

**TADPOLE DEPOSITION IN PHYTOTELMATA: THE ROLE OF BROMELIAD
FEATURES AND ABUNDANCE AND CANNIBALISM IN THE DENDROBATID
FROG *Ranitomeya virolinensis*.**

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**UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
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TITULO: TADPOLE DEPOSITION IN PHYTOTELMATA: THE ROLE OF BROMELIAD FEATURES AND ABUNDANCE AND CANNIBALISM IN THE DENDROBATID FROG *Ranitomeya virolinensis*.*

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PALABRAS CLAVES: Canibalismo; *Ranitomeya virolinensis*; Deposición de larvas; Fitotelmata; *Mezobromelia capituligera*; Santander; Virolín

DESCRIPCION

Un gran número de variables ecológicas influyen sobre la supervivencia de las larvas de anfibios que dependen de fuentes temporales de agua almacenada en fitotelmata. Las restricciones ecológicas en estos ambientes de deposición han permitido la evolución de mecanismos comportamentales de selección de hábitat por parte de los adultos de estas especies. En este estudio investigamos los patrones de deposición de larvas en la rana venenosa de Santander *Ranitomeya virolinensis* y su relación con características ecológicas de los cuerpos de agua, la disponibilidad espacial de bromelias y las conductas agresivas entre larvas. Nuestros resultados indican relaciones significativas entre la elección de los sitios de deposición por parte de los machos de *R. virolinensis* con respecto a la calidad y tipo de fitotelmata. Los machos prefieren las bromelias de gran porte como *Mezobromelia capituligera*, que permiten el almacenamiento de grandes volúmenes de agua, hojarasca y alimento. La abundancia de este recurso determina significativamente la distribución espacial de los machos en los sitios de muestreo. Se observó canibalismo entre larvas de *R. virolinensis*. Este evento conduce a la muerte de las larvas de menor tamaño sin importar el tipo de tratamiento utilizado. Las restricciones ecológicas relacionadas con los hábitats de deposición de larvas en *R. virolinensis*, probablemente han conducido a los machos a conductas de selección y discriminación entre fitotelmata sub-óptimos, y en larvas a conductas agresivas como el canibalismo.

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ABSTRACT

TITLE: TADPOLE DEPOSITION IN PHYTOTELMATA: THE ROLE OF BROMELIAD FEATURES AND ABUNDANCE AND CANNIBALISM IN THE DENDROBATID FROG *Ranitomeya virolinensis*.*

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KEYWORDS: Cannibalism; Dendrobatidae, Phytotelmata; *Mezobromelia capituligera*; *Ranitomeya virolinensis*; Tadpole deposition.

DESCRIPTION

Strong ecological pressures seem to affect survival of amphibian larvae growing in phytotelmata, which has probably led to the evolution of specific habitat selection for reproduction by adults frogs. In this study, we investigated the pattern of tadpole deposition in the Santander poison-dart frog, *Ranitomeya virolinensis*, and tested for relationships between larval abundance and bromeliad features, as well as between bromeliad density and density of calling males. Moreover, we evaluated the incidence of cannibalism among larvae and its potential relationship with tank water volume. Tadpoles were found in phytotelmata of only one bromeliad species (*Mezobromelia capituligera*), and all tadpoles were found alone in phytotelmata. More tadpoles were found in large bromeliads with high water and leaf litter content. In addition, bromeliad density was significantly correlated with the spatial distribution of vocally active males. Cannibalism between tadpoles was observed in experimental tests, always resulting in the death of the smaller tadpole. We suggest that water and food shortage that characterize phytotelmata have led adults of *R. virolinensis* to select bromeliads for larval deposition based on two criteria: bromeliad size, which counteracts desiccation and starving risks, and the absence of conspecific larvae in the bromeliad axils, which counteracts risk of being cannibalized.

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INTRODUCTION

The life history of dendrobatid frogs involves features that are not common among other amphibian species. Adults of many species exhibit strong territorial and aggressive behavior as well as elaborate courtship behaviors. Females oviposit small clutches, and one or both parents attend terrestrial clutches and transport newly hatched tadpoles to aquatic sites where they undergo metamorphosis (Grant et al., 2006). In species of the most basal Dendrobatidae subfamilies (e.g. Colostethinae and Hyloxalinae) all tadpoles are deposited simultaneously in ponds, puddles, or streams (Wells, 1981; Aichinger, 1991; Roithmair, 1994; Juncá, 1998; Downie et al., 2001). In the relatively derived genera (Dendrobatinae Subfamily; e.g. *Ranitomeya*, *Minyobates*, *Dendrobates*, and *Oophaga*), tadpoles are simultaneously or sequentially deposited in small water bodies formed in tree holes, in the axils of bromeliads and heliconiads, or inside big seeds or dead leaves at ground level, all known as phytotelmata (Weygoldt, 1987; Summers, 1990; Caldwell, 1993; Caldwell and Araújo 1998; Summers, 1999; Armbruster et al., 2002; Grant et al., 2006). The pattern of tadpole deposition seems influenced by several abiotic factors such as the availability and volume of water bodies (Jowers & Downie, 2005), amount of food (Kam et al., 1998; Jowers & Downie, 2005), rainfall (Aichinger, 1991; Fandiño et al., 1997), and ambient temperature (Gascon, 1992a, b; Alford, 1999; Fincke, 1999). Moreover, biotic factors potentially affecting tadpole deposition include competition and predation, both at intra- and interspecific level (Caldwell, 1993; Gascon and Travis, 1992; Gascon, 1992 a, b; Caldwell and Araújo, 1998).

