



Published by the British
Herpetological Society

Field evidence of coupled cycles of arthropod predator-tadpole prey abundance in six aquatic systems of an Atlantic Rainforest site in Brazil

Jaime Bertoluci¹, Pedro Luís Bernardo da Rocha² & Miguel Trefaut Rodrigues³

¹Departamento de Ciências Biológicas, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo. Av. Pádua Dias, 11, 13418-900, Piracicaba SP, Brazil ²Instituto de Biologia, Universidade Federal da Bahia. Campus de Ondina, 40170-115, Salvador, BA, Brazil

³Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo. CP 11461, 05422-970, São Paulo, SP, Brazil

We evaluated the patterns of abundance association between tadpoles and their aquatic arthropod predators in natural communities of Atlantic Forest in south-eastern Brazil. We distributed 10 traps in each one of six aquatic systems and counted the numbers of tadpoles and of predators captured monthly for 13 months. For each system, we quantified the temporal association between tadpoles and predator abundances and measured its strength (using Spearman's rho coefficient) for time-lags ranging from -6 to +6 months, followed by testing the hypothesis that the strength of the association differs among time-lag values. The associations were always stronger in streams than in ponds, and strongest ($r^2 > 0.42$) and always significant ($p < 0.016$) when time-lag was zero months, resulting in significant differences of mean values of r^2 across time-lags ($p < 0.001$). A time-lag shorter than one month agrees with predictions from the model of predator-prey coupled cycles. The results also suggest that the importance of secondary factors driving abundance values in streams is stronger than in ponds, where conditions tend to be more unstable. To our knowledge, this is the first evidence of coupled cycles of predator-prey abundance with delayed dependence demonstrated with tadpoles and insects in aquatic forest systems.

Key words: anuran larvae, aquatic invertebrates, predator-prey relationships, tadpoles

Tadpoles represent an important source of food for many aquatic predators (Caldwell et al., 1980; Formanowicz, 1986). In the tropics especially, where amphibian species richness and abundance are very high (Duellman, 1999), numbers of both groups are expected

to represent important factors influencing each other. Predation is usually the major factor influencing tadpole survival (Alford, 1999). Predators may locally reduce the number of tadpoles (Formanowicz, 1986; Alford, 1989). Habitat use by anurans may be influenced by the presence of predators (Kats et al., 1988; Bradford, 1989), leading to an inverse relationship between the abundances of both groups. On the other hand, communities of tadpoles with many individuals could support high numbers of predators which can colonize or reproduce in these habitats. If this is the case, then female frogs might choose sites of oviposition where predators are rare or absent (e.g., Reseratis & Wilbur, 1989). Such dynamics are expected to give rise to coupled cycles of abundances of both groups, time-lagged for one group to respond to changes in abundance of the other group.

Most of the data available concerning abundances of tadpoles and their predators are based on experiments developed under artificial conditions, and are conducted on small spatial scales with very low variation in environmental conditions among replicates (see Parris, 2004 and references therein). Some evidence of interconnected cycles between tadpoles and their predators was found in an array of water bodies in south-eastern Brazil (rocky fields inside the Cerrado domain), where an increase in abundance of aquatic insects (Notonectidae, Belostomatidae, Nepidae and Anisoptera) occurred about five months after peaks of tadpole abundances and was followed by drastic reductions in tadpole density (Eterovick & Sazima, 2000). However, more data encompassing a wide array of ecological conditions are needed. In this work, we demonstrate the existence of coupled cycles of tadpoles and predator abundance in six aquatic systems in a tropical forest. We also quantify the time-lag (from -6 to +6 months, compatible with the dynamics of tadpole development) between them.

Field work was carried out from September 1993 to September 1994 at the Estação Biológica de Boracéia, a 16,450 ha reserve of Atlantic Rainforest located at 900 m above sea level in the coastal mountains of south-eastern Brazil (23°38'S, 45°52'W; see Heyer et al., 1990 for a map). The area is among the wettest in Brazil (Setzer 1946), and the annual rainfall averaged 2024±305 mm from 1973 to 1994 (DAEE, 1994). During the study period, rainfall was irregularly distributed through the year, totalling 1747.3 mm, and the rainy season extended from September to March. Detailed descriptions of the vegetation are available in Travassos & Camargo (1958), Heyer et al. (1990), Wilms et al. (1996); Bertoluci & Rodrigues (2002) present detailed climatic data for the study period.

