

The paradoxical frog *Pseudis paradoxa*: larval habitat, growth and metamorphosis

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The genus *Pseudis* is unique amongst anuran amphibians in that body growth occurs mostly or entirely in the larval phase, with huge tadpoles metamorphosing into adult-sized frogs. Tadpole growth rate, metamorphic duration and tadpole habitat were studied in the paradoxical frog *Pseudis paradoxa* in Trinidad, West Indies, in order to assess the factors which may have led to the evolution of this unique life history. Growth rate was shown to be similar to other tropical tadpoles: *Pseudis* simply continued to grow, rather than progress to metamorphosis. Metamorphic duration fitted well with a model based on tadpole size. Sexual dimorphism in tadpole size was apparent, with females larger than males at metamorphosis. *Pseudis* tadpoles initially possess highly cryptic patterning, which is lost as they grow larger. The costs and benefits of continued growth in the larval phase in a permanent tropical swamp habitat are discussed in terms of potential predators and food availability to both *Pseudis* larvae and adults.

Key words: amphibian tadpoles, anurans, maturation, Trinidad

INTRODUCTION

The paradoxical frog *Pseudis paradoxa* (Linnaeus, 1758) has long intrigued biologists on account of its unusual life history. In most anurans, tadpoles metamorphose at a relatively small size into juveniles, which then undergo considerable growth before reaching adulthood. In *P. paradoxa*, however, larval growth produces enormous tadpoles which metamorphose into small frogs that may already be at adult size. Garman (1877) recounted the history of the frog's name; he was stimulated by an 1876 Brazilian report of a giant tadpole, which gave it the name *Batrachichthys*, i.e. frog-fish. When the enormous tadpoles were first discovered by scientists in Suriname in the mid 18th century, they concluded that development was retrograde: from small frog to larger tadpole to fish. The original name, *Rana piscis*, reflected this interpretation. Linnaeus realised that this view was in error, and renamed the species *Rana paradoxa*. In a later revision, Wagler (1830) devised the generic name *Pseudis* (a pseudo-paradox) as a reminder of how early observers had been misled. McDiarmid & Altig (1999) also describe and illustrate some of the history of this confusion.

The genus *Pseudis* currently contains eleven species (Frost, 2008), with the three species previously named as *Lysapsus* recently re-assigned as *Pseudis* (Aguiar et al., 2007). The phylogenetic relationships of these species have been controversial. Garda et al. (2004) reviewed the literature that placed *Pseudis* and *Lysapsus* as the sub-family Pseudinae within the family Hylidae, while noting that a relationship with the family Leptodactylidae has also been proposed. Faivovich et al.'s (2005) extensive review, combining morphological and molecular data,

confirmed the position of *Pseudis* and *Lysapsus* as closely related taxa within the sub-family Hylinae.

P. paradoxa is a widespread species occurring in Trinidad, Venezuela, the Guianas, Brazil, Argentina, Bolivia and Paraguay. Gallardo (1961) recognized six subspecies on morphological grounds, but these have not yet been subjected to genetic analysis. In Trinidad, where the work reported here was carried out, the subspecies is *P. paradoxa caribensis* Gallardo (Murphy, 1997).

Despite the intriguing nature of the life history of *Pseudis* there have been few detailed investigations into the ecology of the group. Emerson (1988) made a comparison of tadpole characteristics in *P. paradoxa*, *Lysapsus mantidactylus* and *Rana catesbeiana* (another species with large tadpoles) based on museum specimens, but we have not been able to find any previous detailed studies reporting tadpole growth and metamorphosis.

Kenny (1966, 1969, 1977) reported on the distribution and life history of *P. paradoxa* in Trinidad. Kenny's (1969) distribution map shows *P. paradoxa* occurring in the southwest and in the east at Nariva swamp, with an additional population in the Caroni river basin based on frogs that accidentally escaped from captivity in the Bamboo Grove fish farm. Earlier, Ditmars (1936) claimed that *P. paradoxa* occurred in Trinidad only in a single pond at Mayaro on the east coast, but it is unclear how reliable that claim is. Kenny (1969) gave a maximum tadpole length of 230 mm (with a body to total length ratio of 1:3) but did not give any data on variability in length at metamorphosis. At Bamboo Grove in 1960, following a period of dry following, the ponds were slowly flooded in May; frogs began calling once the water was deep enough (Kenny, 1966). The date of spawning was not known, but by July

P. paradoxa tadpoles were 35–55 mm long and by mid October they were 190–220 mm. Metamorphosis occurred from November to January. Kenny reported that frogs took on an adult appearance three days after forelimb emergence but that the long tail (lacking its fins) persisted for 10–14 days. Kenny concluded that in the field *P. paradoxa* took about six months to reach metamorphosis: he noted that this was surprisingly fast given the huge size of the tadpoles in comparison to other local species in similar conditions.

