Development and demography of Phasmahyla jandaia (Bokermann and Sazima, 1978) (Anura, Hylidae) tadpoles in an Atlantic Forest site, southeastern Brazil

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Mortality rates are often high during the anuran tadpole stage, making demographic parameters in this phase of their life cycle important to the understanding of population demography. Nevertheless, information on mortality rates or population size is lacking for most Brazilian anurans. Herein we report on the demographic parameters of *Phasmahyla jandaia* (Hylidae) during the larval stage, including number of individuals through time, mortality rates and time of recruitment. Tadpole recruitment occurred year-round, although froglet recruitment to the terrestrial habitat was restricted to the warm, rainy season. This trend seems to result in high plasticity of the tadpole developmental period. Mortality rates decreased with advancing tadpole stage, totalling 77% during the whole aquatic phase. Survivorship can be regarded as intermediate compared with other anurans for which data are available, and is in accordance with a high investment in egg size and the low number of eggs laid by *P. jandaia*.

Keywords: Anura; *Phasmahyla jandaia*; tadpole survivorship; tadpole development

Introduction

In the 1960s, when Turner (1962) reviewed the literature on anuran demography, tadpole survival rates were unknown and their estimation was a major challenge for tadpole demographic studies. Afterwards, some researchers (e.g. Tinsley and Tocque 1995; Hels 2002; Loman and Lardner 2006) successfully investigated parameters related to tadpole demography, such as tadpole survivorship and time until metamorphosis, but detailed information on developmental dynamics across several larval stages was not provided. Nevertheless, Werner (1986) recognized the importance of studying properties of tadpole growth in general, and among developmental stages in particular, to understand the role of the aquatic phase (often regarded as a "growth phase") in anuran complex life cycles.

Most studies conducted on frog population dynamics indicate that the greatest mortality occurs in the initial phases of the life cycle (eggs and larvae; e.g. Tinsley and Tocque 1995; Hels 2002), mainly as the result of predation or drying of ephemeral aquatic breeding sites (Alford 1999), but also through density-dependent factors (Hels 2002). Although available data stress the importance of studying frog population dynamics during the tadpole stage, most studies on anuran demography

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still focus on the adult phase (Sinsch et al. 2001; Leskovar et al. 2006; Lu et al. 2006; Pellet et al. 2006).

In the Neotropics, even fundamental natural history attributes are poorly known for many anuran species, such as breeding period, duration of the tadpole stage, time of metamorphosis and recruitment of froglets to the terrestrial population (Duellman and Trueb 1994). This is the case for members of the genus *Phasmahyla* Cruz, 1990, a Brazilian Atlantic Forest Domain (*sensu* Ab'Saber 1977) endemic.

Phasmahyla is a small genus of the Phyllomedusinae, comprising four species: *P. guttata* (Lutz, 1924), *P. cochranae* (Bokermann, 1966), *P. jandaia* (Bokermann and Sazima, 1978) and *P. exilis* (Cruz, 1980). Their egg clutches are laid and wrapped by the frogs in the leaves of the marginal vegetation of permanent streams bordered by forest, overhanging the water (Bokermann and Sazima 1978). The tadpoles are neustonic and have umbelliform oral discs (*sensu* Altig and McDiarmid 1999), presumably adapted to feed at the water surface (Cruz 1982, 1990).

The species *P. jandaia* is particularly poorly known because it has been recorded at only a few localities of the Espinhaço mountain range in the state of Minas Gerais, southeastern Brazil (Bokermann and Sazima 1978; Caramaschi et al. 2000; Nascimento et al. 2005; Canelas and Bertolucci 2007; Leite et al. 2008). There are no data on tadpole demography and no consensus on reproductive phenology of adults of *P. jandaia*, as is the case for many Brazilian anurans (Eterovick et al. 2005). Knowledge of the natural history and population dynamics of this species, especially with its restricted distribution, will aid a better understanding of its needs and potential conservation strategies. Studies of population dynamics are especially critical at this time of worldwide decline in amphibian populations, as noted in recent studies (Bell et al. 2004; Pellet et al. 2006). Studies of population dynamics can provide information which will help to differentiate between natural population fluctuations and serious declines.

We studied a population of *P. jandaia* with emphasis on the larval stages, to determine (1) how the total number of tadpoles varies temporally, (2) the periods of recruitment of new tadpoles to the population throughout the year, (3) the annual period of metamorphosis and recruitment of froglets to the terrestrial habitat, and (4) the survivorship of nine out of ten proposed developmental classes from hatching until conclusion of metamorphosis.