Correspondence: Jaime Bertoluci (jaime.bertoluci@usp.br)

Table 1. Number of tadpoles (TAD) and predators (PRED) recorded in six aquatic systems (ponds L1 and L3 and streams R1, R2, R3, and R4) during 13 months.

Month	L1		L3		R1		R2		R3		R4	
	TAD	PRED	TAD	PRED	TAD	PRED	TAD	PRED	TAD	PRED	TAD	PRED
Sep 1993	5	17					15	25			2	1
Oct 1993							15	7				
Nov 1993												
Dec 1993												
Jan 1994												
Feb 1994												
Mar 1994					2	4			5	5	2	1
Apr 1994	5	2									1	16
May 1994	2			3					4	3		1
Jun 1994												
Jul 1994		5										
Aug 1994	508	1	156	5	9	2	16	1	10	9	1	8
Sep 1994							5	2	4			

In order to obtain monthly data on the abundances of tadpoles and their aquatic predators in a diversity of aquatic systems, we sampled four streams and two ponds using funnel traps: Stream 1 (=Site R1 of Bertoluci & Rodrigues, 2002) is a small stream (60 m long, 1.3 m wide, 22 cm maximum depth) located in the primary forest and consisting of interconnected rocky or muddy puddles with dead leaves and sticks. Stream 2 (Site R2; Fig. 5 of Heyer et al., 1990) is a small stream (50 m, 1.8 m, 27 cm) at the forest edge. Stream 3 (Site R3) is a small stream (96 m, 2 m, 32 cm) inside the primary forest and consisting of interconnected puddles with a rocky, sandy bottom and dead leaves. Stream 4 (Site R4) is a small stream (91 m, 2.4 m, 30 cm) inside the forest; its bed is mainly rocky, but some puddles have sand and dead leaves. Pond 1 (Site L1; Edge Pond of Heyer et al., 1990) is a semi permanent pond (80 m², 1 m deep) formed by

the interruption of a small stream and is located at the forest edge. Pond 2 (Site L3; Lago do Aterro of Heyer et al., 1990) is an artificial reservoir of large dimensions and is located at the edge of secondary growth forest; we sampled a 57 m strip of its margin subjected to flooding and bordered by grasses, Cyperaceae and *Typha*. Water temperatures and temperature variation along the year were lower in streams than in ponds, where tadpole species tend to metamorphose faster (Bertoluci, 1997).

We constructed double-entry funnel-traps with two 2L plastic bottles, which result in approximately 1.5L traps. We installed 10 traps at each site; in streams, traps were entirely submerged at the bottom of stream puddles, in ponds, we positioned them near the margins in order to sample different microhabitats. We performed sampling monthly (72 trapping hours) throughout the study period (September 1993 to September 1994). We calculated monthly abundance estimates of tadpoles and potential predators by using the total number of individuals captured in all 10 traps. We assumed that tadpoles are equally susceptible to predators and that predators show no preference for certain tadpoles. Tadpoles of *Rhinella ornata* and *R. icterica* (Bufonidae) are very similar in morphology and behaviour, and were pooled. If prey and predator abundances are dependent, our rationale was that we should detect a significant association between them assuming the appropriate time-lag is taken into account.

