The diet of the African Tiger Frog, *Hoplobatrachus occipitalis*, in northern Benin

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Abstract. The worldwide decline of amphibian populations calls for studies concerning their ecological role within ecosystems and only knowledge about amphibian species' diets may facilitate the identification of their respective position in trophic cascades. Frog consumption by humans has recently increased to a considerable extent in some parts of West Africa. We analyse herein the diet of the most commonly consumed frog species, *Hoplobatrachus occipitalis* (Dicroglossidae), in Malanville, northern Benin. In order to determine its prey spectrum we investigated stomachs of frogs obtained from frog hunters, and stomach-flushed frogs caught by ourselves. Overall, we investigated the gut contents of 291 individuals (83 flushed, 208 dissected), 21% of which had empty stomachs. We identified Coleoptera, Lepidoptera and Formicidae as the most important prey categories in flushed frogs and Pisces, Coleoptera and Araneae in collected frog stomachs. According to these data, *H. occipitalis* is an opportunistic forager, able to predate on terrestrial as well as on aquatic taxa. The prey spectrum revealed by the two different sampling methods differed only slightly. In contrast, the frequency of particular prey categories (e.g., fish) differed strongly. These differences were most probably method-based, rather than reflecting different prey availability among capture sites.

Key words. Amphibia, Anura, Dicroglossidae, diet, savanna, stomach flushing, West Africa.

Introduction

In addition to climate change (Blaustein et al. 2010), habitat degradation and conversion (Cushman 2006, Ernst et al. 2006), and diseases (Daszak et al. 2003), the overharvesting by humans may play a major role in the decline of amphibian populations (Schlaepfer et al. 2005, Warkentin et al. 2009). Since amphibians are important components in trophic cascades, vanishing populations may have crucial effects on ecosystem functioning (Halliday 2008, Mohneke & Rödel 2009). However, only detailed ecological and biological data, such as diet, can facilitate estimating these effects (Duffy 2002, Whiles et al. 2006).

Anuran larvae are mostly grazers or suspension feeders (Ranvestel et al. 2004, Altig et al. 2007), whereas adults predominantly prey on various invertebrates and, in relation to their sizes, sometimes vertebrates. Studies concerning the diet of adult amphibians have been conducted for various species in almost all regions of the World; e.g., the Neotropics (Whitfield & Donnelly 2006, Lima et al. 2010), Asia (Hirai & Matsui 2001b, Yu et al. 2009), Australia (Lemckert & Shouler 2007), temperate America (Mahan & Johnson 2007, Hothem et al. 2009), and Europe (Blackith & Speight 1974, Kovács et al. 2007). Although studies on African anurans are comparatively rarer, the diets of several species have been studied (Inger & Marx 1961, Hughes 1979, Blackburn & Moreau 2006, Kouamé et al. 2008).

The large aquatic African Tiger Frog, *Hoplobatrachus occipitalis* (Günther, 1858) inhabits savannas in sub-Saharan Africa. It is known to be consumed by humans in several countries (e.g., Benin, Burkina Faso, Ghana, Guinea, Ivory Coast, Nigeria). The intensity of exploitation of this species as human food varies among regions as well as between different ethnic groups (Mohneke et al. 2010). The focus of our study was the town of Malanville in northern Benin, where the collection of *H. occipitalis* for local and regional food markets is especially intense, i.e., a group of 30 Nigerian frog hunters collected approximately 450000 frogs within two months (Mohneke et al. 2010). This intense exploitation seems to be unsustainable and may lead to the local decline of *H. occipitalis*. This could have ecological consequences. An Asian *Hoplobatrachus* species, *H. tigerinus* is known to ingest as much as 10% of its own weight in insects per day (Abdulali 1985). In India, the collection of frogs' legs resulted in the survival of tonnage of insects, including disease-carrying mosquitoes and agricultural pests (Oza 1990). Larval *H. occipitalis* are opportunistic carnivores and mainly feed on other tadpoles and mosquito larvae in temporary savanna ponds (Spieler & Linsenmair 1997, Rödel 1998). Detailed knowledge about the amount and composition of the adults' diet is so far limited to two studies from Senegal (Lescure 1971) and Ivory Coast (Tohé 2009). The aim of our study was to a) identify the diet of *H. occipitalis* in northern Benin, as well as to b) evaluate the efficiency and accuracy of stomach flushing versus dissection.