Compared to other water bodies used by amphibians for larval development, phytotelmata are considered ephemeral and poor in terms of food availability and

oxygen (Caldwell & Araújo, 2004). In dendrobatid and other anuran species where larval survival and development depend on phytotelmata, ecological pressures may have led to the evolution of more specific habitat selection by adults (Downie et al., 2001; Armbruster et al., 2002). Adult frogs are thus predicted to make differential use of phytotelmata according to their capacity of water retention (Resetarits, 1996; Armbruster et al., 2002) and leaf litter content, which provides both nutrients and shelter to tadpoles (Kam et al., 1996; Alford, 1999; De Oliveira and Navas, 2004). In turn, the distribution and size of dendrobatid populations should be at least partially explained by the availability and quality of their essential reproductive resources -the phytotelmata (Donnelly, 1989; Kam et al., 1996; Pröhl and Berke, 2001).

The presence, abundance, and size distribution of predators, inter- and intra-specific competitors and cannibalistic larvae are also expected to influence habitat selection for tadpole deposition by adult dendrobatids (Caldwell, 1997; Gascon, 1991, 1992a, b). Intra-specific aggression involves attacks and injuries, which often lead to the elimination of conspecific competitors. Not surprisingly, intraspecific aggression may also lead to cannibalism when the aggressor feeds on the victim (Crump, 1992). Cannibalism between dendrobatid larvae is common (Caldwell & Araújo, 1998, 2004; Alford, 1999), stimulates growth and development in some larvae (Crump, 1992), and seems associated with resource limitation in environments such as phytotelmata (Crump, 1983, 1992; e.g., Summers, 1999). Cannibalism may be partly adaptive and partly the result of indiscriminate predatory behavior by anuran larvae, but their consequences in anuran populations and assemblages are still unclear (Caldwell & Araújo, 1998).

Ranitomeya virolinensis (according to the phylogeny and taxonomy of Grant et al., 2006) occurs at moderate elevations (1700-1900 m) in the Cordillera Oriental of Colombia. Male parents transport and deposit one at a time tadpole exclusively in bromeliads (Ruiz-Carranza & Ramírez-Pinilla, 1992). Field studies on larval

deposition by dendrobatids should improve our understanding of the evolution of parental care in the group and of the behavioral and ecological aspects that affect the species distribution at the type locality.

The aims of this study were 1) to test for a relationship between features of phytotelmata (bromeliad size, volume of water, pool depth, amount of leaf litter and height above ground) and the pattern of tadpole deposition, 2) to test for a relationship between the availability of bromeliads and the pattern of male density, and 3) to evaluate experimentally the incidence of cannibalistic behavior between larvae of *R. virolinensis* and its potential relationship with the volume of water found in phytotelmata

1. MATERIALS AND METHODS

1.1 STUDY AREA AND DETERMINATION OF TADPOLE DEPOSITION SITES

During April-June 2004 and March 2005, we studied a population of *Ranitomeya virolinensis* at the “Costilla de Fara” forest area, (Virolín, Charalá municipality, Department of Santander, Colombia, 6°13´N, 73°05´W; 1820 m elevation), located 2 km south from the type locality, on the western flank of the Cordillera Oriental of Colombia. The rainfall regime is bimodal at the study site, with a first rainy season from February-June, peaking in April (350 mm), and a second one between September-December, peaking in October (390 mm). Annual total rainfall reaches 3000 mm and the mean annual temperature is 18.3° C (IDEAM, Encino and Gámbita weather stations). *Ranitomeya virolinensis* occurs in secondary sub-Andean forests characterized by oaks (*Quercus humboltii* and *Trigonobalanum exelsum*), abundant arums (e.g. *Anthurium* spp.), and epiphytes like bromeliads (e.g., *Mesobromelia capituligera*, *Tillandsia fendleri*), and orchids (e.g. *Epidendrum* spp.). The forest fragments have an approximate canopy height of 25 m and are surrounded by deforested areas where ferns and grasses are common.