Material and methods

Study site

The study was conducted in a pool of a permanent tributary of Fechos stream (20°04′22″S, 43°57′49″W, ca. 1200 m altitude) at the Estação Ecológica (ecological station) of Fechos, Nova Lima municipality, Minas Gerais state, Brazil. The ecological station encompasses 877 ha and is located on the northeastern slope of the Serra da Moeda, within a region known as Quadrilátero Ferrífero, in the southern portion of the Espinhaço mountain range. The Espinhaço has already been recognized as a priority area for amphibian conservation in the state of Minas Gerais, because it is species rich and has high threat levels (Drummond et al. 2005). Leite et al. (2008) reviewed available information on the anurans of the Espinhaço mountain range. The headwaters of Fechos stream are located in an Atlantic forest
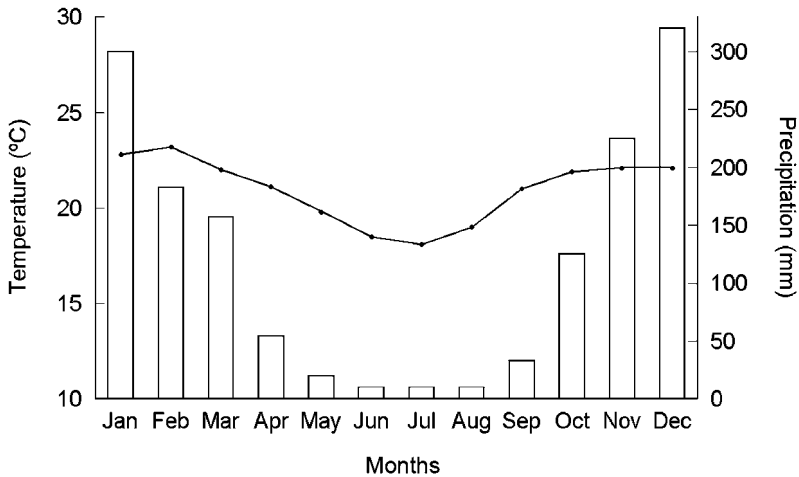
Figure 1. Mean monthly air temperature (°C) (●) mean monthly rainfall (mm) (▲) from 1960 to 1991 at Belo Horizonte, Minas Gerais state, southeastern Brazil (data from the 5° Distrito de Meteorologia de Belo Horizonte).

vegetation formation characterized by mountain slopes and montane meadows on "canga" (a particular flora adapted to iron-rich soils) in the highest regions. The climate in the area is seasonal with a marked dry season from April to September and a rainy season from October to March. Mean annual rainfall is about 1500 mm, and annual mean temperature is approximately 21.5°C. Mean temperature in the coldest month (July) reaches 18.1°C, and it reaches 23.2°C in the hottest month of February (Figure 1; 5° Distrito de Meteorologia de Belo Horizonte, available at: http://www.inmet.gov.br, consulted 16 March 2006).

The pool where we conducted the study is formed by a small concrete dam and has a surface area of about 9 m² (constant over the year) with depths varying from a few cm up to 90 cm. The bottom is composed of mud, pebbles, stones and some fallen branches. Marginal vegetation is composed mainly of giant ferns (*Cyathea delgadii*, Cyatheaceae), ferns (*Blachnum brasiliensis*, Blachnaceae) and "jaborandi" (*Piper* sp., Piperaceae). Immediately below the dam, all the water of the stream is directed into pipes for human use. The pool forms an isolated habitat as careful inspection showed that there are no other pools upstream, and because still pools are the only known suitable habitat for the development of the tadpoles of *P. jandaia*, it is highly unlikely that *P. jandaia* tadpoles occur outside the studied pool. Additionally, tadpoles present in the pool are unable to disperse upstream, because of the strong current, or downstream, because of the physical barrier imposed by the dam. Occasional floods of the dam would result in the death of tadpoles eventually carried downstream into the pipes.

The stream has retained most of its natural features, except for the presence of the dam, which was built in the 1980s. The only disturbance at the site is the monitoring of the water level and dam by the workers of the ecological station, which involves opening the dam and removing excess sediment once a year. This whole procedure is done within a day, and occurred twice during our study (in September 2002 and September 2005). We would remove the tadpoles from the pool before the procedure, which lasted less than an hour in these two instances, returning

them afterwards (the methodology used for tadpole removal was the same used for tadpole sampling; see next section). Conducted in this way, the sediment removal procedure did not seem to cause noticeable alterations in the *P. jandaia* tadpole population, because we did not notice subsequent changes in the number of tadpoles. Additionally, the procedure did not prevent the reproduction of *P. jandaia*, because we observed calling males even on the following night.

