

The diet of the paradoxical frog *Pseudis paradoxa* in Trinidad, West Indies

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The diet of adult and late metamorphic *Pseudis paradoxa* in Trinidad was assessed from stomach contents. *Pseudis paradoxa* consumed a wide taxonomic and size range of invertebrates, mostly insects, but also arachnids, crustaceans (crabs) and annelids. There was little evidence for ontogenetic changes in prey taken, but larger females had taken larger prey than smaller individuals. Although most prey items could have been captured above the water surface, some must have been taken below the surface. The significance of these findings is discussed in the light of *Pseudis*'s unique life history and evolution (individuals are essentially full size at metamorphosis; adults are fully but secondarily aquatic) and in comparison with previous reports.

Key words: feeding ecology, Hylinae, ontogeny, prey size

The eleven species of *Pseudis* (Frost, 2009) are characterized by a unique life history, whereby the tadpoles grow to an exceptionally large size and metamorphose into frogs that are already at the adult stage or close to it, rather than needing to progress through the juvenile phase characteristic of most other other anurans (Downie et al., 2009a,b). Another special feature of *Pseudis* is that, although part of the tree frog subfamily Hylinae (Faivovich et al., 2005), the adults are aquatic, with strongly webbed feet and no sign of adhesive toepads. Because of these features, the feeding ecology of post-metamorphic *Pseudis* is of some interest. For example, do they show any sign of ontogenetic change in prey size preference, and do they feed mainly on aquatic or terrestrial/aerial prey? Four previous studies have reported on the diets of three species of *Pseudis* (Brandão et al., 2003; Duré & Kehr, 2001; Garda et al., 2007; Teixeira et al., 2004), but they have only partly addressed these questions.

Adult *Pseudis paradoxa* were captured as part of a study on *Pseudis* life history from four of the five Trinidad locations reported in Downie et al. (2009a,b). These were Nariva swamp (Bush Bush canal and Manzanilla Road), Bamboo Grove and Columbus Bay, over the period 1996–2001, in June to August. Frogs were captured by hand at night with individuals located at the water surface by

torchlight and/or by call. Captured frogs were conveyed in 2-litre polythene tubs or polythene bags, containing a little swamp water, and with small punched air-holes. Frogs were killed within 3h of capture by an overdose of anaesthetic (MS 222 or Benzocaine). They were then fixed in buffered neutral formalin, after slitting open the abdominal wall to facilitate penetration of the fixative. For wet weights of whole animals, specimens were dried of surface fluid and weighed using an electronic balance accurate to 0.01 g. Snout–vent lengths (SVL) were measured using callipers accurate to 0.1 mm. To assess sex and reproductive state, gonads and fat bodies were removed for inspection and measurement. The presence or absence of any remnant of the tail was also assessed to determine whether any individuals were in the process of metamorphosis. Downie et al. (2009a) report that *P. paradoxa* take 5–11 days to complete metamorphosis, i.e. to develop through Gosner (1960) stages 41–46. Stomach and intestines were removed from each specimen, opened and the contents examined. We counted the number of prey items, classified them to order level (and sometimes to family), to stage (adult or larva) and to habitat (aquatic or terrestrial/aerial). We also measured head to tail lengths (to 1.0 mm) whenever this was possible, using a dissecting microscope and eyepiece graticule. Since intestine contents were generally too fully digested to be recognizable and measurable, we did not include them in our analysis. Identification of contents was made with the aid of a dissecting microscope and reference to preserved museum specimens collected in the neotropical region, particularly from Trinidad.

To provide an index of stomach fullness, we devised an estimate of the size of each content item ($\text{length}^2 \times 0.3 \times \text{length}$ in millimetres, an approximation of cylinder volume). The sums of each stomach's contents were then given a score: 0, 1 = contents sum of 1–99 mm³; 2 = sum of 100–600 mm³; 3 = sum of 600 mm³. These equate to empty, small amount, moderate amount, full stomach.

In total, we analysed the gut contents of 36 frogs: 23 adult males, seven adult females and six late metamorphs (juveniles). Adult sizes were: males – mean±SD SVL 50.5±5.4 mm, mean mass 21.5±7.2 g; females – mean SVL 56.8±8.0, mean mass 29.9±14.0. Mean juvenile tail length was 41.8±29.9 mm. All metamorphs had the coloration typical for frogs rather than tadpoles, but still retained the tail. Mean ± SD stomach fullness scores were: males 1.7±1.0; females 2.3±1.0; metamorphs 1.3±1.2. These scores were not significantly different between the sexes (χ^2 tests, $P>0.05$ in each case). We observed differences in the proportion of individuals with empty stomachs: males 13%; females none; metamorphs 33% (overall 13.9%). Since frogs were captured by locating them at the surface by call or by torchlight, males that were calling may have been those with empty stomachs. Solé & Pelz (2007) have shown that male frogs feed throughout the breeding season, but *P. paradoxa* can be heard calling well before sunset (JRD, personal observation), so it may be some time since calling males have fed.

