Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

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Version of record first published: 28 May 2009.

To cite this article: Jörn Dietl, Wolf Engels & Mirco Solé (2009): Diet and feeding behaviour of the leaf-litter frog Ischnocnema henselii (Anura: Brachycephalidae) in Araucaria rain forests on the Serra Geral of Rio Grande do Sul, Brazil , Journal of Natural History, 43:23-24, 1473-1483

To link to this article: http://dx.doi.org/10.1080/00222930902898709

Journal of Natural History
Vol. 43, Nos. 23–24, June 2009, 1473–1483

Diet and feeding behaviour of the leaf-litter frog *Ischnocnema henselii* (Anura: Brachycephalidae) in *Araucaria* rain forests on the Serra Geral of Rio Grande do Sul, Brazil†

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(Received 16 September 2008; final version received 14 March 2009)

We analysed the diet of *Ischnocnema henselii* from a subtropical *Araucaria* forest through stomach flushing. The identified prey items comprised arthropods such as spiders, ants, orthopterans, collembolans and homopterans. We consider *I. henselii* to be a nocturnal and opportunistic sit-and-wait predator. Small animals are preferred. Because this species lives permanently on the forest floor, we also determined the composition of the habitat's leaf-litter mesofauna. By using Winkler sieve extraction, we obtained a spectrum of small invertebrates that reflected the prey in the stomach contents well. The only exceptions were mites, the most abundant leaf-litter inhabitants, which frogs either avoided or ignored. Our results represent the first information on the diet of *I. henselii* and are discussed in comparison with data on related species and in relation to the relevance of this predator within the food web of subtropical montane rain forests in southern Brazil.

Keywords: Anura; *Ischnocnema henselii*; *Araucaria* forest; stomach flushing; southern Brazil

Introduction

Information on feeding ecology is crucial for understanding anuran life history, population fluctuations, and the impact of habitat fragmentation and modification (Anderson 1999). The *Araucaria* plateau in southern Brazil houses a hot spot of amphibian biodiversity (Kwet 2004). Many species live syntopically in the leaf litter, and so compete for food resources, mainly arthropods. Depending on their degree of specialization, frogs can be narrow-mouthed, poisonous, active foragers (ant specialists) or wide-mouthed, cryptic, sit-and-wait foragers ("non-ant" specialists) (Toft 1981). Generalists are intermediate in foraging mode and morphology.

The genus *Ischnocnema* currently includes 29 species and is widespread in central and southern Brazil and adjacent northern Argentina (Caramaschi and Canedo 2006). Some species occur in the leaf litter of forests, far away from ponds and other sources of water, and have direct development. The life history of many taxa is unknown, including that of *Ischnocnema henselii*. This species, described as *Hylodes*

†This article is dedicated to the memory of the late Marcos Di-Bernardo.

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ISSN 0022-2933 print/ISSN 1464-5262 online

DOI: 10.1080/00222930902898709
http://www.informaworld.com

henselii by Peters (1870), and recently revalidated from synonymy of *Eleutherodactylus guentheri* by Kwet and Solé (2005), is a sibling species to *Ischnocnema guentheri* (Steindachner, 1864). The species occurs in Atlantic rain forests and especially in *Araucaria* forests of Rio Grande do Sul and Santa Catarina, Brazil, and in Misiones, Argentina. Besides a few notes on the habitat where eggs are deposited (forest leaf litter), nothing is known about the ecology of this species (Kwet and Solé 2005). Within the scope of a long-term project on the unique ecosystem of subtropical *Araucaria* forests (Engels 2003), we studied the dietary components of *I. henselii* in the Pró-Mata reserve on the Serra Geral of Rio Grande do Sul. Diet composition was analysed through stomach flushing (Solé et al. 2005) and compared with the arthropod fauna occurring in the feeding habitat, representing the potential prey of *I. henselii*. In anurans, number and size of prey are generally related to the body size of an individual (Zug and Zug 1979; Toft 1980; Ovaska 1991; Lima and Moreira 1993; Lima 1998; Parmelee 1999; Peltzer and Lajmanovich 1999). Given that the body size of adult specimens of *I. henselii* is within the range of smaller frogs in the community (currently comprising 34 anuran taxa recorded at Pró-Mata on the *Araucaria* plateau), we asked the following questions. (1) What is the body size of these frogs in the local *Araucaria* forest population? (2) What kinds of prey are consumed by specimens of different size? (3) Is the size of prey items identified in the stomach contents related to the individual mouth width? (4) Does the consumed prey reflect the composition of the mesofauna living in the feeding habitat of *I. henselii*? (5) Do prey items allow for any conclusions on the predation strategy of these frogs?