Kenny's observations were on a field population. He attempted to grow tadpoles in captivity but had no success (despite success with most other Trinidad species). Dixon et al. (1995) achieved very slow growth of *P. paradoxa* tadpoles from Argentina under laboratory conditions and Walls (1996), reporting in a herpetological hobbyist magazine, noted slow tadpole growth and poor success in achieving metamorphosis.

The life history of *Pseudis* appears contrary to some theories concerning tadpole growth and metamorphosis. For example, Wassersug (1975) suggested that the basic mode of nutrition in tadpoles ought to limit final size because as tadpoles grow larger, their ability to process food does not increase in proportion. Further, Werner (1986) noticed that in different amphibian groups, there is a positive relationship between tadpole size at metamorphosis and adult size. Werner used these data to derive a model based on relative growth and mortality rates of tadpoles and juveniles, but none of his cases approached the situation found in *Pseudis*, where snout–vent length in metamorphs and adults is essentially the same. An aim of the work reported here was to investigate growth rate and tadpole ecology in *Pseudis*, in an attempt to throw light on the unique life history of this species. In addition, these large tadpoles provide an extreme example of the relationship between metamorphic duration and tadpole size demonstrated by Downie et al. (2004) and we therefore measured metamorphic duration as a test of this relationship. In a companion paper, we discuss whether the giant tadpoles of *Pseudis* have any special anatomical features related to their size (Downie et al., 2009).

MATERIALS AND METHODS

Pseudis paradoxa tadpoles, metamorphs and adults were collected over a 21-year period (12 field seasons: June–September) at five main sites in Trinidad, West Indies, with occasional collections made elsewhere. Locations were chosen based on the presence of calling male *Pseudis* and on accessibility. The presence of adult *Pseudis* did not guarantee the presence of tadpoles. The sites were as follows:

Two sites were sampled at Nariva swamp. One was at the canal extending westward to Bush Bush island (10°24.3'N, 61°02'W): at the east end, the canal passes through mangroves, but opens soon into an extensive freshwater swamp. We accessed the canal by boat, and the collection sites were the canal itself and adjacent open pools fringed by dense aquatic vegetation. The other site was further south where the swamp extends close to the

Manzanilla Road, and we were able to access a set of pools just north of the Kernahan Road on foot (10°22.5'N, 61°01'W).

Bamboo Grove, located at Valsayn, just south of the Churchill–Roosevelt Highway (10°38'N, 61°25'W), has been sporadically active as a fish farm during the 21-year sampling period. It contains a set of large ponds on both sides of the access road. The ponds are partly rain-fed, but water is also pumped in to flood them to suitable depth whenever fish are being reared.

Columbus Bay in Icacos (10°05'N, 61°54.3'W) is at the southwestern tip of Trinidad. The beach is fringed by coconut palms. Behind the narrow fringe of palms to the right of the access road is a set of seasonal ponds that support populations of several frog species, including *P. paradoxa*.

Bonasse swamp (10°05.8'N, 61°51'W), also in southwest Trinidad, is 2 km east of the village of Bonasse in Cedros. The area sampled is on the north side of the Southern Main Road, which passes through swamps.

Tadpoles were captured during daylight hours. At Bamboo Grove and in the Nariva canal, it was possible to use a 3 m long seine net (5 mm mesh), but at other sites, the density of the aquatic vegetation made seining impracticable. At these sites, a robust handnet (0.5 mm mesh) with a long wooden handle was the most effective method. The water was generally too turbid and deep to allow tadpoles to be detected visually. On collection, tadpoles were transferred to a large bucket of swamp water and transported within 3 h to the University of West Indies, St Augustine.

Adults were captured at night and were located either visually (sitting on surface vegetation, e.g. lily pads, or floating in the water) or by call. We experimented with several methods of catching the frogs. They are extremely wary and immediately dive when disturbed. The most successful method was to approach a located frog very slowly, with lights off, until close enough to catch it with both hands. Adults were transported to the laboratory in 2 litre polythene tubs or polythene bags containing a shallow depth of swamp water and with small punched air-holes.