We conducted a separate analysis per system (each stream and pond). For each of them, we ran eleven non-parametric bivariate correlation tests between prey and predator abundances, using time-lags from -6 to +6 months. This procedure allowed us to evaluate, in a given system, if (based on *p*-value) and how much (based on *r*²) both abundances were associated, taking into account each time-lag. In order to evaluate the hypothesis that the evidence of coupled cycles was pervasive (common to all systems) we conducted a General Linear Model (GLM) using time-lag as a fixed factor, system as random (blocking) factor, and *r*² as response variable. A high *r*² value for a given time-lag was interpreted as strong evidence to match the coupled cycles of abundance of

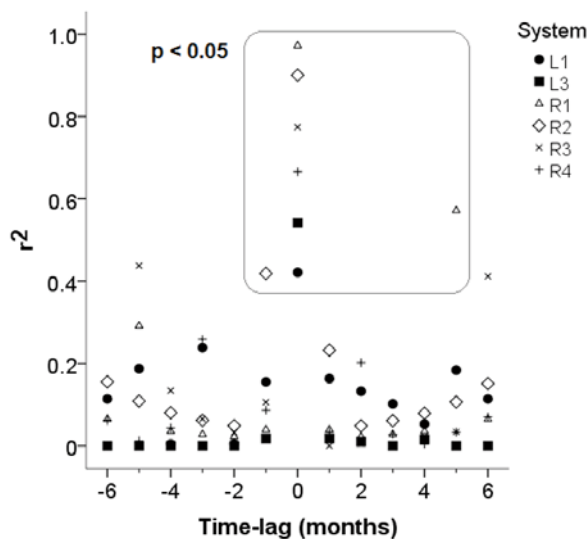


Fig. 1. Distribution of the correlation coefficients (*r*²) between the number of tadpoles and their predators sampled from September 1993 to September 1994 using time-lag values ranging from -2 to +2 months for six aquatic systems in the Atlantic Forest, including two ponds (o) and four streams (x).

tadpoles and their predators. Analyses were performed using SPSS v13.0, and we adopted 0.05 as the significance level in the study.

Among the 78 instances of sampling tadpole and predator abundances (6 systems \times 13 months), usually either none of the groups were captured (57 instances) or both were captured (16 instances). In only five instances was one group captured, which strongly suggests an association between the groups. Sampling resulted in zero captures in six months (November 1993 to February 1994 and June 1994), but all systems presented both groups: the numbers of months with captures per system were 2 (L3 and R1), 3 (R3), 4 (R2) and 5 (L1 and R4). No pair of systems presented captures in identical months, suggesting that a single set of environmental external variables could not explain eventual associations between tadpoles and predators in all systems. The number of tadpoles (0 to 508) and predators (0 to 25) captured per system and month varied by several orders of magnitude (Table 1). We recorded the following species of tadpoles: *Rhinella icterica*, *R. ornata* (Bufonidae), *Aplastodiscus leucopygius*, *Bokermannohyla hylax*, *Dendropsophus minutus*, *Hypsiboas faber*, *H. polytaeniis*, *Scinax hayii*, *S. obtriangulatus* (Hylidae) and *Physalaemus olfersii* (Leiuperidae). We also recorded the following predators: Coleoptera - *Copelatus* sp., *Hydaticus paliatus*, *Laccophilus* sp., *Megadytes* sp., undetermined (Dytiscidae), *Tropisternus* sp., undetermined (Hydrophilidae); Heteroptera - *Curicta* sp., undetermined (Belostomatidae), *Corydalus* sp. (Corydalidae), undetermined (Notonectidae); Odonata - *Anax amazili*, *Aeshna punctata* (Aeshnidae), *Libellula herculea* (Libellulidae); Crustacea - *Aegla* sp. (Aeglidae).

The correlation analyses between tadpole and predator abundances for different time-lags resulted in a consistent pattern across systems: significant (positive) associations were found only when time-lags equal zero (p always < 0.016 , other significant results are represented by time-lag -1 in system R2: $p = 0.023$, and time-lag +5 in system R1: $p = 0.03$), and their corresponding r^2 values were the highest of all analyses ($r^2 > 0.42$, Fig. 1). Interestingly, when time-lag equals zero, r^2 values were systematically higher for streams than for ponds. The GLM detected a significant difference of r^2 among time-lags ($F_{12,60} = 14.210$, $p < 0.001$), confirming that the value at a time-lag of zero is highest (mean = 0.713 while the second highest mean was 0.173; Fig. 1).