Our results provide the first reported data on the diet of *I. henselii* and contribute considerably to our understanding of food webs and of predators that depend on small invertebrates.

Material and methods

We conducted field studies in *Araucaria* forests on the Serra Geral of Rio Grande do Sul, Brazil. The four sites for specimen collection were located in the Centro de Pesquisas e Conservação da Natureza Pró-Mata (CPCN) of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS) in Porto Alegre, and in the nearby *Fazenda Três Estrelas*. Pró-Mata is an area of about 5000 ha, lying between 29°27′ and 29°35′ S and between 50°08′ and 50°15′ W. The study area has a subtropical humid climate with annual precipitation of approximately 2500 mm and is between 850 and 1050 m above sea level. We captured *I. henselii* frogs by hand during random sampling on the *Araucaria* forest floor from November 2004 to March 2005. Back in the field station, we weighed all captured individuals to the nearest 0.1 g on a digital scale and measured them with callipers to the nearest 0.1 mm. We measured snout–vent length (SVL) and the greatest mouth width (MW). We performed stomach flushing by applying a non-anaesthetic method within 2 h of collection (Solé et al. 2005), a method also used recently by Miranda et al. (2006). Shortly after treatment we released the frogs back to the original site of capture. We flushed a total of 79 individuals, of which 62 had stomach contents which were preserved in 70% ethanol. We examined prey samples using a stereo microscope (Zeiss Stemi V6), counted all items, identified them to family or order level, and measured them with an ocular micrometer (length and width, 0.01 mm). We estimated prey volume using the following formula for ellipsoid bodies (Griffiths and Mylotte 1987):

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right)x\left(\frac{w}{2}\right)^2$$

where l = prey length and w = prey width. If only indigestible or incompletely digested body parts remained, we used a regression formula (Hirai and Matsui 2001) to estimate the original prey size. We calculated the relative importance index (I) of each prey category in the diet (Biavati et al. 2004) with the formula:

$$I = \left(\frac{F\% + N\% + V\%}{3}\right)$$

where F% = frequency of occurrence, N% = numeric percentage, V% = volumetric percentage. We analysed the diel feeding activity and hunting strategy by comparing the prey patterns of frogs captured during day and night hours.

To detect any prey selection behaviour (Hirai 2004; López et al. 2007), we also analysed the leaf-litter mesofauna in the habitat of *I. henselii*. In January 2005, we collected the leaf litter from 1 m^2 of the *Araucaria* forest floor at *Fazenda Três Estrelas*. The invertebrate fauna contained within the sample was separated through Winkler sieving (Besuchet et al. 1987), preserved in 70% ethanol and identified to family or order level.

For statistical analyses we used BioStat software (Eberius and Tarara 2001).

Results

Frog samples and stomach content analysis

The 79 captured frogs measured 20–35 mm SVL, and their body weight varied between 0.5 and 4 g (Figure 1). The two parameters were positively correlated with

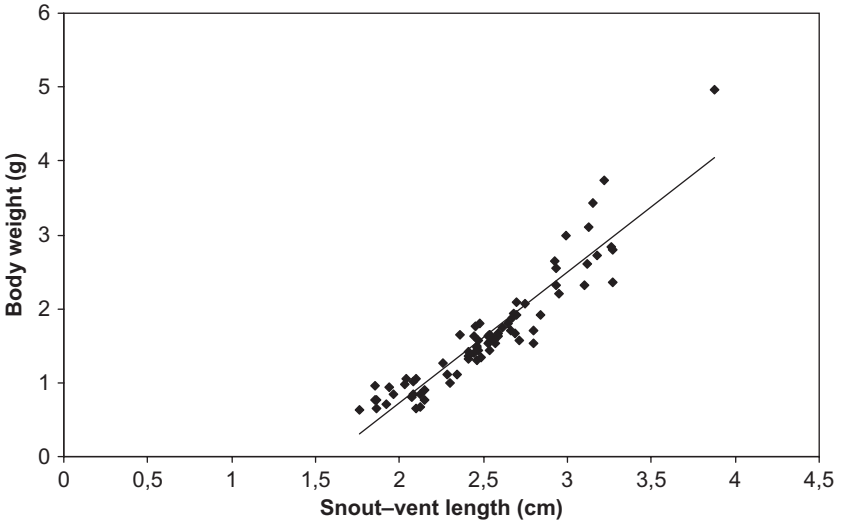

Figure 1. Relationship between body size (snout–vent length) and weight in *Ischnocnema henselii* adults.

each other ($r = 0.9365$, $F = 77$, $p < 0.001$). Our sample included an equal proportion of subadult frogs and grown adults. Mouth width varied from 6 to 12 mm.