To identify the water bodies used for tadpole deposition, we randomly inspected several phytotelmata within a sampling area of about 1 km². Two of us searched in phytotelmatas such as heliconiads, arums, bromeliads and orchids, over two days, looking for tree holes and ponds that could be potentially used as places for tadpole deposition. The search included phytotelmata placed at variable height of trees (up to 25 m height), where epiphytes such as bromeliads and orchids were observed. Carefully, we removed plant leaves and extracted the water inside.

Finally, we collected the plant specimens in which we found tadpoles for subsequent identification.

1.2 BROMELIADS FEATURES AND TADPOLES ABUNDANCE

To test for a relationship between bromeliads features and their tadpole contents, we randomly collected 50 individuals of the only bromeliad species where we found tadpoles, *Mesobromelia capituligera*. Height above ground (HG) was measured with a metric band from the ground to the bromeliad base. Bromeliad size (BS) was determined as the average width of three central bromeliad bracts. Water volume (WV) was measured in a 1000 ml graduated cylinder by extracting the total water content stored in each bromeliad. Pool depth (PD) was the average of measurements from the bottom to the water surface in three central bromeliad bracts. Leaf litter weight (LW) was estimated in the lab as the dry weight of fallen leaves removed from the bromeliad (dried at 63° C for 12 hours until a constant weight was obtained). Finally, we determined the presence or absence of tadpoles per bromeliad (PAT) and the total number of tadpoles per bromeliad (TAT). The last two variables were registered only by carefully removing each of the bromeliads bracts. The larvae were individually kept in plastic containers in order to use them in the cannibalism experiments.

1.3 BROMELIAD AVAILABILITY AND SPATIAL DISTRIBUTION OF MALE FROGS

To determine whether the density of males was related to the density of bromeliads, we randomly laid out seven 4 x 60 m rectangular transects, each including six stations at 10 m intervals. At each station, we counted the number of bromeliads (BD) and the number of vocally active males (MD) by area unit. To improve our estimate of male density, we conducted a parallel sampling to

determine daily patterns and peaks (10:00-11:00 h) of calling activity. Then, we censused twice per day, between 10:00-11:00 h, all males calling at each station, the second time walking in the opposite direction as the first time. All censuses of calling males were conducted by one of us, thus avoiding among-site variation associated with observer differences.

1.4 CANNIBALISM EXPERIMENTS

To evaluate the incidence of cannibalism and its potential relationship to water volume, we placed pairs of tadpoles of different body sizes (with 1 mm precision) in water containers with variable volumetric capacity, and observed the occurrence of attacks and deaths. We then assigned six replicates of tadpole pairs to each one of three experimental treatments and to one control. The low volume treatment (LVT) contained 15 ml, the middle volume treatment (MVT) 50 ml, and the high volume treatment (HVT) 100 ml of water, directly obtained from the bromeliads. Water volume in the containers was kept constant throughout the experiment by re-filling. Tadpoles were not fed during experiments. As experimental control for tadpole mortality, we kept single tadpoles in plastic containers under similar conditions as tadpole pairs. Each container was monitored every 12 h during six consecutive days, noting tadpole condition and recording the time until cannibalism (at 12 h precision). To confirm cannibalism events, we also conducted focal animal observations of tadpoles.

1.5 STATISTICAL ANALYSIS

We checked for normality for our field-compiled variables (HG, BS, WV, PD, LW, BD and MD) by means of a Kolmogorov-Smirnov test. Variables related to the

bromeliad features (HG, BS, WV, PD and LW) were then submitted to a principal components analysis (PCA) to reduce them to a smaller number of factors that could explain the covariance among them. Because one of our output variables was binary, i.e., the tadpoles were present (1) or absent (0) in each bromeliad, we used logistic regression to test for a relationship between bromeliad features (summarized by principal components) and tadpole occurrence. We further tested for a relationship between bromeliad features and the total number of tadpoles per bromeliad (TAT) by means of Spearman's correlation analyses.

To evaluate whether male density (MD) was related to the availability of bromeliads (BD) we carried out Spearman's correlations analysis for each transect, using the stations as the statistical units, and also an overall correlation analysis, using mean value per transect as the statistical units. Finally, to evaluate the effect of water volume on the incidence of tadpole cannibalism, we conducted an analysis of covariance (ANCOVA) using the difference in body size between tadpoles as covariate, and the latency until cannibalism as response variable. Statistical analyses and graphs were performed using SPSS 10.0.1 for Windows (SPSS Inc., 1999).

2. RESULTS

Adults of *Ranitomeya virolinensis* were found mainly on the forest floor and inside cavities formed by tree-roots that grow on a rocky substrate. Males usually call from these territories and sometimes from fallen logs. Territories commonly consist of subterranean, humid and dark cavities, covered by abundant bryophytes, *Selaginella*, and other plants roots. Females are commonly found wandering among the leaf litter and in the refuges formed by rocks. Reproductive events such as courtship, mating, oviposition and egg care probably occur within these male territories.