The stream constitutes a typical habitat for this frog (small, permanent forest stream), being similar to other sites where we recorded populations of the same species (breeding adults and tadpoles), all at streams surrounded by forest, such as in Serra do Cipó (19°15′26″S, 43°32′37″W), Serra da Moeda (20°24′19.0″S, 43°51′04.3″W), and Serra de Ouro Branco (20°28′16.1″S, 43°39′02.5″W). However, in these other localities where we recorded tadpoles of *P. jandaia*, they were rare and hard to locate. The presence of the dam at our study site created a unique situation in which we were able to study the larval stage of a population of *P. jandaia*, following the same cohorts of tadpoles month after month, which would not be feasible in other streams. However, this population differed in one aspect from populations at pristine streams: the dam constituted an artificial mortality source for tadpoles during heavy rains, when the water level would rise over it and carry the neustonic tadpoles into pipes, where they would die. Nevertheless, these events were occasional, and we could still collect important data on tadpole demography which could not be easily collected in pristine habitats.

Sampling methods

From June 2002 to May 2003, and from August 2004 to November 2005, we carefully captured all *P. jandaia* tadpoles present in the study pool with dip nets every 2 weeks, during the day. We counted and classified all the tadpoles captured according to developmental stage (*sensu* Gosner 1960) and kept them in a 40-litre plastic bucket containing water from the stream until all the tadpoles had been captured, to avoid recording the same individual twice. The whole sampling procedure could last up to 3 hours, after which we returned the tadpoles to the pool with no apparent damage.

For analysis we grouped developmental free-swimming stages (*sensu* Gosner 1960) of *P. jandaia* tadpoles into 10 classes: I, Stage 25; II, Stages 26–27; III, Stages 28–29; IV, Stages 30–31, V, Stages 32–33; VI, Stages 34–35; VII, Stages 36–37; VIII, Stages 38–39; IX, Stages 40–41; X, Stage 42. All classes were supposedly equally likely to be sampled by our method, except for class X, during which tadpoles start to leave the water and were probably under-sampled. Hence, we did not consider Class X in the estimates of most demographic parameters, for which we considered Class IX as the last completely aquatic tadpole class.

The increase in the number of *P. jandaia* tadpoles present in each class between samplings (2-week intervals) allowed us to detect recruitment of new individuals into a developmental class in several instances. For this purpose, we used the formula $r_{C(t)} = n_{C(t)} - n_{C(t-1)}$, where $r_{C(t)}$ corresponds to the minimum number of individuals that could be considered as recruited into a given class (C) in the time interval t; $n_{C(t)}$ is the number of individuals (n) present in class C at time t, and $n_{C(t-1)}$ is the number (n) of individuals present in the same class (C) at time t–1. The time interval from t–1 to t corresponds to the interval between samples (15 days).

We could only detect recruitment into a class when the number of individuals at time *t* was greater than at time *t*–1 so we worked on the most conservative scenario of minimum recruitment. Individuals may achieve a given developmental class by coming to it from the previous class or by remaining in the class from time *t*–1 to time *t*; these two cases could not be distinguished without confining or marking tadpoles. If a given number of tadpoles develop from a given class (C) into the following class (C+1) but the same number of tadpoles develop from the previous class (C–1) into C, while others remain in their original classes, the changes in class C would be unnoticed by our method. Nevertheless, our results allowed the recognition of large cohorts that could be followed during the whole developmental process, indicating that developmental asynchrony within cohorts may not be large enough to mask the general developmental pattern.

To detect more precisely the recruitment of new *P. jandaia* individuals into the population (recently hatched larvae) we divided Class I (stage 25 of Gosner 1960) into two different Sub-classes, I.1 and I.2. The first included only the smallest tadpoles measuring less than 2.0 cm, which we considered to be those most likely to have hatched in the previous 15 days (that is, since the last sampling). The second included the remaining tadpoles in Stage 25. We considered the increase in number of individuals in Sub-class I.1 as recruitment of new tadpoles to the population, which we could detect even when the whole Class I was reduced from time *t*–1 to time *t*. This subdivision made the detection of new hatchings more accurate because of the relatively long duration of Gosner's Stage 25 (Gosner 1960), when growth is more noticeable than development.

We assumed the occurrence of successful breeding (recruitment of new larvae into the population) when either Class I.1 or I had at least 10 individuals more at time *t* than at time *t*–1, that is, $r_{I(t)}$ and/or $r_{I.1(t)} \geqslant 10$. When both the class and the subclass had an increase of 10 or more individuals, the largest number was considered as the number of new tadpoles in the population.

We estimated the total number of tadpoles of *P. jandaia* entering each developmental class (I–IX) during the study by summing the positive $r_{C(t)}$ values of all samples in which they were obtained. We used these data to estimate survival and mortality rates. To make this estimation, we assumed class recruitment and mortality rates to be constant over time.

