian monitoring program of the National Park (see Assemian et al. 2006) we searched for frogs along various transects. A transect was 600 m in length and 2 m width (surface searched for frogs per transect walk: 1,200 m^2). Each transect was walked for 24 times; every transect walk lasted app. 45 min. A detailed description of the collecting method and the general transect design is given by Rödel & Ernst (2004). Between March 2004 and February 2005 we collected 30 adult females of both species, on two transects (BT5 and BT6; compare Assemian et al. 2006) in swampy parts of the rainforest (see Appendix). We collected 14 *P. ghanensis* during the rainy season and 16 during the dry season. From *P. phyllophilus* we collected 18 specimens during the rainy and 12 specimens during the dry season. Snout-vent-lengths of the living frogs were taken with dial callipers (accuracy ± 0.5 mm). Unfortunately the frogs were too small and too fragile to employ stomach-flushing, as e.g. described by Joly (1987) and Solé et al. (2005). Hence, frogs were euthanized in a chlorobutanol solution and thereafter dissected. Stomachs were preserved in 70% ethanol and stomach content analyzed in the laboratory with the aid of a dissecting microscope. For every specimen we determined and counted the prey items, and thereafter dried and weighed the prey (Sartørius scale; accuracy

± 0.0001g). We distinguished between insect orders, arachnids (Arachnida), crustaceans (Isopoda), myriapods (Diplopoda), and other animal remains and plant parts (Dierl & Ring 1992, Tachet et al. 2003). As the frogs had to be killed for the analyses we decided to restrict the study to females. The specimens hence could be additionally used for research questions that concern the reproductive effort and strategies of both species (N.G. Kouamé unpubl. data). The frogs are deposited in the collection of the Laboratoire d'Environnement et de Biologie Aquatique at the University Abobo-Adjamé, Abidjan (Appendix).

Statistical analysis

For a quantitative analysis of the frogs' diets we calculated: the percentage or the frequency of presence F (Rosecchi & Nouaze 1987, Gray et al. 1997, Young et al. 1997); the exact percentage of prey weight P (Hyslop 1980) and the index of occurrence of the percentage of weight Ip [Ip = (F.P*100)/(ΣF.P); Ip may vary from 0 to 100, Natarajan & Jhingran 1961]). The different prey categories were classified according to the scheme of Simenstad (1970). As principal prey we defined those prey items that summed to more than 50% of the Ip index. As secondary prey we defined those items that accomplished the Ip index to more than 75%. We used the index of shared prey $\mathbf{C_\lambda}$ according to Morisita (1959) modified according to Horn (1966) to evaluate the prey overlap between the two species. C_λ would be 0 is the prey composition in both species would be completely different; C_λ is 1 if the prey of both species is identical. A C_λ value larger than 0.6 represents a significantly different trophic niche (Zaret & Rand 1971).

Results

Snout-vent-lengths in female *P. ghanensis* varied from 17.5-20.5 mm; SVL in *P. phyllophilus* ranged from 14.5-21.0 mm. Hence both species showed no significant size differences (Mann-Whitney-*U*; Z = 1.138; p = 0.255; N = 60). During 240 transect walks we recorded 394 *P. ghanensis* (2.2 individuals per transect-hour) and 303 *P. phyllophilus* (1.7 frogs / t-h). We recorded *P. ghanensis* on transects BT1

Tab. 1. Number of particular prey items (n) in stomachs of *Phrynobatrachus ghanensis* and *P. phyllophilus* (each N = 30).

	Phrynobatrachus ghanensis		*Phrynobatrachus phyllophilus*	
	n	stomachs	n	stomachs
Coleoptera	6	4	10	9
Dermaptera	–	–	2	2
Diptera	8	7	2	2
Heteroptera	–	–	2	2
Hymenoptera	61	30	69	18
Isoptera	2	2	2	2
Lepidoptera	4	3	2	2
Orthoptera	3	3	3	2
Thysanoptera	2	2	2	2
Arachnida	10	9	5	4
Isopoda	3	2	0	0
Diplopoda	2	2	0	0
other animals	7	7	8	8
plants	5	5	11	11

(10 specimens), BT4 (5), BT5 (125), BT6 (242) and BT7 (12). We found *P. phyllophilus* on BT4 (2), BT5 (238) and BT6 (63). The number of individuals per transect was not significantly different (Wilcoxon paired-test, Z = -0.944; p = 0.345; N = 5). For a short habitat description of the transects see Assemian et al. (2006).