The exploration of the study area led to the identification of a single type of phytotelmata used by *R. virolinensis* males for tadpole deposition: *Mezobromelia capituligera*, a bromeliad species found on the ground and on tree branches at different heights above the ground. More tadpoles were found in the largest bromeliads that contain higher water volumes (Fig. 1) and leaf litter. Tadpoles were not recorded in 67% of the evaluated bromeliads. These bromeliads were small and the water retention was poor ($X_{BS} = 5.92$, $SD = 2.47$; $X_{WV} = 113.23$, $SD = 95.42$). Tadpoles were found in the remaining bromeliadas (33%), which corresponds to large bromeliads with great capacity of water retention. ($X_{BS} = 8.90$, $SD = 1.60$, $MIN = 6.5$, $MAX = 11.30$; $X_{WV} = 325.44$, $MIN = 110$, $MAX = 670$). The number of tadpoles per bromeliad was variable ($X = 6.50$, $SD = 7.06$, $MIN = 1$, $MAX = 26$,) and, in all the cases, we found a single tadpole in each bromeliad axil ($n = 146$). The PCA resulted in the extraction of two components that explained 88% of the total variance among bromeliad features. The first principal component (PC1) explained 67% of the variance and it was positively correlated with the bromeliad size (S), water volume (WV), depth (PD), and with leaf litter weight (LW).

The second principal component (PC2) explained 21% of the variance and was correlated only with the bromeliad height (HB) (Table 2).

The logistic regression indicated a significant relationship between the bromeliad morphometric features (PC 1) and the presence (1) or absence (0) of tadpoles ($r^2 = 0.49$, $P = 0.001$, $n = 49$ bromeliads; Fig. 2). The bromeliad height above ground (PC 2) was not related to the probability of larvae deposition in bromeliads under the logistic regression model ($r^2 = 0.01$, $P = 0.855$, $n = 48$ bromeliads). The phytotelmata morphometric features were also significantly correlated with the abundance of larvae per bromeliad (Spearman $\rho = 0.622$, $P = 0.001$, $n = 48$; Fig 3). In contrast, the bromeliad height above ground was not related to the number of tadpoles found inside them (Spearman $r = 0.045$, $P = 0.762$, $n = 48$). Density of males was related to density of bromeliads in the overall correlation analysis (Spearman $\rho = 0.680$, $P = 0.001$, $n = 42$), although this relationship was not evident in the individual test for three out of the seven transects (Spearman ρ , $P > 0.05$; Fig 4).

Water volume significantly affected the latency time until cannibalism (ANCOVA: $F = 5.232$, $P = 0.023$; Fig 5), which is attributable to the shorter latency at the low-volume treatment. Neither size difference between the pairs of tadpoles (ANCOVA: $F = 8.94$, $P = 0.363$) nor its interaction with water volume (ANCOVA: $F = 0.254$, $P = 0.780$) significantly affected latency time until cannibalism. In all cases, the larger tadpole killed the smaller one ($n = 18$). Tadpole aggression consisted of abrupt bites by means of their oral disc, which caused the loss of body parts (mainly of the tail) and ripping of organs such as intestines and eyes. These wounds caused tadpole death, while all control larvae remained alive throughout the experimental time.

3. DISCUSSION

More tadpoles of *Ranitomeya virolinensis* were found in large phytotelmata with apparently high potential for the storage of water and food. Additionally, our experiments provided evidence of the occurrence of cannibalism on smaller larvae, which occurs sooner when tadpoles are growing in lower water volume. Next, we will discuss the way in which these factors may interact with tadpole deposition behavior by adults of this species.

3.1 BROMELIAD FEATURES AND ABUNDANCE

Bromeliad size, water volume and depth, and leaf litter content were strongly correlated and were also the most important predictors of tadpole abundance (see Table 2). *Ranitomeya bombetes*, a species considered taxonomically close to *R. virolinensis* (Taran Grant, pers. com.), apparently corroborates this pattern, because males also deposit their larvae in large bromeliads with high amount of leaf litter (Suarez, 2004). It has been observed that the selection of temporary water bodies which store considerable water volumes increases the reproductive success of species that develop in these habitats (Resetarits, 1996), probably because large ephemeral water bodies buffer the impact of desiccation, which is in turn determined by evaporation and lack of precipitation (Rowe & Dunson, 1995; Skelly, 1997). Some dendrobatid females lay unfertilized eggs to feed tadpoles (*Oophaga* spp.); however in other dendrobatids as in many Neotropical anuran species that breed in phytotelmata, the storage and proliferation of nutrients such as detritus, insect larvae, and microinvertebrates increase the chances of tadpole

survival until metamorphosis (Armbruster et al., 2002; De Oliveira and Navas, 2004). The leaf litter constitutes a predictable source of nutrients and probably serves as a refuge against predators (Alford, 1999; Armbruster et al., 2002). Thus, the differential use of large bromeliads with high water and leaf litter content may favor the development of *R. virolinensis* tadpoles, because it counteracts factors such as desiccation, food shortage and, eventually predation.