We estimated the survival probability in a given developmental class of *P. jandaia* tadpoles by dividing the number of individuals recruited into a class during the whole study by the number of tadpoles recruited into the population (added to Class I or Subclass I.1 from time *t*–1 to time *t*) during the whole study. Tadpole recruitment did not occur in classes other than Class I because there were no suitable breeding habitats upstream and a careful search confirmed the absence of egg clutches or tadpoles at any portion of the stream other than the studied pool. We estimated survival rates of *P. jandaia* tadpoles among classes by dividing the number of individuals entering to a given class C during the whole study by the number of individuals recruited to class C–1 during the whole study. We estimated mortality at class C–1 by subtracting its survival rate from 1.0. We present quantitative data as mean ($\pm$SD; range; sample size).

Results

The number of tadpoles of *P. jandaia* captured per sampling day varied from 0 to 316, in 52 sampling days distributed over 27 months. The absence of tadpoles in the second sampling conducted in January, both samplings conducted in February 2003
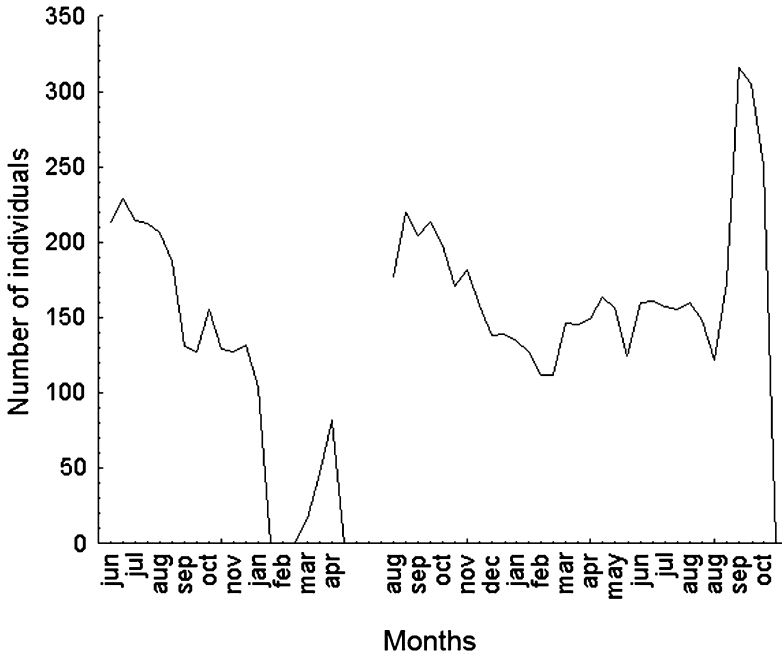
Figure 2. Total number of individuals of *Phasmahyla jandaia* in the pool formed by the dam of Estação Ecológica de Fechos, Nova Lima (Minas Gerais, southeastern Brazil), from June 2002 to May 2003 (Jun to Apr on *x*-axis) and from August 2004 to November 2005 (Aug to Oct on *x*-axis). Each mark on the *x*-axis corresponds to one sampling, and samplings were separated by 15 days. The corresponding month is provided every two samplings.

and the sampling conducted in November 2005 was supposedly caused by storms that flooded the dam, carrying all the tadpoles present into the pipes and consequently killing them. Other representative reductions in the number of tadpoles (of about 50 individuals) were found on two occasions (September 2002 and October 2005) when storms also caused flooding of the dam, although in smaller proportions (Figure 2). We detected smaller decreases in the larval segment of the population (up to 32 tadpoles) in other instances ($n=18$), nevertheless, these could not be related to any specific causal factor and occurred in both the rainy and the dry seasons.

Excluding samplings with no tadpoles, and the following periods when the population was being re-established (from January to May 2003 and November 2005), the mean number of tadpoles present was 169 individuals per sample (± 47; 104–316; $n=44$ samplings). We recorded the largest numbers of tadpoles in June and July 2002, from September to October 2004, and in September and October 2005 (the largest number recorded was in September 2005). We recorded the smallest numbers of tadpoles from September to December 2002, from March to April 2003, and in February 2005 (Figure 2).