We found prey items in the stomachs of all 60 frogs (Tab. 1). In total we found six different major prey categories consumed by *P. ghanensis* (Insecta, Arachnida, Isopoda, Diplopoda, other animals and plants) and four major prey categories in *P. phyllophilus* stomachs (Insecta, Arachnida, other animals and plants). In Table 2 the percentage of prey categories (Ip) consumed by both species is summarized. Both species mainly preyed on insects, 81.8% and 80.5%, respectively. Coleoptera and Hymenoptera dominated the diet of both species. However, whereas *P. ghanensis* mainly preyed on hymenopterans (predominantly ants), *P. phyllophilus* seemed to prefer beetles (Tab. 2). Hymenopterans (predominantly ants) were important prey items for both species through both seasons (Tab. 2), but especially for *P. ghanensis* during the rainy season. During the dry season arachnids became of increasing importance for both species. During the dry season flies became the most dominant prey item for *P. ghanensis* and this species then also captured more woodlice and butterflies (Tab. 2). *Phrynobatrachus phyllophilus* switched from predominant beetle prey in the rainy season to hymenopterans and arachnids in the dry season. Eleven stomachs of *P. phyllophilus* contained plant items, eight stomachs were almost completely filled with plants parts, accounting for the high percentage of this "prey item" (Tabs. 1+2). However, neither in *P. ghanensis* (Mann-Whitney-*U*; Z = - 0.793; p = 0.427) nor in *P. phyllophilus* (Mann-Whitney-*U*; Z = 0.390; p = 0.696), prey composition differed significantly between the two seasons. Likewise the trophic niche of both species did not differ significantly, neither during the rainy (C_λ = 0.49), nor during the dry season (C_λ = 0.39).

Tab. 2. Percentage (Ip% Index, see Materials and methods) of prey categories consumed by female *Phrynobatrachus ghanensis* and *P. phyllophilus* throughout a whole year (complete), during the rainy (rainy) or dry (dry season, respectively (Sample size in parentheses).

	Phrynobatrachus ghanensis			*Phrynobatrachus phyllophilus*		
Season / Prey category	complete (N = 30)	rainy (N= 14)	dry (N= 16)	complete (N= 30)	rainy (N= 18)	dry (N= 12)
Coleoptera	5.07	4.02	6.47	56.77	69.34	1.16
Dermaptera	–	–	–	0.04	–	0.78
Diptera	6.75	0.30	25.76	0.10	0.16	–
Heteroptera	–	–	–	0.22	–	3.88
Hymenoptera	65.55	82.81	16.98	22.61	17.62	35.40
Isoptera	0.02	0.05	–	0.18	–	3.3
Lepidoptera	1.51	–	10.54	0.03	–	0.48
Orthoptera	2.88	2.41	1.60	0.49	–	8.73
Thysanoptera	0.01	–	0.04	0.09	0.14	–
Insecta (Σ)	81.79	89.59	61.39	80.53	87.26	53.73
Arachnida	3.93	0.37	17.72	1.30	0.05	11.06
Isopoda	11.75	7.71	16.87	–	–	–
Diplopoda	0.50	1.43	–	–	–	–
other animals	1.5	0.66	2.66	3.00	3.10	1.75
plants	0.53	0.24	1.36	15.17	9.59	33.46

Discussion

Whereas in some reptile assemblages competition for food seems to play a role, or species differ to a high degree in specializing on particular diets (Toft 1985, Akani et al. 2001, Luiselli 2006), it is assumed that competition for food is only of minor importance in anurans that generally feed on a huge variety of prey items (Toft 1980a, b, Kuzmin 1995, Hofer et al. 2004, Ernst & Rödel 2006). For example the herpetofauna of Lamto, a forest-savanna mosaic in Central Ivory Coast, consists of species with a specialised diet (snakes) and species that feed on very diverse prey items (amphibians, lizards and some snakes, Barbault 1974b). Particular prey preferences in lizards are often correlated with habitat and foraging mode, although this correlation seems to differ between different ecosystems (Huey & Pianka 1981, Gasnier et al. 1994). Wild (1994) reports competition for food between a toad, *Bufo camerunensis* and a reptile, the ground dwelling chamaeleon *Rhampholeon spectrum*, the toad out-competing the reptile.

So far competition for food in amphibians was only recorded in laboratory experiments with unnaturally high densities (Kuzmin 1995) or tadpoles in very special natural habitats (Woodward 1982, Osborne & McLachlan 1985, Rudolf & Rödel 2005). It seems that food normally cannot be considered a limited resource for amphibians. In Lamto the arthropods, mostly consumed by the various anuran species, were extremely abundant (Barbault 1974a). With a few exceptions adult anurans are known to be exclusively carnivorous (but see below) and to especially feed on a variety of small arthropods (Kam et al. 1998, Hirai & Matsui 1999; but e.g. only termites and ants in *Hemisus marmoratus*, Barbault 1974a, Rödel et al. 1995), and hence are generally regarded as opportunistic feeders (e.g. Inger & Marx 1961, Barbault 1974a, Duellman & Trueb 1986). This is reflected in seasonal shifts in food composition (Inger & Marx 1961, Toft 1980a, b) or by profound differences of prey composition in populations of one species, living in different areas or habitats. These "preferences" are then directly dependant on the availability of the respective prey species. For example the frog *Aubria subsigillata* predominantly feeds on fish in Gabon (*Epiplatys* spp.) but not in Ghana (Knoepffler 1976, Hughes 1979).