The lack of correlation between tadpole abundance and bromeliad height above ground suggests that this factor does not affect the use of phytotelmata by adult males. The same phenomenon was observed by Armbruster et al. (2002), who studied the assemblages of macrofauna in bromeliad tanks in Ecuadorian Amazonia. On the other hand, it has been suggested that adults of *Scinax perpusillus* use the lower bromeliads because they contain more water, nutrients, shade and protection against predators (De Oliveira and Navas, 2004). The apparent lack of selectivity by males *R. virolinensis* regarding tank elevation was confirmed in parallel experiments (unpublished data), where artificial containers at different elevations were colonized and used after 6 months.

In several anuran species, the selection of larval deposition sites is not only related to their physical characteristics, but to biotic factors such as the presence of predators and intraspecific competitors or cannibals (Caldwell, 1993; Caldwell and Araújo, 1998; Downie et al., 2001). It has been suggested that in temperate anurans, interspecific competition determines to a greater extent than predation the structure of aquatic assemblages (Formanowicz, 1986; Lawler and Morin, 1993; Horat and Semlitsch, 1994; Skelly, 1997). In contrast, anuran larval communities in the tropics seem to be more structured by the kind of co-occurring predators (Magnusson & Hero, 1991; Gascon, 1991; 1992). Adult and larval insects have been detected and recognized frequently as effective competitors of tadpoles in pools and phytotelmata (Magnusson and Hero, 1991; Fincke et al., 1997; Caldwell, 1993). We suggest that interspecific interactions do not play an

important role in the selection of bromeliads for tadpole deposition in *R. virolinensis*, since we did not record any insect (e.g. odonates, coleopters, or mosquitoes) or larvae of other amphibian species during the study. Instead, the effect of intraspecific competition together with the aggressive and cannibalistic behaviors (see cannibalism) might be crucial for explaining tadpole distribution and life history.

Our results suggest that the spatial distribution of *R. virolinensis* males at the study area is significantly related to the availability of bromeliads for tadpole deposition (Fig 4). In *Oophaga pumilio* the increase in density of bromeliads is correlated with an increase in adult population size, suggesting that the availability of tadpole rearing sites is a limited resource for these frogs (Donnelly 1989). Considering that *R. virolinensis* tadpoles depend on temporary water bodies for their development, it is possible to suggest that the population size can be regulated during the larval stage, as it has been suggested for other frogs (Wilbur, 1987; Caldwell, 1993; De Oliveira and Navas, 2004), but we need evidence from manipulative experiments to confirm this speculations.

3.2 CANNIBALISM

Our results showed that in experimental conditions cannibalism between *R. virolinensis* tadpoles took place whenever two or more larvae were put together. Under experimental conditions, cannibalism occurs in a very short time, although this time is correlated with the water volume stored in the pools (Fig 5). As has been suggested for species of the scaphiopodid anuran *Scaphiopus* (Pfennig and Frankino, 1997), our result indicates that the use of larger water bodies may decrease the risk of cannibalism between tadpoles. Although the effect of size difference between tadpoles on the time until cannibalism was not statistically significant, the smaller tadpole was in all the cases killed by the larger one. Larval

deposition in phytotelmata that lack conspecific larvae should increase tadpole survival (Caldwell, 1993; Summers and Amos, 1997). In *R. ventrimaculata*, the presence of conspecific larvae influences the selection of larval deposition sites by adults (Summers, 1999). In *Dendrobates auratus*, deposition of tadpoles in a previously used pool results in new larvae being consumed by the oldest (usually larger) ones (Summers, 1990). We predict from these results that, under natural conditions, males of *R. virolinensis* should differentially use bromeliads with high volumetric potential and select axils free of conspecific tadpoles.

Cannibalism is common in some dendrobatid species, and especially in those species that deposit their tadpoles in phytotelmata, which are considered poor in terms of resources' availability (Weygoldt, 1987; Crump, 1992). Although cannibalism may confer benefits regarding resources acquisition (Crump, 1983; Summers and Amos, 1997), our results indicate that cannibalism between *R. virolinensis* tadpoles occurred even when food conditions are favorable. Thus, cannibalism may also represent an indiscriminate behavior that would eliminate competitors and predators, rather than (or in addition to) a behavioral adaptation to low food conditions (Crump, 1992; Caldwell, 1993; Caldwell and Araujo, 1998; Summers, 1999), but this hypothesis deserves further testing.

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ATTACHMENTS

Table 1. Experimental conditions of *Ranitomeya virolinensis* tadpoles during the test for the relation among water volume and the cannibalism incidence. Artificial containers were used with tadpole pairs under three volume treatments: Low volume treatment (LVT); middle volume treatment (MVT) and high volume treatment (HVT).