Tadpoles and adults used for morphometric investigations were killed by an overdose of anaesthetic (MS 222 or Benzocaine) as soon as possible after collection. They were then fixed in buffered neutral formalin or Bouin's fluid. For wet weights of whole animals, specimens were dried of surface fluid and weighed using an electronic balance accurate to 0.01 g or 0.001 g. Lengths were measured using callipers accurate to 0.1 mm; for very small specimens we used a dissecting microscope fitted with an eyepiece micrometer. In *P. paradoxa*, as tadpoles grow, the vent becomes a large structure often damaged during storage. Because the vent was not a reliable point to use for the end of the body, we used the base of the hindlimbs instead (snout–hindlimb length; SHL).

Tadpoles were staged after fixation using Gosner (1960). Since tadpoles range considerably in size over Gosner stages 26–28 (assessed mainly by hindlimb form), their lengths and weights were also noted on staging.

Metamorphs and adults were sexed by opening the abdomens of fixed specimens and examining the gonads.

Tadpoles for laboratory growth experiments were transferred to glass tanks in the laboratory, containing dechlorinated tap water mixed with swamp water. Airstones were located at both ends of the tanks. Laboratory air temperature was approximately 28 °C, and water temperature 26 °C.

Since tadpole numbers captured in any year or at any site were small, we have pooled results from all years and sites in our analysis. For most statistical analysis, Minitab Statistical Analysis Software, version 13.3, was used, with the exception of slope *t*-test comparisons of total length and SHL with mass regressions and growth rates of laboratory reared tadpoles, which were calculated by hand. Regression analysis was used to determine mass-length relationships of wild caught tadpoles and metamorphs. χ^2 analysis was used to determine differences in sex ratio of tadpoles and adults caught in the wild. We used the Mann-Whitney U-test for comparing sizes between males and females, as the data were not normally distributed.

RESULTS

General observations

Pseudis paradoxa tadpoles were found both in permanent swamps (Nariva canal) and in large ponds that may dry out in the dry season from December to May (Bamboo Grove fish farm; Columbus Bay). Although most of our observations were made in the rainy season during June–September, we were able to confirm that the Columbus Bay site does dry out (observed in May). The fish farm ponds are regularly allowed to dry out seasonally and lie fallow.

Tadpoles tended to be caught amongst dense vegetation (reeds, grasses) rather than in open water. Water at all sites was never clear: rather, these were nutrient-rich waters with high algal content.

The seasonally dry sites were fish-free, with the exception of the fish farm, where *P. paradoxa* was able to co-exist with some fish species. Fish of several species, mainly carnivorous (Phillip & Ramnarine, 2001) were abundant in the Nariva canal site, again indicating the capacity of *P. paradoxa* tadpoles to co-exist with fish. Other common potential predators present at all sites were cayman (*Caiman crocodilus*) and herons (JRD once saw a heron, species not identified, taking a large *P. paradoxa* tadpole from the swamp at Bonasse).

At Bamboo Grove fish farm, we once caught enough large tadpoles in a small seine net to suggest that tadpoles might be shoaling, but at all other sites and times, tadpoles were found singly and usually after considerable hand net effort. For example, at Bonasse swamp on one occasion, more than 30 casts with a hand net caught fewer than five *P. paradoxa* tadpoles, but many more (>30) *Scinax ruber* tadpoles.

Water depth at sites where we found tadpoles was generally in the range 50–80 cm. Water temperature (measured late morning at Bonasse swamp in July, a few centimetres below the surface) was around 28 °C.

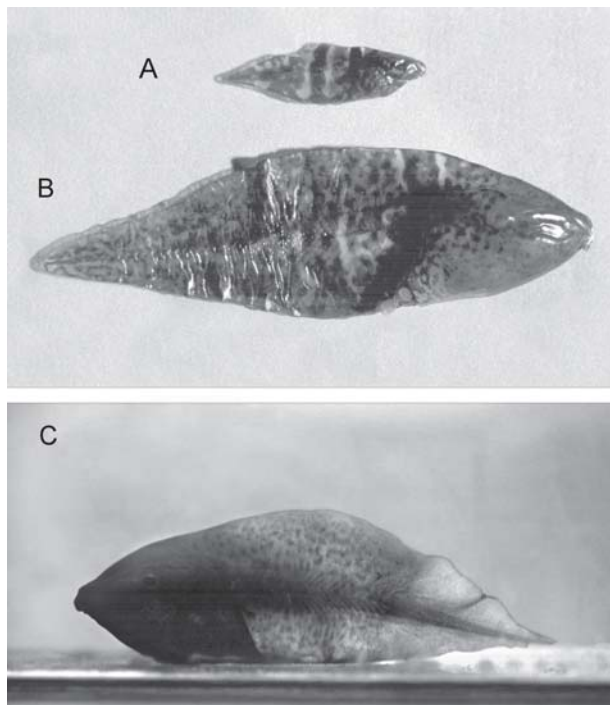


Fig. 1. Changing appearance of *Pseudis paradoxa* tadpoles with growth. A) 26 mm tadpole, showing strong vertical striping. B) 66 mm tadpole. C) 180 mm tadpole. A,B photographed out of water, anaesthetized. C photographed in water.