Material and methods
Study site and period

The study took place in northern Benin, close to the borders of Burkina Faso, Niger and Nigeria. All specimens were collected in close proximity to the river Niger, near Karimama (N 12°04.062'; E 003°10.680') and Malanville (N 11°52.590'; E 003°22.667'). This region is characterized by a dry Sudan savanna with an annual precipitation of approximately 755 mm (Faoclim 2 – worldwide agroclimatic data base, http://freegeographytools.com/2007/fao-world-climate-data). First rainfalls normally occur in late June and last until mid-September. Our data were collected at the end of the dry season (May and June) in 2009.

Stomach contents

There are various approaches to investigating the diet of amphibians. Individuals can be directly observed (mostly very difficult) or faeces can be collected (many prey items may be completely digested or unrecognisable). However, the two most common methods are dissection and stomach flushing. There are only a few studies comparing these both methods directly (Leclerc & Courtois 1993, Wu et al. 2007). We applied both methods. No frog was killed for this study.

Stomach flushing. Adult *Hoplobatrachus occipitalis* were captured during the night (2300 to 0400 h) in flooded rice paddies, at riversides and temporary ponds, and immediately (within one hour after capturing) stomach flushed on site, as described in Solé et al. (2005). We recorded weight (spring scale: 0 to 300 g, accuracy: ± 0.2 g), snout–vent length (digital dial calliper: 0 to 150 mm, accuracy: ± 0.01 mm), and sex of each frog. For flushing, we used two types of flexible PVC tubes with diameters of 5 mm for larger and 3 mm for smaller frogs. The tube was attached to a syringe, which was filled with pond or river water (according to the respective capture site). Regurgitated items were stored in formalin (5%) and later transferred to ethanol (70%). At the beginning of our study, we kept 10 flushed frogs in plastic containers for three days to check for potential complications due to the stomach flushing (e.g., injuries, death). All these frogs survived unharmed. All other individuals were immediately released after flushing.

Stomach sampling. Stomachs of *H. occipitalis* were collected in the rice paddies of Malanville on three different days. The respective frogs had been killed by Nigerian frog hunters during the preceding nights (sampling time: 1900 to 0300 h) by beating the frogs to death with long wooden sticks (Mohneke et al. 2010). The hunters gutted the frogs in the early morning and allowed us to separate the stomachs from the remaining innards. Each of these frogs was weighed with a spring scale (details see above) before they were disembowelled by the hunters. The stomachs were fixed in formalin (5%).

Diet analyses

The stomach content of each frog was examined individually. The collected stomachs were sliced lengthwise to extract the entire stomach content. All items were transferred into ethanol (70%) for subsequent identification. Prey items were counted, identified to a particular taxonomic category (mostly order level), and length, width and depth were measured (to the nearest 0.01 mm) with a digital calliper under a dissecting microscope. The volume of completely preserved food items was calculated using the formula of a prolate ellipsoid $V = 4/3\pi$ (½ × length) × (½ × width)². The original volumes of partly digested Formicidae were calculated with the regression method as described by Hirai & Matsui (2001a).