A total of 183 prey items were retrieved from those stomachs that had contents; besides 109 animal prey subjects, there were also 37 plant remains and 37 undetermined items. There was no statistically significant relation between the individual mouth width and the number of up to six prey items found in the 61 frogs with animal remnants in their stomachs (Figure 2). The most frequent prey items were spiders, ants, orthopterans, collembolans and homopterans. We calculated the relative importance of all taxa and spiders and orthopterans were the top prey items (Table 1).

The length of animal prey isolated from the stomachs varied from a few up to 15 mm with a positive correlation ($p < 0.001$) between mouth width and maximum prey size (Figure 3). The average prey volume increased significantly with individual mouth width (Figure 4, $p < 0.01$). About 95% of prey animals measured less than 10 mm, and approximately 80% had a volume < 20 mm^3, indicating that frogs of this species feed predominately on small prey.

The mesofauna of the Araucaria *forest litter*

We isolated over 3000 animals by Winkler sieving of the leaf-litter sample. About 50% were mites, 25% were collembolans and 10% were ants (Table 2).

Discussion

Diet of adult I. henselii *frogs*

We collected all *I. henselii* frogs in exactly the same *Araucaria* forest habitat as that described by Kwet and Solé (2005). Our sample of stomach-flushed frogs represented the range of adult growth stages (Kwet and Di-Bernardo 1999) so the

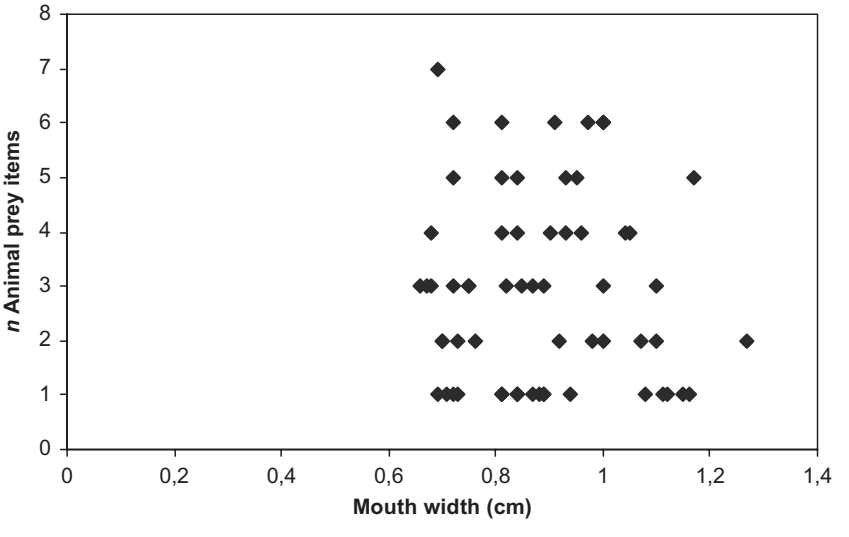

Figure 2. Relationship between mouth width and number of ingested animal prey items.

Table 1. Stomach content of 62 *Ischnocnema henselii* adult frogs collected on the litter of a subtropical *Araucaria* rain forest.

Prey animals	*n*	Volume (%)	IRI
ARTHROPODA			
Arachnida			
Araneae	24	6.9	**11.2**
Opiliones	1	0.3	0.5
Pseudoscorpiones	1	–	0.4
Crustacea			
Isopoda	2	10.7	4.4
Insecta			
Collembola	9	0.5	3
Coleoptera (Im.)	6	18.1	8.5
Coleoptera (Lv.)	4	1.1	2
Dermaptera	3	2.1	1,9
Diptera	6	0.6	2.6
Heteroptera	3	0.2	1.3
Homoptera	9	16.8	8.8
Hymenoptera – Formicidae	14	2.8	5.8
Hymenoptera – others	4	0.3	1.7
Lepidoptera (larvae)	1	0	0.4
Orthoptera	10	20.3	**10.9**
Myriapoda			
Chilopoda	7	9.4	5.6
Diplopoda	3	0.2	1.3
MOLLUSCA			
Gastropoda	2	9.7	4.1
Total	**109**		