Although at some sites and on some occasions most tadpoles caught were of similar size, suggesting a single breeding episode, this was not always the case. For example, at Columbus Bay in early August 1996, we collected tadpoles at <1.0 g weight but also individuals in the middle of metamorphosis (weight >13.0 g) from the same pond. Similarly at Bonasse swamp on 21 July 2003 we collected tadpoles over the size range <0.1 g to 10.0 g. The only time we captured a pair in amplexus was in late June 1982, two weeks after heavy rains (though there had also been short wet spells in late April and mid May that year). The pair produced a large number of eggs but they were all infertile. At the same site, four weeks later, we caught tadpoles that were 1–2 g (stage 27). At Nariva canal, we collected late tadpoles and metamorphs in late September 1995, but no small tadpoles. The site was sampled monthly until February 1996 but no more tadpoles were ever found.

Although we did not make systematic observations on the behaviour of tadpoles kept in tanks in the laboratory, in general, when kept in clean water, tadpoles tended to remain rather static, lying at the bottom of the tank. Larger tadpoles spent time with their heads at the surface, possibly gulping air, and with the body hanging down almost vertically. In more turbid water, tadpoles were more active, swimming about at the bottom of the tank.

The appearance of tadpoles altered noticeably as they grew (Fig. 1). Very small tadpoles had strongly marked vertical stripes at the junction of the body and the anterior part of the tail with irregular dark blotches on the posterior

Table 1. Comparison of body sizes of late metamorphic (stages 45–46) *P. paradoxa* with adults caught in the field. Statistics (all comparisons using Mann-Whitney): b x d mass, $W=124.0, P=0.08$ NS; b x d length, $W=136.0, P=0.02$; a x c mass, $W=28.0, P=0.27$ NS; a x c length, $W=29.0, P=0.20$ NS; c x d mass, $W=39.0, P=1.00$ NS; c x d length, $W=45.0, P=0.17$ NS; a x b mass, $W=331.0, P=0.04$; a x b length, $W=349.0, P=0.004$. Summary: only significant differences are adult females longer than males; adult males heavier and longer than stage 45–46 males.

Sex and stage	n	Mean size \pm SD	
		Mass (g)	SVL(mm)
a) Male, st 45–46	10	17.8 \pm 5.9	44.9 \pm 3.2
b) Male, adult	19	21.2 \pm 6.2	50.9 \pm 4.8
c) Female, st 45–46	3	27.2 \pm 11.0	47.9 \pm 4.7
d) Female, adult	7	29.9 \pm 14.0	56.8 \pm 8.0

tail. The body was grey with dark blotches. As tadpoles grew, the striped pattern became less clear and had disappeared entirely in the largest tadpoles, which had dark grey bodies. The anterior tail had irregular dark blotches and the posterior tail was relatively lacking in pigmentation.

Tadpole sizes, growth and metamorphosis

Field-collected specimens, preserved after collection. Figure 2 shows log-log plots of the mass–length relationships of 40 field-collected *P. paradoxa* tadpoles ranging from stages 25–42. Only specimens with undamaged tails were included in the analysis. Figure 3 presents the same dataset arranged by stage. Masses ranged from 0.26 to 67.68 g (a 93.25 g tadpole was excluded because of damage to its tail) and total lengths from 28.3 to 188.2 mm. Figures 2 and 3 also show the equivalent data for male ($n=10$) and female ($n=3$) specimens near the end of metamorphosis (stages 45–46). The highly significant mass–length relationships shown in Figure 2 (along with the lack of difference in slope between the relationships for total length and SHL) indicate that *P. paradoxa* tadpoles maintained the same relative dimensions as they grew. We did not obtain any significant relationships between mass and length for metamorphs, but our sample size was small. Figure 3 demonstrates considerable increase in mass and length at the early stages, with a levelling off as tadpoles approached metamorphosis. Table 1 compares the sizes of male and female metamorphs with adults caught in the field. Females were larger than males; field-caught adults were larger than metamorphs, but not greatly so. Differences were rarely statistically significant, due to high variability and the small sample sizes of females. The most significant difference obtained was between adult and late metamorph males where we had the largest sample sizes. The differences may have been reduced by the inclusion of recent metamorphs in our “adult” sample, since once the tail has disappeared, there is no obvious way of assessing age. Although our