Phrynobatrachus spp. usually occur in very high abundances in African forest (Ernst & Rödel 2006) as well as in savanna ecosystems (Barbault 1967, Gardner et al. 2007). During the rainy season in Lamto four *Phrynobatrachus* species accounted for 8.6% of the savanna amphibians and for 74% of the anurans in the gallery forest (Barbault 1972). During the core rainy season these *Phrynobatrachus* species achieved densities of up to 1453 individuals per hectare in a swampy valley (Barbault 1972). Such densities might result in a competition for food. However, the limiting factor for amphibian populations in Lamto was not food, but rainfall (Barbault 1974b).

In our study both species occurred often in sympatry, namely swampy parts in primary rainforests. Their microhabitat choice seemed to be the same (N.G. Kouamé unpubl. data) and the two species occurred in comparable densities. The observed densities were far lower than those in Lamto, hence already contradicting the potential importance of competition for food between the two species. This was further supported by the fact that the differences in food composition between the two species were not significant.

In our study all stomachs were filled. Thus it seems that both species frequently feed all year round. Although it is believed that frogs do not normally feed on plants, it is known that some frogs may have considerable amounts of plant material in their stomachs. Simon (1983) found more plant material in breeding than in non-breeding individuals of a New Guinean microhylid frog. We detected more plants during the dry season than during the rainy season. Hence, we would not *a priori* exclude the possibility that some plants are devoured deliberately during less favourable periods and were not only swallowed randomly. This possibility is further supported by the fact that the high percentage of plant material in the dry season diet of *P. phyllophilus* was due to some stomachs completely filled with plants (for frogs that deliberately feed on plants compare Da Silva & De Britto-Pereira 2006 and other literature cited therein). The *Phrynobatrachus* species' ability to digest plant matter is completely unknown.

However, and as expected, insects in general and beetles and ants in particular were dominant in the prey of both frog species investigated. The dominance of ants and beetles in the diet was also revealed in six Congolese *Phrynobatrachus* species by Inger & Marx (1961). They partly observed differences in diets between the sexes, altitudes and seasons. *P. anotis* ate more beetles during the dry, more ants in the wet season. In contrast *P. perpalmatus* consumed beetles, cicadas and spiders in the wet season and beetles, cicadas and flies in the dry season. *Phrynobatrachus rungwensis* (termed *P. gutturosus* is this publication) and *P. natalensis* preyed much on termites, but only during the wet season. Only in *P. perpalmatus* ants did not play an important role, which might be explained by the aquatic habitat of the frog, from which the ants were nearly absent. In the other five *Phrynobatrachus* species Inger & Marx (1961) explained the dominance of ants in the prey samples with the overall dominance of these insects. A similar preference for beetles like in *P. perpalmatus*, and the scarcity of ants was recorded from the prey of the semi-aquatic *P. accraensis* at the end of the dry season (Rödel 1995, termed *P. francisci* in this paper). We observed similar, although not significant seasonal switches in food composition like Inger & Marx (1961). Even though we have not simultaneously recorded the availability of the respective prey, we presume that the food choice in the two *Phrynobatrachus* species most likely can be explained by differences in the availability of the various arthropod taxa. The differences in the consumption of ants and beetles as dominant food may hence reflect some so far undetected differences in the frogs' micro-habitat choice and / or activity patterns, rather than being the result of current competition for food. Further in-detail-analyses of the habitat requirements and the species' behaviour may help clarifying this point.

Acknowledgements

We are especially grateful to the "Office Ivoirienne des Parcs et Réserves" and the "Direction des Eaux et Forêts de Côte d'Ivoire" for the access permit to Banco National Park. The research permission was issued by the "Ministère de l'Enseignement Supérieur et de la Recherche Scientifique", Republic of Côte d'Ivoire. This paper is part of the projects "Banco-Santé-Ecologique" at the "Laboratoire d'Environnement et de Biologie Aquatique" of the University Abobo-Adjamé, Abidjan and the BIOLOG-program of the German Ministry of Education and Science (BMB+F; Project W08 BIOTA-West, FZ 01 LC 00410). Timo Moritz commented on a previous draft of the manuscript. These supports are gratefully acknowledged!