These results demonstrate that coupled cycles of abundance exist among tadpoles and their predators in the wild, irrespective of the aquatic system under analysis (as suggested by Eterovick & Sazima, 2000, who show that time-lags between the cycles are about five months). The lower r^2 values in ponds could suggest that secondary factors other than predator-prey interaction have a greater effect on the abundances of prey and predators than in streams (e.g., constraints on tadpole development in streams related to low temperatures and low food abundance). We suggest that future studies investigating this subject are based on samples taken more frequently than one month to better characterize the time-lag.

Acknowledgements: We thank Amauri Marcato, Eleonora Trajano, Wolfgang Wilms and Antonio (the caretaker of Estação Biológica de Boracéia) for help in the field; Museu de Zoologia da USP for logistical support; CAPES and FAPESP (process number 96/6701-3) for grants to JB; Fundação de Amparo à Pesquisa do Estado da Bahia by a scholarship to PLBR during part of his association with the project. We specially thank three anonymous referees and the editor Robert Jehle, whose comments greatly enhanced the original manuscript. All authors were supported by scholarship from CNPq.

REFERENCES

- Alford, R.A. (1989). Variation in predator phenology affects predator performance and prey community composition. *Ecology* 70, 206–219.
- Alford, R.A. (1999). Ecology: resource use, competition, and predation. In *Tadpoles: the biology of anuran larvae*, 240–278. McDiarmid, R.W. & Altig, R. (eds.). Chicago: The University of Chicago Press.
- Bertoluci, J.A. (2007). Fenologia e seleção de hábitat em girinos da Mata Atlântica em Boracéia, São Paulo (Amphibia, Anura). Unpublished Doctoral Thesis, Universidade de São Paulo, Brazil. 123 pp.
- Bertoluci, J. & Rodrigues, M.T. (2002). Seasonal patterns of breeding activity of Atlantic rainforest anurans at Boracéia, Southeastern Brazil. *Amphibia-Reptilia* 23, 161–167.
- Bradford, D.F. (1989). Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implications of the negative effect of fish introductions. *Copeia* 1989, 775–778.
- Caldwell, J.P., Thorp, J.H. & Jervey, T.O. (1980). Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia* 46, 285–289.
- DAEE (Departamento de Águas e Energia Elétrica) (1994). *Lay-out dos Registros Diários*. São Paulo, Departamento de Águas e Energia Elétrica do Estado de São Paulo.
- Duellman, W.E. (1999). Distribution patterns of amphibians in South America. In *Patterns of Distribution of Amphibians: a Global Perspective*, 255–328. Duellman, W.E. ed.). Baltimore: The Johns Hopkins University Press.
- Eterovick, P.C. & Sazima, I. (2000). Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. *Amphibia-Reptilia* 21, 439–461.
- Formanowicz, D.R., Jr. (1986). Anuran tadpole/aquatic insect predator prey interactions: tadpole size and predator capture success. *Herpetologica* 42, 367–373.
- Heyer, W.R., Rand, A.S., Cruz, C.A.G., Peixoto, O.L. & Nelson, C.E. (1990). Frogs of Boracéia. *Arquivos de Zoologia, São Paulo* 31, 231–410.
- Kats, L.B., Petranks, J.W. & Sih, A. (1988). Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* 69, 1865–1870.
- Parris, K.M. (2004). Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecography* 27, 392–400.
- Resetarits, W.J., Jr. & Wilbur, H.M. (1989). Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70, 220–228.

- Setzer, J. (1946). *Atlas Climático e Ecológico do Estado de São Paulo*. São Paulo, Comissão Interestadual da Bacia Paraná-Uruguai.
- Travassos, L., Camargo, H.F.A. (1958). A Estação Biológica de Boracéia. *Arquivos de Zoologia, São Paulo* 11, 1–21.
- Wilms, W., Imperatriz-Fonseca, V.L. & Engels, W. (1996). Resource partitioning between highly eusocial bees and

possible impact of the introduced africanized honey bee on native stingless bees in the Brazilian Atlantic Rainforest. *Studies on Neotropical Fauna and Environment* 31, 137–151.

Accepted: 16 October 2012