Table 1. Stomach content items from 36 *Pseudis paradoxa* from Trinidad, West Indies. Frequency (F) is the number of frogs containing a contents category. Number (N) is the total number of each category identified. The %S column shows the size contribution of each category to the total gut contents. Columns %N and %S give a comparison with the results of Teixeira et al. (2004); + and – refer to higher and lower representations in our study, respectively; A means absent from Teixeira et al. (2004). We have assumed that Hymenoptera in Teixeira et al. (2004) are ants, and that Odonata and Diptera are adults. Categories recorded in Teixeira et al. (2004) but absent from our sample are Isopoda (0.5%) and Gastropoda (1.5%).

Contents category	Frequency	% F	Number	% N	% S
Insecta					
Coleoptera (adults)	6	8.7	6	7.4 ⁻	3.8 ⁻
Diptera (adults)	9	13.0	14	17.3 ⁻	0.7 ⁻
(larvae)	4	5.8	5	6.2 ^A	2.5 ^A
Hemiptera Heteroptera	4	5.8	4	4.9 ⁺	1.1 ⁻
Homoptera	4	5.8	4	4.9 ⁻	0.3 ⁻
Hymenoptera ants	3	4.3	3	3.7 ⁺	1.0 ⁺
bees	1	1.4	1	1.2 ^A	<0.1 ^A
Lepidoptera (adults)	1	1.4	1	1.2 ^A	0.3 ^A
(larvae)	4	5.8	4	4.9 ⁺	10.6 ⁺
Odonata (adults)	6	8.7	8	9.9 ⁺	12.5 ⁺
(nymphs)	1	1.4	1	1.2 ^A	1.0 ^A
Orthoptera	8	11.6	9	11.1 ⁺	38.6 ⁺
Dictyoptera	3	4.3	3	3.7 ^A	23.5 ^A
Unidentified insect	1	1.4	1	1.2 ⁺	<0.1 ⁻
Arachnida					
Araneae	7	10.1	9	11.1 ⁺	3.3 ⁻
Acari	1	1.4	1	1.2 ^A	<0.1 ^A
Crustacea					
Decapoda	2	2.9	3	3.7 ^A	0.5 ^A
Annelida					
Hirudinea	2	2.9	2	2.5 ^A	<0.1 ^A
Other					
Plant fragments	2	2.9	2	2.5 ^A	<0.1 ^A

Table 1 shows the distribution of stomach contents across our sample, including a comparison between our results and those of Teixeira et al. (2004). Table 2 extends this comparison to three previous studies on the diet of adult *Pseudis*. The comparisons cannot be precise because of differences in methodology, but clear differences do emerge. Duré & Kehr (2001) and Garda et al. (2007) found rather low proportions of individuals with stomach contents; Duré & Kehr (2001) recorded the only individuals preying on vertebrates (amphibians, fish). Our Trinidad study provides the widest diversity of prey categories, despite representing one of the smallest samples. A common feature is that Diptera provide most prey numerically (except in one case) but not in terms of size (mass or estimated volume in the various studies), where small numbers of large grasshoppers, odonates, spiders or frogs predominate, except in the case of *Pseudis* (= *Lysapsus*) *limellum*, where Diptera are top or third in volume/mass in two studies.

Teixeira et al. (2004) and Duré & Kehr (2001) found a significant relationship between frog size and prey size in *P. paradoxa*, but not in *P. bolbodactyla* or *P. limellum*. In our case, Spearman rank correlations revealed positive but non-significant coefficients of correlation for the whole adult sample ($r_s=0.323$) as well as for males only

($r_s=0.361$), and a significant correlation in females ($r_s=0.536$, $P=0.003$), despite a small sample size ($n=7$). Inspection of the data for individual frogs showed that both large and small prey items were captured across the adult *P. paradoxa* size range. Lima (1998) showed strong relationships between frog size and prey size in a study of six species of Amazonian leaf litter frogs, in addition to prey type preferences in some species. Hirai (2002) also found evidence for an ontogenetic prey-size increase in *Rana nigromaculata*, an inhabitant of rice paddy fields, an environment quite similar to that utilized by *P. paradoxa*. The relative lack of such relationships in *Pseudis* and the wide size range of prey taken may reflect the prey availability, but could also result from *Pseudis*'s unusual life history, where post-metamorphic individuals change little in size (Downie et al., 2009a).