In order to characterize the diet of *H. occipitalis* in general, several indices, adopted from diet studies in fish and amphibians, were used (e.g. Pinkas et al. 1971, Guidali et al. 2000, Dietl et al. 2009). Each calculation was done for stomach flushing and sampling, respectively. The number of stomachs containing a particular prey category was evaluated as the frequency of occurrence (FO_i) and the proportion of FO_i [$FO\%_i = (FO_i/n_{\text{stomachs with diet}}) \times 100$]. For each prey category, we calculated the total volume as the sum of all prey items of category i (V_i) as well the proportion of V_i relative to the total volume of all measured food items [$V\%_i = (V_i/\Sigma V_{i...n}) \times 100$]. The importance of each prey category related to the entire range of food items in all samples was identified via the index of relative importance $IRI_i = (\%N_i + \%V_i) \times \%FO_i$ (Pinkas et al. 1971). We used the Mann-Whitney U-test to search for potential prey differences in relation to the frogs' sizes, weights and sex and to compare the two methods. The χ²-test was chosen to compare frequencies. For correlative analyses, we applied the Spearman-Rank correlation. All statistical analyses were conducted with R 2.9.0 (http://www.r-project.org).

Results
Investigated animals

83 frogs were flushed and the stomachs of 208 individuals were collected. The weight of the frogs ranged between 24 and 176 g (mean ± SD: 74.5 ± 25.8 g, n = 279), with flushed frogs being slightly lighter (stomach sampling: range 24–176 g, 75.1 ± 24.4 g, n = 196; stomach flushing: range 35–148 g, 73.1 ± 29.0 g, n = 83). However, this difference was not significant (Mann-Whitney U-test: W = 7172, p = 0.12, n_{sampling} = 196, n_{flushing} = 83). Snout–vent length was only measured in flushed individuals (range 67.82–108.32 mm; mean ± SD: 83.79 ± 10.40 mm, n = 83). Since size and weight were tightly correlated (Spearman-Rank correlation: r_s = 0.91, p < 0.001, n = 83), we used only weight for subsequent analysis. Due to the killing method of the frog hunters (see Mohneke et al. 2010), heads were damaged and vocal sacs of male frogs were often not recognizable. Sex was thus only identified in flushed frogs (n_{males} = 37, n_{females} = 44, two frogs were too young for sexing). In flushed frogs, the sexes differed neither in size (Mann-Whitney U-test: W = 893, p = 0.46, n_{males} = 37, n_{females} = 44) nor in weight (W = 915.5, p = 0.34, n_{males} = 37, n_{females} = 44).

Stomach filling

In total, 20.62% (sampling: 20.19%; flushing: 21.69%) of the frogs had empty stomachs. The proportion of stomachs

containing prey items did not differ between the two methods (χ^2-test: χ^2 = 0.015, df = 1, p = 0.90, $n_{stomach\ sampling}$ = 208, $n_{stomach\ flushing}$ = 83). Whether a stomach contained prey items or not was independent from weight (all samples: Mann-Whitney U-test: W = 6556.5, p = 0.98, n = 279, stomach sampling: W = 3314, p = 0.81, n = 198; stomach flushing: W = 577, p = 0.93, n = 83), size (stomach flushing only: W = 631.5, p = 0.47, n = 83), as well as from sex (stomach flushing only: χ^2-test: χ^2 = 0.150, df = 1, p = 0.70, n_{males} = 37, $n_{females}$ = 44).

Overall, we recorded 1259 prey items, 718 were gathered by stomach sampling and 541 by stomach flushing. The number of items ranged between one and 87 per stomach (9.8 ± 5.5, n = 231, sampling range: 1–40, 4.3 ± 4.4, n = 166; flushing range: 1–87, 8.3 ± 16.7, n = 65). There was no difference in the number of items found per stomach related to sex (stomach flushing only: W = 475.5, p = 0.79, n = 63), nor to sampling method (Mann-Whitney U-test: W = 599.5, p = 0.50, n = 231). We detected no correlation between the number of food items and the weight of the frogs (r_s = -0.029, p = 0.67, n = 219).

ed through dissection (sampling range: 0.16–7885.63 mm³, 296.58 ± 967.17; flushing range: 0.05–6429.96 mm³, 58.72 ± 333.68; Mann-Whitney U-test: W = 67248, p < 0.001, $n_{sampling}$ = 465, $n_{flushing}$ = 430; Figure 1). When testing all frogs or those that had been collected by the frog hunters only, the mean size of prey was not correlated to the frogs' weight (Spearman-Rank correlation: all frogs: r_s = 0.03, p = 0.35, n = 895; frog hunters samples: r_s = 0.07, p = 0.13, n = 465). Prey size was weakly negatively correlated to the weights of the flushed frogs (r_s = -0.11, p < 0.05, n = 430).