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Appendix

Field numbers, size and origin of *Phrynobatrachus* females examined in this work. Vouchers will be all deposited in the collection of the Laboratoire d'Environnement et de Biologie Aquatique at the University Abobo-Adjamé, Abidjan. BT = Banco transect; SVL = Snout-Vent-Length.

Species	Specimens	SVL (mm)	Transects	Date of capture
P. ghanensis	No.1	20.0	BT6	10.03.2004
P. ghanensis	No.2	18.5	BT6	07.04.2004
P. ghanensis	No.3	17.5	BT6	07.04.2004
P. ghanensis	No.4	18.0	BT6	18.05.2004
P. ghanensis	No.5	20.5	BT6	18.05.2004
P. ghanensis	No.6	19.0	BT6	18.05.2004
P. ghanensis	No.7	20.0	BT5	02.06.2004
P. ghanensis	No.8	19.0	BT5	02.06.2004
P. ghanensis	No.9	18.0	BT5	29.06.2004
P. ghanensis	No.10	20.0	BT6	29.06.2004
P. ghanensis	No.11	19.0	BT5	30.06.2004
P. ghanensis	No.12	19.0	BT5	30.06.2004
P. ghanensis	No.13	20.0	BT5	07.07.2004
P. ghanensis	No.14	18.0	BT5	08.07.2004
P. ghanensis	No.15	18.0	BT5	08.07.2004
P. ghanensis	No.16	18.0	BT6	05.08.2004
P. ghanensis	No.17	20.0	BT6	01.09.2004
P. ghanensis	No.18	19.5	BT6	01.09.2004
P. ghanensis	No.19	17.5	BT5	16.09.2004
P. ghanensis	No.20	19.5	BT5	16.09.2004
P. ghanensis	No.21	18.5	BT5	16.09.2004
P. ghanensis	No.22	18.0	BT5	28.12.2004
P. ghanensis	No.23	17.5	BT5	28.12.2004

Species	Specimens	SVL (mm)	Transects	Date of capture
P. ghanensis	No.24	18.5	BT6	28.12.2004
P. ghanensis	No.25	18.5	BT6	28.12.2004
P. ghanensis	No.26	18.5	BT6	25.01.2005
P. ghanensis	No.27	19.0	BT6	25.01.2005
P. ghanensis	No.28	19.0	BT6	25.02.2005
P. ghanensis	No.29	20.0	BT6	25.02.2005
P. ghanensis	No.30	18.0	BT6	25.02.2005
P. phyllophilus	No.31	20.0	BT5	06.04.2004
P. phyllophilus	No.32	19.0	BT5	06.04.2004
P. phyllophilus	No.33	19.0	BT6	06.04.2004
P. phyllophilus	No.34	19.0	BT6	06.04.2004
P. phyllophilus	No.35	19.0	BT5	07.04.2004
P. phyllophilus	No.36	18.5	BT5	07.04.2004
P. phyllophilus	No.37	18.0	BT6	07.04.2004
P. phyllophilus	No.38	19.0	BT5	18.05.2004
P. phyllophilus	No.39	20.0	BT5	02.06.2004
P. phyllophilus	No.40	21.0	BT5	02.06.2004
P. phyllophilus	No.41	20.0	BT5	02.06.2004
P. phyllophilus	No.42	20.0	BT5	02.06.2004
P. phyllophilus	No.43	20.0	BT5	03.06.2004
P. phyllophilus	No.44	17.0	BT6	29.06.2004
P. phyllophilus	No.45	18.0	BT6	08.07.2004
P. phyllophilus	No.46	20.0	BT6	08.07.2004
P. phyllophilus	No.47	19.0	BT5	05.08.2004
P. phyllophilus	No.48	18.0	BT5	05.08.2004
P. phyllophilus	No.49	18.0	BT6	05.08.2004
P. phyllophilus	No.50	19.5	BT5	01.09.2004
P. phyllophilus	No.51	18.0	BT5	01.09.2004
P. phyllophilus	No.52	18.5	BT5	01.09.2004
P. phyllophilus	No.53	14.5	BT5	01.09.2004
P. phyllophilus	No.54	20.0	BT6	16.09.2004
P. phyllophilus	No.55	19.5	BT5	18.10.2004
P. phyllophilus	No.56	20.0	BT6	22.11.2004
P. phyllophilus	No.57	18.5	BT5	28.12.2004
P. phyllophilus	No.58	20.0	BT5	28.12.2004
P. phyllophilus	No.59	18.5	BT5	25.01.2005
P. phyllophilus	No.60	18.5	BT5	25.01.2005

Manuscript received: 3 May 2007

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