Teixeira et al. (2004) recorded 11 juveniles still in possession of a tail. They were unable to determine the sex of the juveniles, although Downie et al. (2009b) have shown that the gonads of the two sexes are distinguishable even in late tadpole stages. Unfortunately, Teixeira et al. (2004) do not comment specifically on juvenile gut contents. Our data show that juveniles can take prey of the same types as adults while retaining a substantial tail (one juvenile male with a 34.6 mm tail had consumed a 15 mm damselfly).

Table 2. Study and species comparison of *Pseudis* stomach contents. A: *P. paradoxa* (A), this study; B: *P. paradoxa* and *P. (= Lysapsus) limellum* data from Duré & Kehr (2001); C: *P. bolbodactyla* data from Teixeira et al. (2004); D: *P. bolbodactyla* data from Brandão et al. (2003); E: *P. (= Lysapsus) limellum* data from Garda et al. (2007). Prey types given to order level where possible: Duré & Kehr (2001) specified “larvae” as one prey type, so all larvae in the other studies were treated as a single prey type in this comparison: “larvae” did not rank in the top three by number or volume/mass for any *Pseudis* species.

Species	Sample size	% with prey in stomach	Prey types	Top three prey types, in descending order, by:	
				Number	Volume/mass
A: <i>P. paradoxa</i>	36	86.1	15	Diptera Orthoptera Araneae	Orthoptera Dictyoptera Odonata
B: <i>P. paradoxa</i>	50	42.0	13	Diptera Coleoptera Hemiptera	Amphibia Coleoptera Hymenoptera
B: <i>P. limellum</i>	75	61.3	13	Diptera Acari Hymenoptera	Diptera Osteichthyes Orthoptera
C: <i>P. bolbodactyla</i>	59	94.9	12	Diptera Homoptera Coleoptera	Araneae Coleoptera Diptera
D: <i>P. bolbodactyla</i>	18	77.8	10	Heteroptera Coleoptera Orthoptera	Orthoptera Hymenoptera Araneae
E: <i>P. limellum</i>	172	52.9	13	Diptera Homoptera Odonata	Odonata Araneae Diptera

A question hardly addressed in the previous studies is whether *Pseudis* feed solely on terrestrial/aerial prey, or whether they can also capture prey under water, as pipid frogs do (Tinsley et al., 1996). Duré & Kehr (2001) reported seeing *Pseudis* foraging “from the leaves of floating aquatic plants”. Teixeira et al. (2004) noted that prey found in *Pseudis* stomachs could be seen on the leaves and stems of emergent vegetation: they also collected one of their frogs out of water.

In Trinidad, we found *P. paradoxa* in the Nariva swamp, a large drainage basin that is mainly freshwater but influenced by saltwater on its eastern side (Bacon, 1990), in permanent ponds of a fish-farm (Bamboo Grove), or in temporary ponds at the margins of longer-term swamps (Columbus Bay). Frogs were generally found around the margins where there was dense emergent and floating vegetation, and most of the prey items we identified were insects and arachnids characteristic of emergent or terrestrial vegetation. However, in our sample 19 prey items (23% of the total) are aquatic or have aquatic life stages: two leeches, three crabs, one damselfly nymph, one gerrid bug, four dytiscid beetles and five fly larvae, one chironomid and four oxycerines. Of these, gerrids live on the surface film and the leeches may be inadvertent prey, originally attached to something else. The crabs

could be aquatic, although Trinidad has several species of tree-climbing and freshwater/terrestrial crabs (Hagen, 1977). The *P. paradoxa* female whose stomach contained two crabs was captured on a low branch of a mangrove tree where Nariva swamp exits into a tidal river. Although some of the prey with aquatic life stages may have been captured above the water surface, a small number – the damselfly nymph and the fly larvae – suggest that *P. paradoxa* is capable of predation under water.

In conclusion, we have confirmed and extended the generalist nature of foraging in *P. paradoxa*: these frogs capture prey over a wide size and taxonomic range; ours is the first report of crab-eating. In addition, our data suggest that *P. paradoxa* captures some, though a small proportion, of its food from under the water. We have also shown that prey capture begins before metamorphosis is complete.

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