The volume of stomach contents (sum of all measured preys items in one stomach) ranged between 0.16 and 11527.29 mm³ (828.23 ± 1839.22 mm³, n = 197). Stomachs of frogs that had been collected by the frog hunters contained significantly more prey volume than flushed frogs (stomach flushing: range 0.16–6429.96 mm³, 443.04 ± 962.59 mm³, n = 57; stomach sampling: range 0.24–11527.29 mm³, 985.06 ± 2076.29 mm³, n = 140; Mann-Whitney U-test: W = 3219, p < 0.05, n = 197). The volume of stomach contents was positively correlated to the *H. occipitalis* weight, irrespective of the method (Spearman Rank correlation: r_s = 0.18, p < 0.05, n = 186).

Volume of food items

Stomach contents at a more advanced stage of digestion became increasingly difficult to identify both taxonomically as well as in volume. In order to avoid wrong categorizations and misestimates in body sizes of the prey items we included solely feebly digested or nearly intact items for the content analysis. Therefore, no volume calculations were carried out in 21.5% of the prey items in the flushed and in 35.2% in the collected stomachs. Flushed, single prey items were significantly smaller in size than those collect-

Prey composition

Most prey items were arthropods such as spiders or insects, but vertebrates, i.e., fish and amphibians, were also common. The most common prey of flushed frogs were termites, whereas beetles, due to their frequency of occurrence and greater individual size, were the most important prey animals. Ants and adult moths also had a high index of relative importance in the flushed frogs. In the collected stomachs, fish were the most common and most important
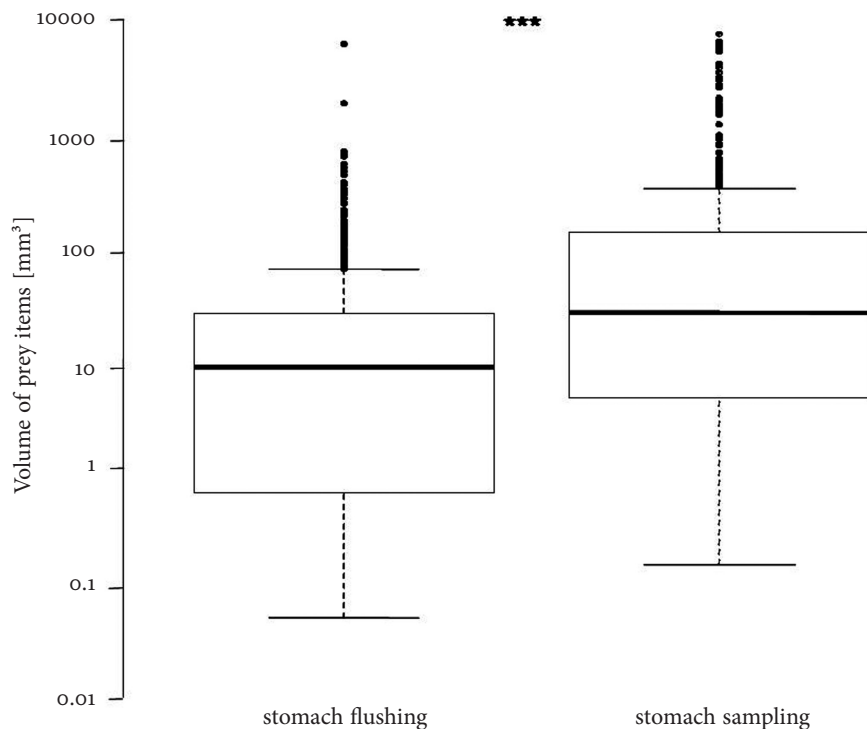

Figure 1. Volume of *Hoplobatrachus occipitalis* prey. Given are the calculated volumes of all measured food items in mm³ of collected and flushed frog stomachs. The scale on the Y-axis is logarithmic; $n_{sampling}$ = 465, $n_{flushing}$ = 430.