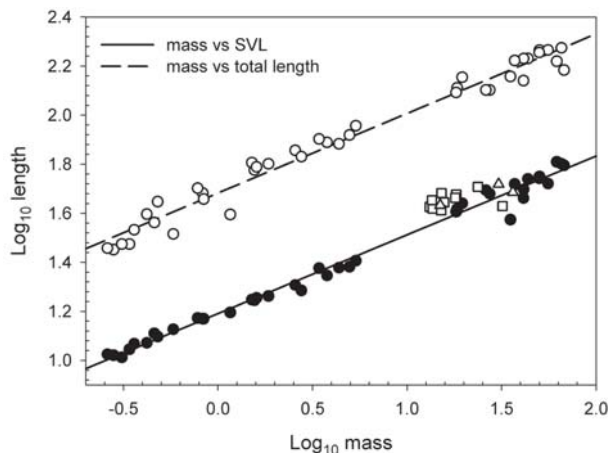


Fig. 2. Log-log plots of *P. paradoxa* tadpole and late metamorph (stages 45, 46) mass (g) against length (mm). Solid line, SHL; dashed line, total length. Closed circles = tadpole SHL; open circles = tadpole total length; squares = male metamorph SHL; triangles = female metamorph SVL. Regression line statistics: tadpole mass versus SHL, $y=1.19+0.32x, r^2=0.99, P<0.001$; tadpole mass versus total length, $y=1.68+0.32x, r^2=0.97, P<0.001$. Slopes of the two regression lines not significantly different: $t=0.368, P>0.05$.

sample of females at metamorphosis was small, they were already larger than male metamorphs.

The sex ratio of both adults and late metamorphs was biased towards males. This may not be surprising for adults, which were largely located by call. However, it was unexpected for metamorphs. Combining our two samples of metamorphs from single locations (Columbus Bay – five males to one female; Bonasse swamp, grown in

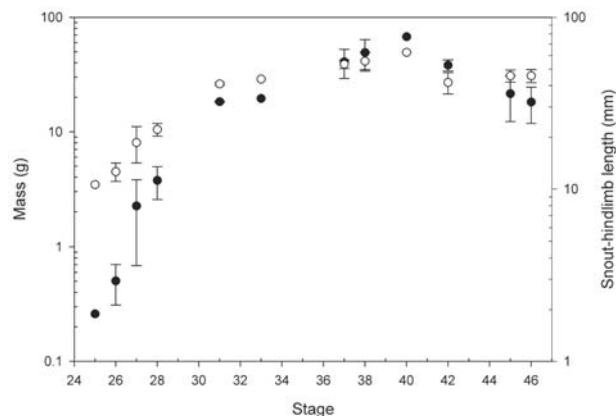


Fig. 3. Relationship between size and Gosner stage in *P. paradoxa* tadpoles and late metamorphs (stages 45, 46). Closed circles = mean mass (g) on logarithmic scale; open circles = mean SHL (mm); error bars are \pm SD.

Table 2. Data collected on laboratory-reared *P. paradoxa* metamorphs.

Tadpole number	Total length at forelimb emergence (mm)	SHL at completion (mm)	Completion date	Metamorphic duration (days)	Tail stump length (mm)	Sex
1	150.2	42.3	18 September	10	2.0	male
2	230.8	47.5	25 September	5	5.0	male
3	182.0	52.3	30 September	5	14.0	female
4	172.0	46.0	8 October	11	13.5	male
5	194.0	44.1	13 October	10	10.0	male

the laboratory – four males to one female) gives a sex ratio significantly different from 1:1 ($\chi^2=4.45$, $P<0.05$).

Field-collected specimens, grown in the laboratory. We made two attempts to grow *P. paradoxa* tadpoles in the laboratory, in 2002 and 2003. In 2002 eight tadpoles were grown in two $80 \times 40 \times 40$ cm tanks over a period of 12 days using initially clean dechlorinated water at a depth of 30 cm. They achieved length increases of 5.9–46.7%