The increase in number of individuals in Class I or Sub-class I.1 between consecutive samples indicated the occurrence of at least 17 successful reproductive events, represented by the recruitment of new tadpoles into the population. Six of these reproductive events occurred in 2002–2003, and 11 in 2004–2005, and they occurred in both the rainy and the dry seasons (Figure 3).
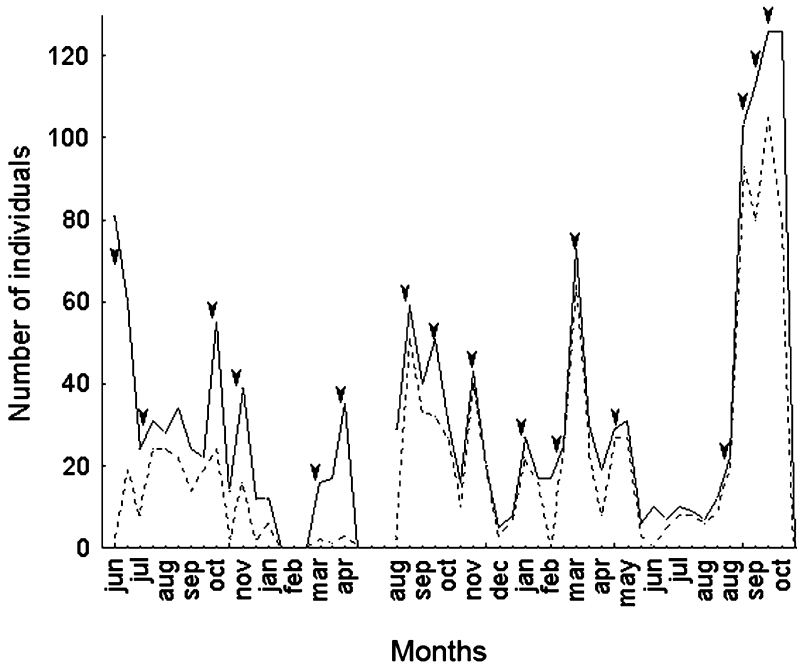
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Figure 3. Number of *Phasmahyla jandaia* individuals in developmental Class I (line) and in the Sub-class I.1 (dotted line; see Material and methods) in the pool formed by the dam of the Estação Ecológica de Fechos, Nova Lima (Minas Gerais, southeastern Brazil), from June 2002 to May 2003 and from August 2004 to November 2005. Arrows indicate detected tadpole recruitments into the population. Each mark on the *x*-axis corresponds to one sampling, and samplings were separated by 15 days. The corresponding month is provided every two samplings.

Table 1. Developmental class-specific summary of demographic parameters of the tadpole segment of a *Phasmahyla jandaia* population, between June 2002 and May 2003 and between August 2004 and November 2005, in a small creek at the Estação Ecológica de Fechos, Nova Lima (Minas Gerais state, southeastern Brazil); see text for details.

Developmental class	Total number of recruited individuals	Cumulative survival rate	Survival rate	Mortality rate
I	493	1.000	0.651	0.349
II	321	0.651	0.763	0.237
III	245	0.497	0.833	0.167
IV	204	0.414	0.725	0.275
V	148	0.300	0.953	0.047
VI	141	0.286	0.972	0.028
VII	137	0.278	0.905	0.095
VIII	124	0.252	0.903	0.097
IX	112	0.227	–	–

At least 493 individuals hatched and entered the population as tadpoles during the study (Table 1). We found one egg clutch containing 13 embryos in November 2002, hanging 94 cm from the water surface, wrapped and attached to the lower surface of a *Piper* sp. (Piperaceae) leaf.

Excluding the instances when no tadpoles were captured, individual tadpoles of *P. jandaia* in Classes I–VI occurred in all months throughout the study, including from April to August 2005, when we observed a reduction in Classes VII–X (Figure 4A–J). We found no tadpoles in developmental Class X from the end of June to the beginning of September 2002, in August and the beginning of September 2004, and from the end of March to the end of July 2005 (Figure 4J). Individuals in developmental Class X occurred from the end of September 2002 to January 2003 (first sampling), from October 2004 to the beginning of March 2005 and from August to October 2005. In 2004–2005, the larval segment of the population was not eliminated by storms until November 2005, when there was a storm that coincided with the end of the study, and the highest abundances of Class X occurred from the end of October 2004 to the end of February 2005 (Figure 4J). According to our data, recruitment of froglets to the terrestrial habitat occurs from September to March, with a peak from October to February, months with higher temperatures and humidity values. The developmental period of *P. jandaia* could not be precisely determined, though we estimated it to last at least 4 months, based on a large cohort that could be followed throughout development (Figure 4) and from our field observations.

The highest mortality rates seemed to occur in the first developmental classes, especially from Class I to Class II, when about 35% of tadpoles died (Table 1). Only 30% of the tadpoles hatching reached Class V, indicating 70% mortality from Class I to V. About 23% of tadpoles in Class I reached Class IX (Table 1). After this they reach Class X and leave the aquatic habitat and are hard to detect. According to our data, about 23% of tadpoles that hatched should potentially leave the aquatic habitat successfully. Mortality rates were not constant over development, tending to decrease in more advanced developmental classes. Among the classes, mortality rates were lower than 10% from Class V onwards (Table 1).