Table 1. Stomach contents of *Hoplobatrachus occipitalis*. N = number of prey items, N_m = number of measured items used for volume calculations, N% = percentage of N, FO = frequency of occurrence, FO% = percentage of FO, V = sum of volume of prey items in mm³, V% = percentage of V, IRI = index of relative importance, prey categories comprising several stages are divided in adults (a), larvae (l) and egg (e); the three most important prey categories are highlighted; number of stomachs containing prey items: stomach flushing = 65, stomach sampling = 166.

stomach flushing	Prey animals	N	N_m	N%	FO	FO%	V	V%	IRI
	ANNELIDA								
	Oligochaeta	1	1	0.19	1	1.54	111.17	0.44	0.96
	ARTHROPODA								
	Arachnida								
	Araneae	28	25	5.18	12	18.46	283.14	1.12	116.25
	Crustacea								
	Decapoda	2	0	0.37	2	3.08	na	na	na
	Amphipoda	1	1	0.19	1	1.54	20.70	0.08	0.41
	Insecta								
	Blattodea	1	1	0.19	1	1.54	51.69	0.21	0.60
	Coleoptera (a)	75	55	13.86	29	44.61	5819.27	23.04	**1646.61**
	Coleoptera (l)	2	2	0.37	2	3.08	61.02	0.24	1.88
	Dermaptera	7	6	1.29	6	9.23	679.16	2.69	36.77
	Diptera (a)	9	9	1.66	4	6.15	30.34	0.12	10.98
	Diptera (l)	3	3	0.56	1	1.54	69.40	0.28	1.28
	Hemiptera	5	5	0.92	5	7.69	102.33	0.41	10.23
	Hymenoptera								
	Formicidae	38	38	7.02	12	18.46	304.55	1.21	**151.94**
	others	5	3	0.92	3	4.62	145.64	0.58	6.93
	Isoptera	91	87	16.821	5	7.69	325.48	1.29	139.30
	Lepidoptera (a)	62	29	11.46	19	29.23	3853.58	15.26	**781.05**
	Lepidoptera (l)	6	6	1.11	6	9.23	234.01	0.93	18.79
	Odonata (a)	2	1	0.37	2	3.08	298.01	1.18	4.77
	Odonata (l)	1	1	0.19	1	1.54	117.67	0.47	1.00
	Orthoptera	9	7	1.66	6	9.23	982.44	3.89	51.27
	Phasmatodea	6	5	1.11	5	7.69	164.67	0.65	13.55
	unidentified (a)	29	0	5.36	24	36.92	na	na	na
	unidentified (e)	55	55	10.17	1	1.54	8.40	0.03	15.69
	Myriapoda								
	Diplopoda	2	2	0.37	2	3.08	998.98	3.96	13.31
	MOLLUSCA								
	Bivalvia	1	1	0.19	1	1.54	88.31	0.35	0.82
	Gastropoda	1	1	0.19	1	1.54	58.50	0.23	0.64
	VERTEBRATA								
	Amphibia								
	Anura (a)	2	2	0.37	2	3.08	7081.62	28.04	87.42
	Anura (l)	82	82	15.16	1	1.54	1320.87	5.23	31.37
	Mammalia	1	0	0.19	1	1.54	na	na	na
	Pisces	11	2	2.03	9	13.85	2042.34	8.09	140.13
	unidentified	3	0	0.56	3	4.66	na	na	na
	TOTAL	541	430	100	168	258.46	25253.31	100	3283.94