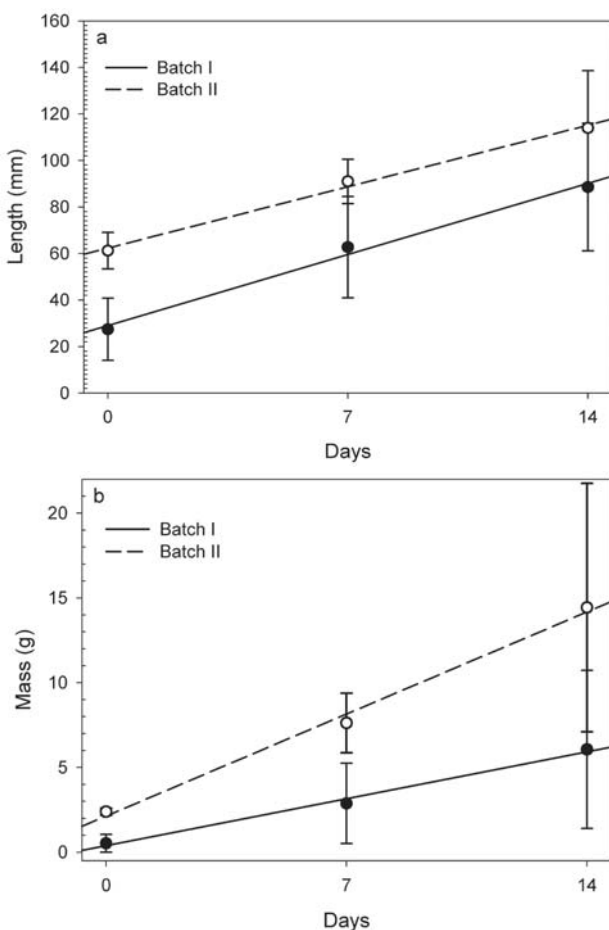


Fig. 4. Growth rates of two batches (I = small initial size; II = medium initial size) of *P. paradoxa* tadpoles grown in the laboratory. A) Mean total length (mm); B) mean mass (g). Error bars are \pm SD. For mass, slopes not significantly different ($t=1.92$, $P>0.05$). For total length, slopes not significantly different ($t=0.51$, $P>0.05$). Closed circles = batch I, open circles = batch II.

and weight increases of 28.9–189.2% over this period. However, we did experience some problems and one died and the others were in poor condition at the end.

We fed the tadpoles on a mixture of coarsely chopped cucumber (suggestion of Andrew Stevenson, pers. comm.), chopped lettuce and fish food flakes so that food was always available. The water rapidly became very cloudy and full of sediment, and we changed it at about four-day intervals. Despite this, some tadpoles developed pale patches on their skin and became listless, suggesting poor health.

In 2003, we allocated 13 tadpoles collected at Bonasse swamp in mid July among three $160 \times 40 \times 40$ cm tanks: a single large (10.6 g) tadpole in one; five medium size (2 g) and seven small (0.02–1.2 g) in the others. Each tank was provided with 2–3 cm of swamp water supplemented with dechlorinated tap water to a total depth of about 30 cm. We used fish food flakes (both high-protein flakes and algal pellets) and chopped cucumber as food. Although the water was changed frequently several tadpoles died. However, five were reared through to metamorphosis from small initial sizes and the recorded growth rates were very substantial. Figure 4 shows the length and wet weight increases recorded over a 14-day period from soon after collection, for the small and medium initial-size batches. Growth rates for the two batches were not significantly different.

The tadpoles that eventually reached metamorphosis were in the weight range of 1–2 g on collection (21 July), probably within 3–4 weeks of spawning based on when the rainy season started that year. The five that completed metamorphosis did so from 18 September to 13 October (i.e. 12–16 weeks after spawning). Table 2 shows data collected on these metamorphosing individuals. Note that some of the specimens still had significant tail stumps when killed at the end of the experiment. The metamorphic durations recorded in Table 2 are therefore slight underestimates.

DISCUSSION

Tadpole behaviour and appearance

Kenny (1966, 1969) reported that at small sizes, *P. paradoxa* tadpoles lived among the vegetation around the edges of water bodies; at larger sizes, they spent more time in mid water and could often be found hanging vertically from the surface, possibly feeding on surface food. Kenny's (1969) figures of tadpoles at small and large sizes are similar to those we show in Figure 2. There have been few reports on tadpole habitat choice, especially where

Table 3. Estimates of time that would be taken to reach *P. paradoxa* size at metamorphosis, based on measured growth rates of two Trinidad species. Graphical length extrapolations linear; weight extrapolations based on \log_{10} . Data on *M. trinitatis* from Downie et al. (2005); *L. fuscus* from Downie et al. (2004) and Downie & Weir (1997).