Discussion

The decrease in number of tadpoles in a population can be caused by death, metamorphosis or emigration. In the studied population of *P. jandaia*, the decrease in numbers of tadpoles could only be attributed to death or metamorphosis, because emigration was highly unlikely. Both during floods and in the months when tadpoles in the advanced developmental classes were not present, the reductions in number of tadpoles detected should be associated with tadpole death, which could be caused either by natural factors or by tadpoles being carried into the pipes at instances when the dam flooded. Heavy rains, which caused floods of the dam, could be regarded as the main cause of mortality in the studied tadpole segment of the population. Such rains usually happen in the beginning of the rainy season and in the rainiest months, occurring only occasionally in other periods (as in May 2003 during the present study). In a pristine stream, floods would not cause the death of all the tadpoles carried downstream, although floods might still have a negative impact on tadpole survival. In such circumstances, tadpoles could establish themselves in other pools after the flood, although they would face the risk of physical injuries during the
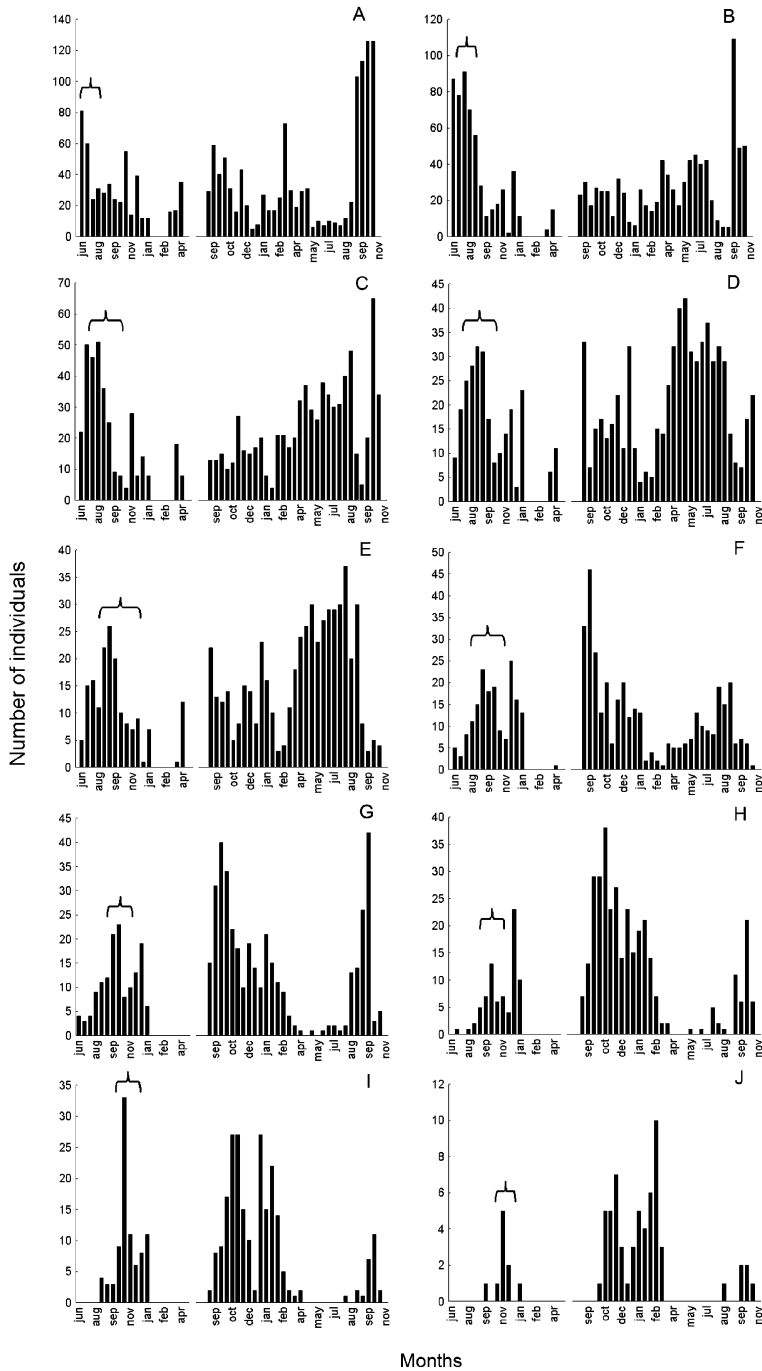
Figure 4. Number of *Phasmahyla jandaia* tadpoles by developmental classes: (A) Class I; (B) Class II; (C) Class III; (D) Class IV; (E) Class V; (F) Class VI; (G) Class VII; (H) Class VIII; (I) Class IX; (J) Class X, recorded every 15 days, in the pool formed by the dam of the Estação Ecológica de Fechos, Nova Lima (Minas Gerais, southeastern Brazil), between June 2002 and May 2003 and August 2004 and November 2005. Brackets indicate a large cohort that was used to estimate developmental period.

process, and they might be carried to microhabitats unsuitable for their needs. Whereas floods can be clearly associated with tadpole mortality in the present study, in a pristine stream they would result in a combination of tadpole mortality and emigration from a given population.