Table 1 continued

stomach sampling	Prey animals	N	N$_m$	N%	FO	FO%	V	V%	IRI
	ARTHROPODA								
	Arachnida								
	Araneae	54	45	7.52	35	21.08	2179.03	1.580	**191.89**
	Collembola	1	1	0.14	1	21.08	9.29	0.007	0.088
	Crustacea								
	Decapoda	2	1	0.28	2	1.21	0.24	0	0.34
	Insecta								
	Blattodea	2	2	0.28	2	1.21	277.34	0.201	0.58
	Coleoptera (a)	72	45	10.03	45	27.11	5564.73	4.035	**381.22**
	Coleoptera (l)	3	3	0.42	3	1.81	9.11	0.007	0.77
	Dermaptera	1	1	0.14	1	0.60	0.35	0	0.08
	Diptera (a)	27	19	3.76	19	11.45	254.42	0.184	45.15
	Diptera (l)	18	16	2.51	10	6.02	337.02	0.244	16.57
	Hemiptera	32	23	4.46	26	15.66	3615.40	2.622	110.87
	Hymenoptera								
	Formicidae	49	49	6.83	19	11.45	293.47	0.213	80.55
	others	8	6	1.11	8	4.82	133.43	0.097	5.84
	Isoptera	58	41	8.08	8	4.82	459.18	0.333	40.54
	Lepidoptera (a)	19	17	2.65	18	10.84	1140.28	0.827	37.66
	Lepidoptera (l)	26	25	3.62	19	11.45	2133.17	1.547	59.15
	Mecoptera	1	1	0.14	1	0.60	15.18	0.011	0.09
	Mantodea	3	1	0.42	3	1.81	530.74	0.385	1.45
	Odonata (a)	8	4	1.11	8	4.82	1554.47	1.127	10.80
	Odonata (l)	4	2	0.56	4	2.41	330.88	0.240	1.92
	Orthoptera	36	20	5.01	29	17.47	4553.92	3.302	145.28
	Phasmatodea	14	8	1.95	13	7.83	205.07	0.149	16.43
	unidentified (a)	74	0	10.31	52	31.33	na	na	na
	unidentified (l)	2	0	0.28	2	1.21	na	na	na
	unidentified (e)	16	16	2.23	7	4.22	46.52	0.034	9.54
	Myriapoda								
	Chilopoda	1	1	0.14	1	0.60	102.87	0.075	0.13
	MOLLUSCA								
	Gastropoda	9	9	1.25	8	4.82	1978.51	1.435	12.96
	VERTEBRATA								
	Amphibia								
	Anura (a)	9	7	1.25	8	4.82	26379.25	19.128	98.22
	Mammalia	2	1	0.28	2	1.21	6010.64	4.358	5.59
	Pisces	150	101	20.89	56	33.74	79794.02	57.860	**2656.68**
	Reptilia								
	Squamata	1	0	0.14	1	0.60	na	na	na
	unidentified	16	0	2.23	16	9.64	na	na	na
	TOTAL	771	509	100	461	277.71	140078.24	100	4122.18

prey animals. They were present in 33.8% of stomachs and the index of relative importance (IRI = 2646.7) was almost seven times higher than the second most important prey category beetles (IRI = 381.22). Furthermore, spiders were frequently found in the frogs collected by the frog hunters. Table 1 summarizes the spectrum of recorded prey items.

Although most prey types were found in both collected and flushed stomachs, the relative occurrence of each cat-

egory differed significantly with the method used (χ²-test: χ² = 60.57, df = 35, p < 0.01, n = 1259). Gravel, vegetation and rice grains were also frequent in the investigated stomachs, with the latter being the most common non-food item (1–6 grains per stomach, 1.6 ± 1.0, n = 40). Vegetation was gathered from 33 stomachs and 10 contained grains of gravel.