IRI, Index of Relative Importance; top prey are indicated in bold print.

animals identified as ingested prey presumably cover the dietary composition of *I. henselii* at our study site, Pró-Mata. In comparison with the leaf-litter mesofauna, as recorded by the Winkler sieve technique, the difference in mite abundance was striking: in the leaf litter, mites dominated the invertebrate spectrum, but not a single acarid was found in any of the over 60 stomachs containing animal remnants. It is most likely that the frogs avoided eating mites, as similarly found in dietary studies for most *Eleutherodactylus* and *Ischnocnema* species (Simon and Toft 1991). Apart from these findings, the overall frequency of particular prey items roughly reflected the composition of the leaf-litter mesofauna (Figure 5) with the exception of spiders. A preference for spider prey is well known for other leptodactylid and brachycephalid frogs (Toft 1980, 1981). Generally, the availability of prey in the environment is an important condition for predators with a small feeding territory (Houston 1973; Blackith and Speight 1974; Löw and Török 1998; Meyer et al. 1999; Hirai 2004). The plant material found in many stomachs was most probably ingested unintentionally together with rapidly swallowed animal prey, as described for other anurans (Blackith and Speight 1974; Hirai and Matsui 1999; Solé and Pelz 2007).

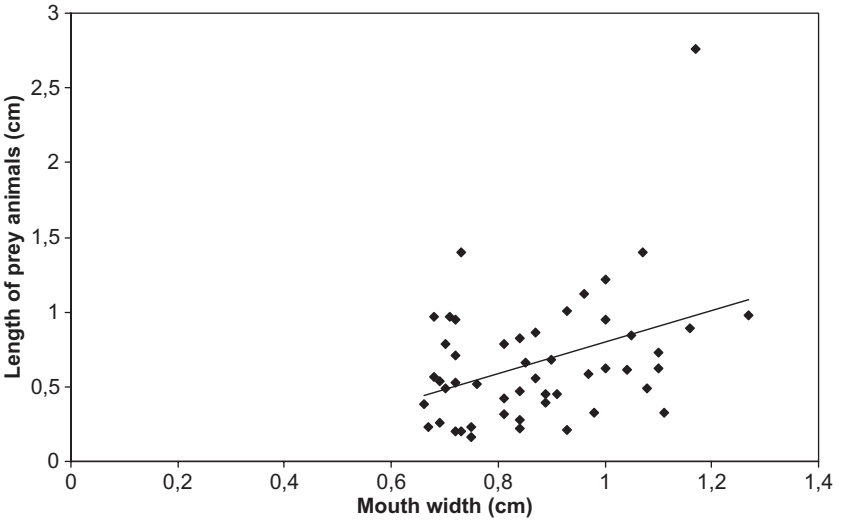

Figure 3. Relationship between mouth width of hunting *Ischnocnema henselii* frogs and length of prey animals.

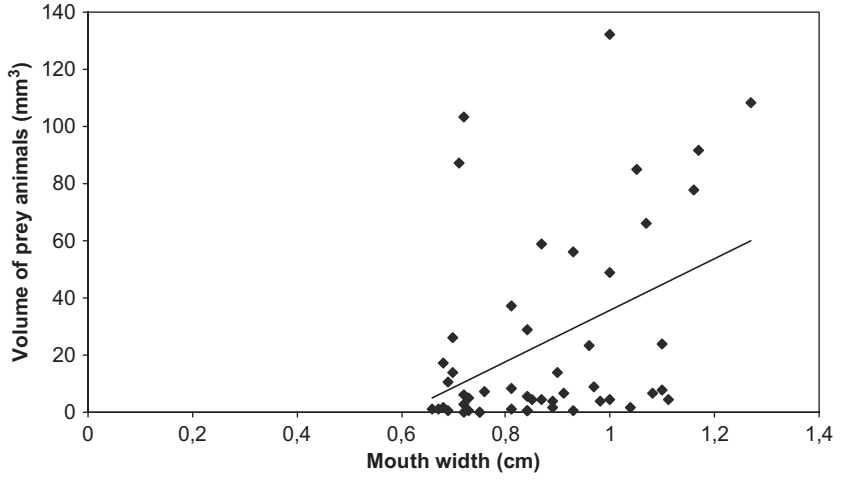

Figure 4. Relationship between mouth width of hunting *Ischnocnema henselii* frogs and the volume of prey animals.