The periods of highest abundance of *P. jandaia* tadpoles in the pool during the study corresponded with the dry and cold months (June–September), especially near the end of the winter (September). In contrast, the periods of lowest abundance were in the rainy season (December–March). Our results showed that tadpole recruitment occurs throughout the year, but the recruitment of froglets to the terrestrial habitat, as well as heavy rains (which tend to cause massive mortality events), both occur most often during the rainy season. The total number of *P. jandaia* tadpoles in the studied population tends to increase during the dry season and decrease during the rainy season.

Aspects of the reproductive biology of *P. jandaia* have been briefly described (Bokermann and Sazima, 1978; Eterovick and Fernandes, 2001; Eterovick and Sazima 2004). All of these studies were based on a single population of the species at its type locality at Serra do Cipó (19°15′26″S, 43°32′37″W). The breeding phenology of *P. jandaia* was not considered in detail in these works, which may explain some of the differing results obtained in the present study. It is also possible that variation exists among populations at different localities or from time to time. Bokermann and Sazima (1978), when describing the species, noticed the presence of tadpoles in several developmental stages from September to April and post-metamorphic froglets from November to January. We observed *P. jandaia* tadpoles in most developmental stages throughout the year and recruitment of froglets to the terrestrial habitat during a longer period than Bokermann and Sazima (1978), from September to March (with a peak from October to February). Eterovick and Sazima (2004) considered the onset of the rainy season (October–December) as the typical period of calling activity for the species. In the studied population, though, breeding occurred throughout the year, which was confirmed by the continuous recruitment of tadpoles. Eterovick and Fernandes (2001) also considered *P. jandaia* as able to breed both during the dry and the rainy seasons. Continuous breeding with froglet recruitment restricted to warmer and rainy periods of the year has also been recorded for other anuran species such as *Hypsiboas albopunctatus* and *Scinax* sp. at a Cerrado locality in central Brazil (Barreto and Moreira 1996).

In species with complex life cycles, such as anurans, timing of juvenile recruitment is an important attribute of fitness, affecting survivorship and reproductive success (Berven 1990). It constitutes a critical period for survivorship, because individuals reaching a new environment are highly vulnerable to predation and unpredictable food location and acquisition (Alvarez and Nicieza 2002). In anurans, time to and size at metamorphosis can be selectively adjusted to maximize fitness, but seasonal factors, such as temperature variation, can have important effects on such attributes (Werner 1986). The phenology of juvenile recruitment by *P. jandaia* is probably an adaptation that allows froglets to reach the terrestrial habitat in periods of high temperatures and humidity, which favour survival. Such conditions are also expected to favour a higher abundance of the insects and other arthropods (Wolda 1988a; 1988b) that constitute an important food source for the froglets. In addition, the warm and moist weather may favour froglet hydration and activity, increasing chances of success in the terrestrial environment. For instance, the rainy season was positively associated with higher survivorship of juvenile *Rana*

sylvatica (Berven 1990). Although *P. jandaia* breeds year-round, seasonal variation may be important enough to direct metamorphosis to a restricted period.

Etkin (1964) suggested that the positive effect of temperature on developmental rates would result in froglet recruitment during the warm season, whereas low temperatures would inhibit development and recruitment to the terrestrial habitat during the cold season. This mechanism may explain the pattern of recruitment observed in *P. jandaia*, though studies on the direct effects of environmental variables on growth and development of *P. jandaia* tadpoles are still needed.

The measurement of the duration of the larval period of an anuran species under natural conditions is a difficult task, especially for a species with continuous reproduction and whose tadpoles cannot be marked without potentially affecting the studied parameters, such as *P. jandaia*. Additionally, anuran larvae are known to have plastic growth and developmental rates, resulting in variable larval periods (Wilbur and Collins 1973). The developmental period of the tadpoles of *P. jandaia* may be influenced by environmental factors (e.g. temperature) affecting developmental rates (Leite et al. unpublished data), and resulting in longer developmental periods for tadpoles that experience lower temperatures during their time in the aquatic habitat. Tadpoles hatched at the onset of the rainy season (October–December) could therefore metamorphose before April, when developmental rates are hypothesized to decrease (Leite et al. unpublished data). On the other hand, tadpoles that hatch later and do not metamorphose by the end of April may not transform at least until the beginning of August (four additional months), when developmental rates increase again and make the conclusion of development possible. As indicated by Werner (1986), seasonality may preclude the existence of a unique optimal size at metamorphosis, the size of froglets being determined by the amount of time spent in the tadpole stage until the appropriate season to metamorphose.