Treatment	Water volume (mL)	Number of tadpoles by container	Time (day)	Number of replicates
LVT	15	2	6	6
MVT	50	2	6	6
HVT	100	2	6	6
Control				
LVT	15	1	10	6
MVT	50	1	10	6
HVT	100	1	10	6

Table 2. Results of the principal component analysis for five variables that represent features of bromeliads potentially or actually used for larval deposition by males of *Ranitomeya virolinensis*. Cells include loadings (interpretable as correlation coefficients) between the original variables and the principal components, as well as the percentage of covariance explained by the first two principal components.

Variable	PC 1	PC 2
Bromeliad size (BS)	0.926	0.112
Water volume (WV)	0.028	- 0.143
Pool depth (PD)	0.940	- 0.073
Leaf litter weight (LW)	0.865	0.148
Height above ground (HG)	- 0.031	0.992
Covariation explained (%)	67.00	21.00

Figure 1. Relationship between the number of tadpoles of *Ranitomeya virolinensis* found in the bromeliad *Mezobromelia capituligera* and some of its attributes: Size, water volume, water depth and leaf litter weight.

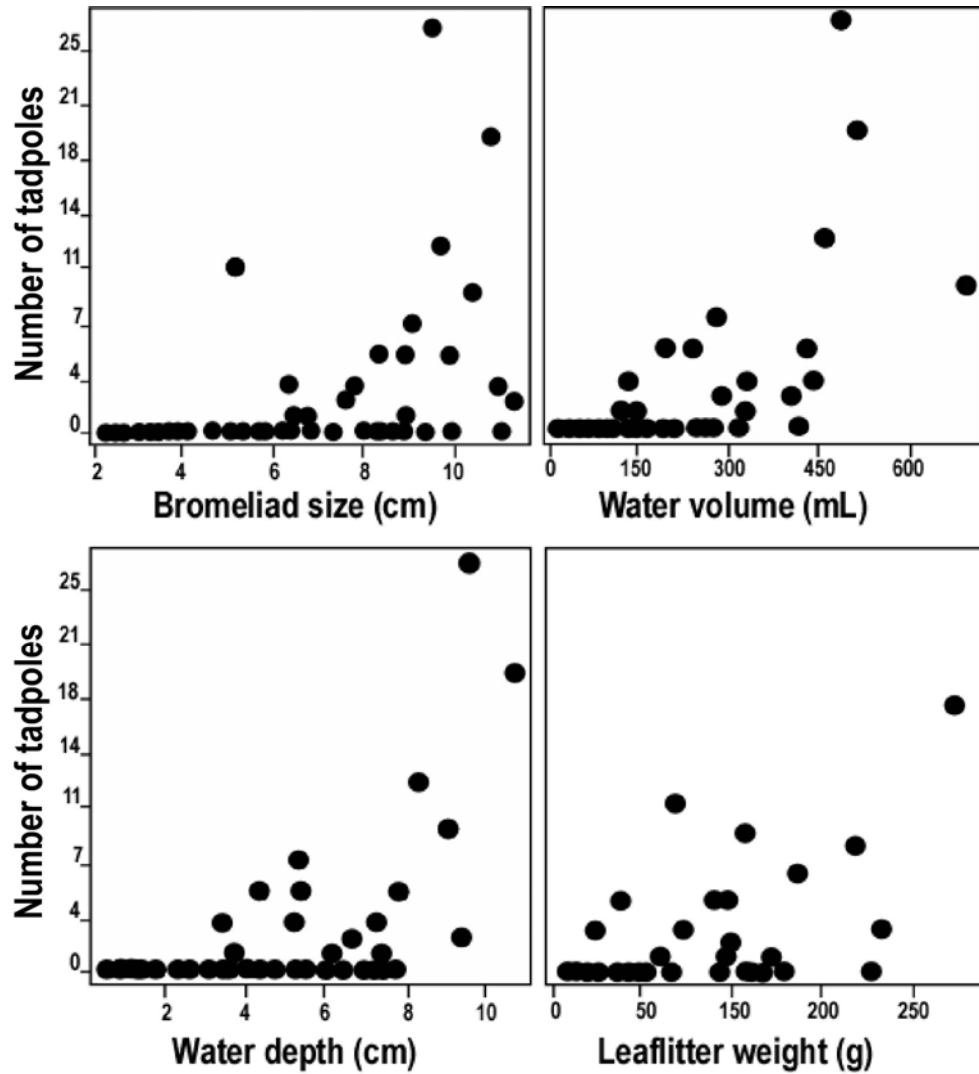


Figure 2. Presence (1, upper fill circles) and absence (0, lower fill circles) of *Ranitomeya virolinensis* tadpoles as a function of the principal component I (positively correlated with bromeliads' size, water volume, water depth and leaf litter weight). Open circles represent the expected probability according to a logistic regression analysis (See results).