Species	Initial weight (mg)	Initial length (mm)	Stage 42 weight (mg)	Stage 42 length (mm)	Time to stage 42 (days)	Time to <i>Pseudis</i> stage 42 weight (days)	Time to <i>Pseudis</i> stage 42 length (days)
<i>Mannophryne trinitatis</i>	37	15.3	352	35.0	29.7	103	243
<i>Leptodactylus fuscus</i>	6.6	8.6	240	34.2	19.6	49	137

tadpoles undergo considerable size change. Smith & Doupnik (2005) found that large tadpoles of the American bullfrog *Rana catesbeiana* preferred a vegetated substrate to open water, but report that earlier stage, smaller tadpoles did not show this preference. They suggest that large bullfrog tadpoles are relatively immune to predation by the aquatic invertebrate predators common among pond margin vegetation. Kopp et al. (2006) report that vegetation reduced predation rate by water bugs in two tadpole species. In ponds where *Pseudis* are found, dragonfly and beetle larvae are common among the vegetation at pond margins (JRD, pers. obs.). The vertical striping of the tadpole's body may act as effective camouflage against visual predators in such a habitat (Ruxton et al., 2004). The loss of this patterning at larger sizes may reflect reduced vulnerability to predators, though the larger tadpoles then become prey for vertebrate predators such as herons and cayman. A study of their escape responses is needed to test how well they can evade these larger predators.

Tadpole dimensions, growth rate and metamorphic duration

Bokermann (1967) reported a Brazilian *P. paradoxa* specimen 270 mm long with a damaged tail and suggested that its full length could have been 320–330 mm. De La Riva (1999) reported on a Bolivian specimen 260 mm long. The longest *P. paradoxa* tadpole Emerson (1988) found in museum collections (from 71 specimens, collected in a variety of countries) was 230.5 mm. None of our field-collected specimens reached these very large sizes, but one of our laboratory-reared tadpoles metamorphosed at a maximum length of 230.8 mm, about the same as the maximum Kenny (1969) reported from Trinidad. It is clear that, as in many other anuran species, size at metamorphosis is highly variable (Wilbur & Collins, 1973).

A key question about *P. paradoxa* tadpoles is: do they exhibit exceptional growth rates? This is difficult to answer categorically because tadpole growth rate varies with species, temperature, density, food availability, etc. The only previous information on *Pseudis* growth is Kenny's (1969) somewhat anecdotal account, and Emerson (1988) felt that the figures did not indicate exceptional growth rates. To eliminate some of the confounding variables, we compared the *P. paradoxa* growth rate we measured with two other species, *Leptodactylus fuscus*

and *Mannophryne trinitatis* (Table 3) reared under similar laboratory conditions (Downie & Weir, 1997; Downie et al., 2005). We derived linear equations for growth rate in the two species, then extrapolated these to find the time it would take to reach *Pseudis* metamorphic size. Given our estimate for *Pseudis* larval duration of 12–16 weeks (see Results), the extrapolations do not suggest that *Pseudis* growth rate is exceptional.

We also investigated whether metamorphic duration in *P. paradoxa* is exceptional. Kenny (1969) reported that “while the fins are resorbed completely within three or four days, the massive myotomes persist for up to two weeks”, but he did not record precise details on individuals. We found that our laboratory-reared tadpoles took 5–11 days (mean 8.2) to metamorphose completely. Cais (1982), as cited by de Souza & Kuribara (2006), reported metamorphic duration of about 10 days. Downie et al. (2004) compared metamorphic durations in 14 species of anurans from five families with the frogs kept under conditions similar to those used here for *P. paradoxa*. For most species, they were able to derive significant relationships between metamorphic duration and body size (mass, snout–vent length, tail length). Downie et al. (2004) used actual body masses, rather than \log_{10} mass: this was appropriate for the fairly small mass range in their sample, but not for the much larger mass reached by *P. paradoxa*. Here we excluded the mass–duration relationship and used the data in Table 2 to test whether *P. paradoxa* metamorphic durations fit with the relationships Downie et al. (2004) derived for tail length and SVL (Table 4). The durations we measured for *P. paradoxa* are very close to expectation based on SVL, but lower than expected for the relationship based on tail length. The commonsense conclusion that metamorphosis should take longer in larger tadpoles is therefore confirmed in the largest tadpole known.

Sexual dimorphism and sex determination

A key result of this study is that males and females were dimorphic in size at metamorphosis. After metamorphosis, frogs grew slightly (SVL 13.3% for males, 18.6% for females), but essentially maintained the difference present at the end of metamorphosis (females longer than males: 6.7% at metamorphosis, 11.6% as adults, SVL). We do not have data to test whether the differences in size at metamorphosis were the result of differences in growth

Table 4. Comparison of actual and predicted metamorphic duration in *P. paradoxa*. Predictions using relationships derived in Downie *et al.* (2004). Length and metamorphic duration data from Table 2. Note that actual metamorphic durations are underestimates, since tail stumps were still present. SHL data used are derived from metamorphic completion since data were not available from initiation.