Predation strategy of I. henselii

Rocha et al. (2000) stated that searching for frogs at night should be easier because of the reflective aspect of the eyes of most frogs when illuminated with a head lamp. In the case of *I. henselii*, however, it was easier to detect and capture these small frogs in the thick leaf-litter carpet during daylight hours than during the night. Most species of *Eleutherodactylus* and *Ischnocnema* are nocturnal hunters (Duellman 1978; Duellman and Trueb 1986).

Table 2. Small animals isolated by Winkler sieving from a litter sample collected at an *Araucaria* forest site where most of the *Ischnocnema henselii* frogs were captured.

Taxa	*n*	%
ARTHROPODA		
Arachnida		
Acari	1622	53.4
Araneae	77	2.5
Crustacea		
Isopoda	2	0.1
Insecta		
Collembola	746	24.6
Coleoptera (Im.)	43	1.4
Coleoptera (Lv.)	92	3.1
Diptera	3	0.1
Heteroptera (Im.)	12	0.4
Heteroptera (Lv.)	18	0.6
Homoptera (Im.)	2	0.1
Homoptera (Lv.)	4	0.1
Hymenoptera – Formicidae	319	10.5
Hymenoptera – Non-Formicidae	2	0.1
Lepidoptera (Lv.)	2	0.1
Myriapoda		
Chilopoda	3	0.1
Diplopoda	18	0.6
ASCHELMINTHES		
Nematoda	8	0.3
ANNELIDA – Clitellata		
Oligochaeta	9	0.3
MOLLUSCA		
Gastropoda	4	0.1
Undetermined	49	1.6
Total	**3035**	100

According to our analyses of stomach contents, these frogs are opportunistic foragers. They seem to prefer spiders, and appear to neglect mites, but the overall spectrum of their prey consumption suggests a generalist strategy. The number of ants found in the stomachs of our frogs supports the data on several closely related species such as *Eleutherodactylus coqui*, *E. cundalli*, *E. gossei*, *E. johnstonei*, *E. planirostris* and *Pristimantis acuminatus*, which are considered as preferential ant eaters (Lavigne and Drewry 1970; Toft 1981; Ovaska 1991). Real specialists, however, contrast in their prey consumption by extreme proportions of termites or ants (Solé et al. 2002; Biavati et al. 2004).

As with other predators, in anurans the diversity of consumed prey items depends on the foraging strategy (Emerson 1976). Active hunters feed mostly on small and slow-moving animals, especially those which they can remove from social aggregations, such as ant and termite nests and paths. Sit-and-wait predators can, by chance, capture