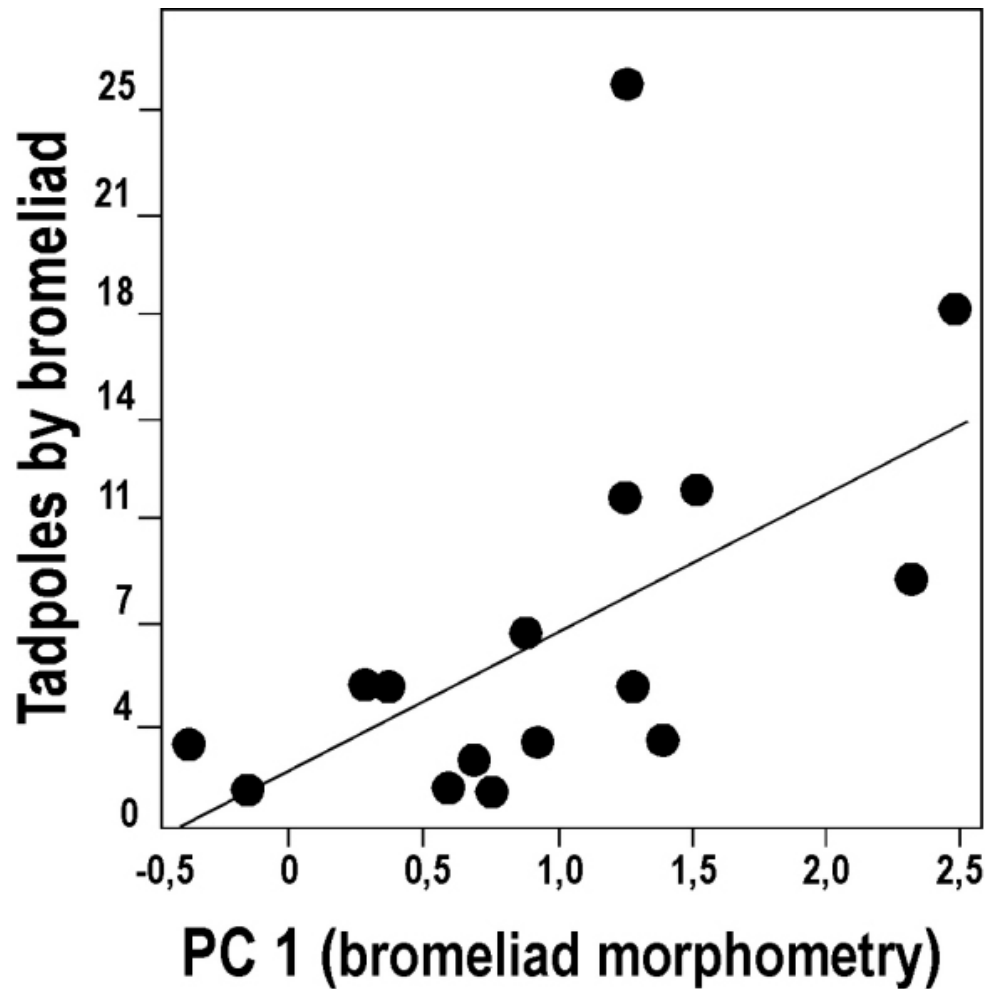


Figure 3. Relationship between the amount of tadpoles of *Ranitomeya virolinensis* per bromeliad and the principal component I (positively correlated with bromeliads' size, water volume, water depth and leaf litter weight).