Discussion

We analysed the dietary composition of *Hoplobatrachus occipitalis* in rice paddies and small rivers close to the river Niger around the end of the dry season of 2009. We identified fish, beetles, moths and ants as the most important prey. Our data on overall prey composition thus partly differed from other studies on *H. occipitalis*. In a Senegalese population, Lescure (1971) found predominantly beetles, ants and spiders by dissection. In southern Ivory Coast, Hymenoptera (including ants) were the most important prey category of dissected *H. occipitalis*, followed by beetles and amphibians (Tohé 2009). It is known that many anurans change their feeding habits according to the seasons; e.g., Toft (1980) found dietary differences according to the respective supply in Peru, and Inger & Marx (1961) reported a seasonal dietary change in various Central African anuran species. In contrast, three of four analysed *Hyperolius* species did not show any change between the dry and wet seasons in Nigeria (Luiselli et al. 2004). Differences in diet composition may be based upon prey availability, varying between seasons and/or habitats (Kovács et al. 2007). Both factors may explain differences between our study, conducted in a dry savanna around the end of the dry season, and other populations (Lescure 1971, Tohé 2009). Gravel, rice grains, and plant matter within the stomachs have most likely been accidentally ingested (Aszalós et al. 2005, Kutrup et al. 2005). On the other hand, some frog species are known to feed on plants (Das 1996, da Silva & de Britto-Pereira 2006) and gravel could aid the digestion of the diet (Evans & Lampo 1996). To clarify if these "prey items" are deliberately ingested, direct observations are necessary.

The type of frogs' prey items is often associated with a specific foraging mode. Active feeders may predate upon large numbers of smaller prey that often occurs in aggregations. Toft (1980) called these frogs "ant-specialists". Solitary prey like beetles or spiders are preferred by "sit and wait" feeders, which have been defined as "non-ant specialists" (Toft 1980, Lima et al. 2010). Ants were consumed by *H. occipitalis* in different quantities. Lescure (1971) found them in 42.9% of the analysed stomachs (13.6% of all ingested prey items). Tohé (2009) did not distinguish between members of Hymenoptera. However, 18% of the investigated stomachs contained individuals of this insect order. This group, probably mostly ants, made up 30% of all ingested prey items in his analysis. In our study, ants occurred in 11.4% of the collected and 18.5% of the flushed stomachs and amounted to 6.8% and 7.0% of all identified categories, respectively. Thus, ants were not avoided in northern Benin, but played a less dominant role in comparison to other diet components. Termites, which represent another aggregation taxa, are generally of less importance (Lescure 1971, this study) in, or even absent (Tohé 2009) from, the diet of

H. occipitalis. The dietary composition of our *H. occipitalis* populations speaks in favour of these frogs behaving as opportunistic "sit and wait" predators (Guidali et al. 2000).

Terrestrial invertebrates usually dominate the diet of anurans, even in aquatic or semiaquatic species (Hirai & Matsui 2001b, Mahan & Johnson 2007). Likewise, most of the prey ingested by *H. occipitalis* was made up by terrestrial species. However, aquatic animals like tadpoles, water bugs, and especially fish occurred as well (Lescure 1971, Tohé 2009; this study). A very high proportion of collected stomachs (N% = 20.9) contained fish. This suggests that *H. occipitalis* is capable of capturing prey above as well as under the water surface as has been reported for only a few other frog species such as *Aubria subsigillata* (Knoepffler 1976), *Lithobates catesbeianus* (Hothem et al. 2009), or *Xenopus laevis* (Inger & Marx 1961).

The high proportion of fish was surprising, particularly since in the study of Tohé (2009), fish accounted for only 3.7% of the prey, even though he studied a *H. occipitalis* population at a fish farm, whereas our frogs predominantly originated from rice paddies. The fish species in our samples (cichlids, cyprinids and catfish) cannot persist in temporary waters and thus likely migrated into the rice paddies when these were flooded.