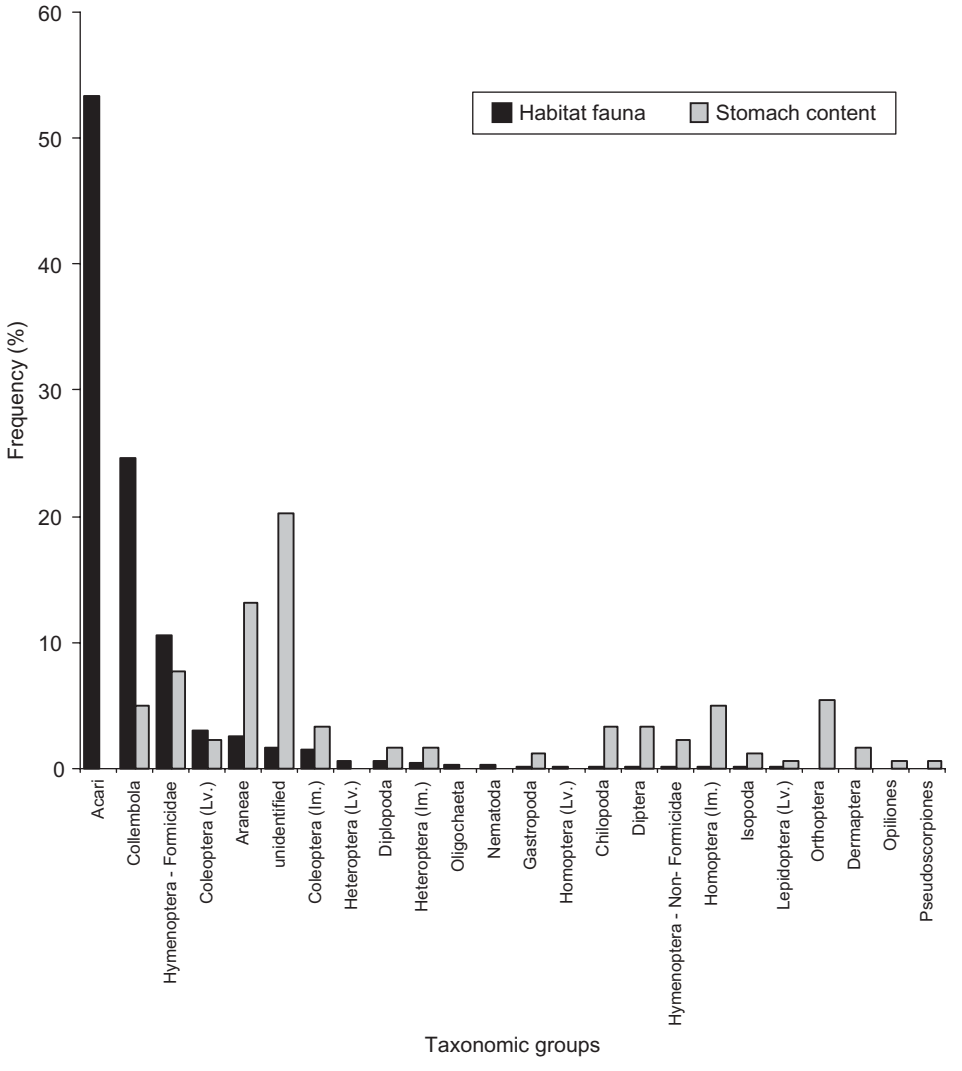

Figure 5. Prey items as found in the stomachs of adult *Ischnocnema henselii* frogs and composition of the litter fauna in the frogs' habitat.

single, larger animals, such as spiders, homopterans, orthopterans and beetles (Huey and Pianka 1981; Toft 1981; Strüssmann et al. 1984; Lima and Moreira 1993). These larger insects represented a large proportion of consumed prey items in the stomachs of flushed *I. henselii* frogs, both in terms of numbers and volume, so we consider them to be sit-and-wait foragers, as is the case for the majority of *Eleutherodactylus* species (Toft 1980, 1981; Woolbright 1985).

Position of I. henselii *in the predator hierarchy of a subtropical* Araucaria *forest*

Ischnocnema henselii is a ground-living frog endemic to the subtropical rain forests on the margin of the *Araucaria* plateau in southern Brazil (Kwet and Solé 2005). There

are currently 34 recognized species of anurans recorded for the 5000 ha area of our study site (Kwet and Di-Bernardo 1999; Kwet 2001, 2004). With a SVL under 40 mm in females (Kwet and Solé 2005), *I. henselii* is one of the smaller frogs at the site. Nevertheless, we found stomach prey items measuring about 30 mm in length. This means that adult frogs are capable of foraging on many medium-sized arthropods, although apparently smaller prey items are preferred. As to feeding ecology, *I. henselii* shares a relatively broad nutritional niche with quite a number of sympatric species. Its emancipation from water bodies for reproductive purposes, first described for the sibling species *I. guentheri* (Lutz 1946), allows it to spend all of its life on the forest floor. It is possible that competition for prey with syntopic species, which for a time have to approach ponds outside the forest, may be reduced at least during the breeding season. This could result in a temporary monopolization of the leaf-litter surface as a lucrative feeding habitat, ultimately increasing the fitness of this frog species. However, more field studies are required to test this hypothesis.

Acknowledgements

Our research was part of the FAPERGS/DLR-BMBF project "*Araucaria* forest" and was realized within the agreement between PUCRS and the University of Tübingen. We would like to thank T. Miranda and M. Ebner (LPB of the PUCRS) for help during field work, A. Kwet (State Museum of Natural History Stuttgart) for supporting our project and A. Angulo, S. Thomson and J. López for critical reading of previous versions of the manuscript. We thank Sabine Heinle (Brasilien-Zentrum Tübingen) for preparing the figures. We appreciate the facilities provided by the IMA staff of PUCRS. J.D. received a DAAD graduate student fellowship through the University of Tübingen.

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