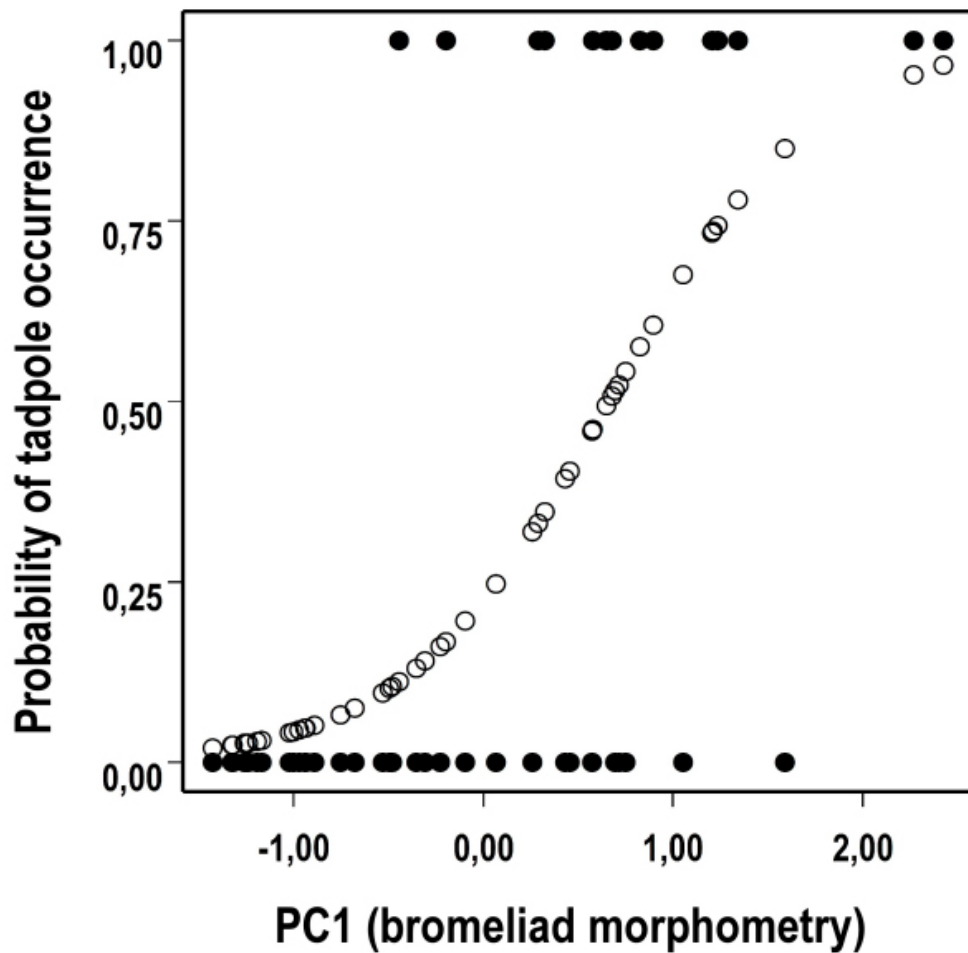


Figure 4. Relationship between bromeliads' density and density of vocally active males of *Ranitomeya virolinensis* across the stations and transects at the study site. Symbols represent values at each station. The line indicates a regression model estimated with the average transect values as the statistical unit.

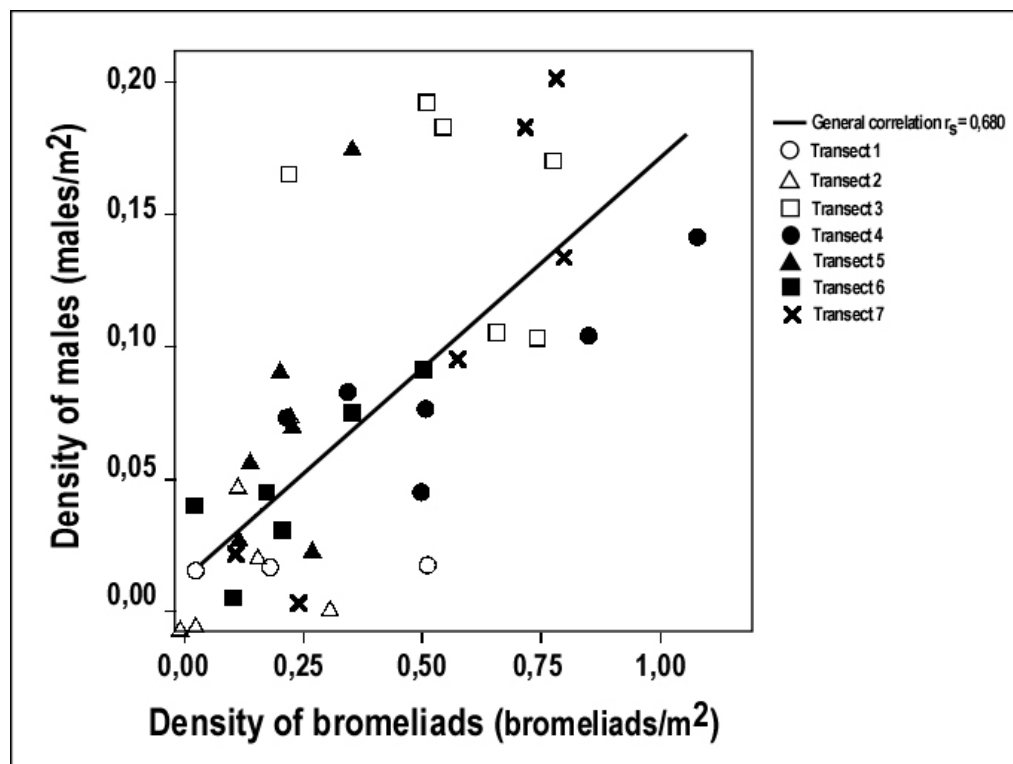


Figure 5. Relationship between the time until cannibalism (latency), the size difference between tadpole pairs, and the water volume in the container. Figure shows that latency is lower when the water volume in containers is small.