Duration (y) and length (x) relationship	Mean <i>Pseudis</i> length at start of metamorphosis (mm)	Predicted mean metamorphic duration (days)	Actual mean metamorphic duration (days)
a) SHL $y=0.18x+0.96$	46.4	9.3	8.2
b) Tail $y=0.135x+0.42$	139.4	19.2	8.2

rate or growth period or both, but such data would clearly be of interest. Because of the long period of growth between metamorphosis and maturation in other anurans, few studies have looked for evidence of sexual dimorphism at metamorphosis. In one such study, Vorburger (2001) found no difference in either size at metamorphosis or time to reach metamorphosis between male and female *Rana ridibunda*. Emerson (1988) noticed that there appeared to be two size classes amongst her sample of larger *P. paradoxa* tadpoles, but she did not examine them internally.

CONCLUSION

Werner's (1986) analysis of size at metamorphosis in three anuran families showed a positive correlation between metamorphic size and adult size in ranids and hylids, though little relationship in bufonids where metamorphic size is always small. He suggested that the optimal size at metamorphosis was based on the balance between two general factors: aquatic versus terrestrial growth rate, and aquatic versus terrestrial mortality rate. However, metamorphic size in *Pseudis* would be an extreme outlier in Werner's analysis. This could be partly explained by *Pseudis* being a fully aquatic frog in the adult stage, but other fully aquatic adult frogs, such as the pipids, have conventional life histories, with significant post-metamorphic growth prior to maturity. How can we explain the radical shift in life-history pattern found in *Pseudis*?

Pseudis tadpole growth rate does not appear to be exceptionally fast, but neither is there any decrease in growth with size. Most of the *Pseudis* sites we found were in permanent swamps, so there is rarely any risk of the habitat drying up, even during the relatively long larval life span. One of our sites was more temporary, but located at the edge of a more permanent swamp: *Pseudis* may have colonized when the permanent swamp extended after heavy rains. We had no evidence that larval period was likely to be limited by desiccation.

The main problem for anuran larvae in permanent swamps ought to be predation by invertebrates at small tadpole size and by vertebrates when larger. The cryptic patterning of the larvae at small sizes suggests that predation is indeed a factor that they have partly adapted to. A study of escape responses in larger tadpoles is needed to determine how well they are able to evade large predators:

the general murkiness of swamp water may protect them against visual predators such as herons and cayman.

A possible advantage of the *Pseudis* life-history pattern is that it allows relatively rapid attainment of maturity. As Emerson (1988) noted, we need a suitable comparator to determine this. Downie *et al.* (2009) found that at metamorphosis, *Pseudis* males are already producing sperm and that females have ova at late pre-vitellogenic stages. Attainment of maturation in a 60–70 mm snout–vent length frog after 12–16 weeks would be very rapid by temperate region standards, but we lack data for tropical anurans. Two Trinidad species of comparable adult sizes are *Hyla geographica* and *Hyla crepitans* (Murphy, 1997). It would be of interest to assess their post-metamorphic growth rates in the field.

Another factor might be adult feeding rates. Werner's (1986) model suggests that once anurans are of adequate size, their growth rate on land surpasses that in the water because of the higher quality of their food. Published reports on adult *Pseudis* diet (e.g. Duré & Kehr, 2001; Teixeira *et al.*, 2004) show that they feed mainly on adult insects out of the water rather than on aquatic prey as pipids do (Tinsley *et al.*, 1996). This could possibly restrict their growth rate as adults, shifting the life-history balance to the larval phase.

Finally, what has been the physiological mechanism of the shift to late, large-size metamorphosis? Emerson (1988) suggested that certain features of *Pseudis* tadpoles could be explained by enhanced secretion of the hormone prolactin. She had no direct evidence for this suggestion and the hypothesis of prolactin as an antagonist of thyroid hormone has fallen out of favour (Rose, 2005). Since each anuran species has a characteristic range of size at metamorphosis this is a character subject to selection, operating on the size at which the hormonal mechanism stimulating transformation is activated. In *Pseudis*, we suggest a heterochronic process that would delay such activation. However, as Downie *et al.* (2009) have shown, *Pseudis* tadpoles are not simply large conventional tadpoles. The development of various organ systems has been altered, concomitant with the delay in metamorphosis.

We set out to throw light on the unusual life history of the paradoxical frog. This and the companion paper have revealed some intriguing details, but more work will need to be done to elucidate the ecological and evolutionary factors which have led to this set of features.

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