While qualitative prey composition was similar between both methods applied, quantitative results were different. We identified beetles, moths and ants as the most important prey categories in flushed frogs, and fish, beetles and spiders in collected frog stomachs. Prey size was significantly smaller in the flushed frogs, potentially indicating that not all large food items may have been flushed out. Since fish were by far the largest prey items, this would explain why they were seemingly so rare in the flushed animals. Generally, altered abundance of particular prey items might be related to site, prey availability varying between habitats (Hirai & Matsui 1999), as well as between natural and human-dominated landscapes (Solé et al. 2009). For instance, a large aquatic African rainforest frog, *Aubria subsigillata,* was reported to mainly predate upon fish in Gabon (62% of all individuals investigated had ingested fish, Knoepffler 1976), whereas frogs from Ghana did not contain any fish (Hughes 1979). We captured our frogs within rice paddies (as did the frog hunters), in shallow branches of rivers, as well as in temporary ponds and near a well of a village. However, we found fish in nine flushed individuals: three captured in the paddy fields, six from the riverside, and one from a temporary pond. It therefore seems unlikely that our observed differences in fish abundance were habitat-specific. Most probably, the differences can be ascribed to the sampling approach. Stomach flushing might be less effective in terms of larger food items like fish.

The reliability of stomach flushing data was evaluated in various taxa. In penguins e.g., the effectiveness is relatively high, but decreases with ingestion time (Gales 1987). In a study on the diet of fishes, the efficacy of flushing also varied with the type of prey in combination with time after ingestion (Petridis & O'Hara 1988). Fitzgerald (1989) concluded in his methodical comparison of diet analyses in crocodiles, that problems will always occur with regard to prey item size. In contrast, Leclerc & Courtois (1993) dissected some flushed frogs and found that less than 1% of the total volume had remained in their stomachs. Wu et al.

(2007) likewise found that nearly 95% of the total volume and prey item number could be recovered through flushing. Unfortunately, we cannot provide such data since we were not permitted to flush the animals before they were killed by the Nigerian frog collectors and abstained from killing the frogs we caught. Hence, it remains unclear if some of the larger and/or a certain part of ingested items remained in the stomachs after flushing.

Many authors have reported that size of prey is related to the snout–vent length and mouth width of anurans (Houston 1973, Toft 1980, Dietl et al. 2009) and/or that diet preferences change with age (Lima & Moreira 1993, Hirai 2002, Blackburn & Moreau 2006). We could not find any correlation between prey size and frog weight in our study (however, only subadult to adult frogs were examined), although the prey covered a broad spectrum concerning weight and size. Most of the examined frogs had well-filled stomachs. The volume of all ingested items in one frog adds up to a maximum of 11,500 mm³ and was found in a medium-sized individual. The potentially enormous quantity of daily consumption underlines the potentially important position of *H. occipitalis* within its ecosystems, especially where the species is very abundant such as on river banks in the dry season, in swamps or rice paddies. Since the consumption of *H. occipitalis* by West Africans is locally dramatically increasing (Mohneke et al. 2010), notable effects on the ecosystem of the species' potential decline are not unlikely. Regardless of the methodological approach, our data, based on nearly 300 individuals, very probably provide a representative picture of the species' diet, at least in this particular region (rice paddies and Sudanese savanna near a large river) and season (dry season). It is known that *H. occipitalis* migrates from river sites (occupied in the dry season) to newly formed savanna ponds in the wet season (Spieler & Linsenmair 1998). This switching of habitats may be also reflected in a change of prey items. Furthermore, *H. occipitalis* tadpoles are known to be very efficient predators of, e.g., other tadpoles and mosquito larvae (Rödel 1998, 2000). A decline of adult frogs will consequently result in smaller numbers of tadpoles. In the wake of unsustainable harvesting of frogs, a dramatic increase of pest insect populations was reported from India (Abdulali 1985, Oza 1990). It would therefore be interesting to investigate the diet of *H. occipitalis* during the wet season in their breeding habitats, far from the rice paddies and riversides, as well as the exact composition and quantities of the tadpoles' prey.

Acknowledgements

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