Predation is usually identified as an important source of mortality for tadpoles of several species under natural conditions – e.g. *Lithobates sylvaticus* (Herreid and Kinney 1966); *Rana aurora* (Calef 1973); *L. catesbeianus* (Cecil and Just 1979); *R. aurora* and *R. pretiosa* (Licht 1974); *Scaphiopus couchii* (Newman 1987). We recorded *Odonata* naiads (Anisoptera), adult and larval aquatic beetles (Dysticidae and Hydrophilidae) and heteropterans (Belostomatidae and Nepidae) living in sympatry with *P. jandaia* tadpoles. These taxa are already known to prey upon tadpoles (Alford 1999; Kopp et al. 2006; P.C. Eterovick personal observation) and could be considered as potential predators of *P. jandaia* larvae.

Prey capture by invertebrate tadpole predators is usually restricted by prey size (Crump 1984; Henrikson 1990; Kehr and Schnack 1991; Caldwell 1994). Several studies suggest that tadpole mortality rates due to predation decrease as the tadpoles develop (e.g. Tejedo 1993; Eklöv and Werner 2000). According to Petranka (1985), large numbers of tadpoles may die during the first developmental stages, but as the population is numerically reduced, mortality rates remain stable for most anuran species. This author considers the possibility that factors other than predation may contribute to this pattern, acting in later developmental stages. The mean length of *P. jandaia* tadpoles increases as they develop (F.S.F. Leite, unpublished data), whereas mortality rates decrease. This pattern indicates that body size may play an important role in the vulnerability of tadpoles of *P. jandaia* to predation. When tadpoles reach developmental Class V, they may be less vulnerable to predators,

which would increase their survivorship and keep it high until Class IX. If this is the case, then predation pressures would represent an important factor controlling tadpole numbers in populations of *P. jandaia*, especially in the early classes. It is also possible that predation rates are reduced in the later developmental stages of *P. jandaia* tadpoles because of the continuous selection of individuals that are more efficient at avoiding predators. Tadpoles of several species have already been shown to reduce activity levels in the presence of invertebrate predators, thereby reducing predation risk (Tejedo 1993; Eklöv and Werner 2000). Some individuals may even be more efficient than others in detecting predator presence and behaving to avoid detection by the predator.

We estimated the chances of a recently hatched *P. jandaia* tadpole completing its aquatic developmental period as 23%. Nevertheless, this probability does not take mortality during Class X into account. It is important to consider that during Class X the froglets will leave the aquatic habitat, and this transition is a great risk to an individual experiencing a completely new environment (Alford 1999). We noticed water bugs (Belostomatidae) and spiders (Trechaleidae) to be particularly abundant at the borders of the studied pool. It is also important to stress that the studied population had an additional mortality factor imposed by the occasional flooding of the dam. However, because these events caused mortality of all tadpoles regardless of their class, we can assume that our survivorship estimates throughout the tadpole classes are not biased by these events. In a pristine stream, heavy rains would carry tadpoles downstream, killing them or not, but still removing them from the local population.

We found no records in the literature of survivorship estimates throughout the larval stages for neotropical anurans. In temperate areas, studies on tadpole survivorship have been conducted in natural or semi-natural areas and it has been shown to vary considerably among species. For example, Calef (1973) estimated 5% survival for *Rana aurora* tadpoles, and a similar survival rate was found for *R. aurora* and *Lithobates sylvaticus* from egg to metamorph (Licht 1974). On the other hand, 62.5% of *L. sylvaticus* tadpoles survive until metamorphosis (Seigel 1983). Hels (2002) estimated very low survival rates from eggs to froglets for *Pelobates fuscus* (from 0 to 3.5%) in Denmark. Survival may also vary considerably among different sites, as in *Pseudacris triseriata*, where tadpole survival varied from 0 to 100%, depending on the oviposition site (Smith 1987). The survival rates we estimated for *P. jandaia* can be considered intermediate if compared with data available for other frogs. We expected that this species would not have very low survival rates because it has a high investment in size, but not in number, of eggs, which is known to vary from 13 (present study) to 30 (Bokermann and Sazima 1978) per clutch.

Herein, we provide information that could aid the conservation of *P. jandaia*. The study was conducted at a single site and in conditions that were not strictly natural (a pool formed by a human-made dam), so results should be considered cautiously. Nevertheless, this study presents the only detailed dataset on tadpole demography for a Brazilian anuran and shows important features, such as time of tadpole recruitment, metamorphosis and breeding activity period, which were not likely to be masked by possible bias caused by human interference at the site. Impacts on the microhabitats where tadpoles develop (e.g. stream pools) will cause greater declines in tadpole numbers if they happen during the winter, whereas impacts in the marginal vegetation can potentially disrupt breeding activities at any

time of the year. Structural or climatic changes that alter the physical properties of the stream margins (e.g. humidity, prey availability) can potentially increase froglet mortality. The froglet recruitment period is presumably selectively adjusted to occur during the warm, rainy season, which probably means that the conditions experienced during this period are the most suitable for froglet survivorship.

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