

Correspondence

Preference and competition for breeding plants in coexisting *Ranitomeya* species (Dendrobatidae): does height play a role?LISA MARIA SCHULTE¹, DENNIS RÖDDER¹, RAINER SCHULTE² & STEFAN LÖTTTERS¹¹) Trier University, Department of Biogeography, 54286 Trier, Germany²) INIBICO – Instituto de Investigación de la Biología de las Cordilleras Orientales, Tarapoto, Peru

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In environments harbouring highly diverse biota, the coexistence of species with similar life histories requires functional resource partitioning and niche segregation, i.e., avoidance of competition through specialization (HARDIN 1960, CHESSON 2000, INDERMAUR et al. 2009). The degree of resource partitioning is positively correlated with species richness, and megadiverse areas often show high degrees of species specialization (KNEITEL & CHASE 2004). Many species exploit spatially and structurally distinct resources for the development of their progeny (MOCK & PARKER 1997). These phenomena are well studied in anuran amphibians. Among these vertebrates, both microhabitat utilisation for clutch deposition and larval morphological adaptation are highly diverse (MCDIARMID & ALTIG 1999, HADDAD & SAWAYA 2000, HADDAD & PRADO 2005). Moreover, segregation into species-specific acoustic niches, i.e., spatial and temporal structures, are common and locally remarkably well defined (HÖDL 1977).

One example of anuran species coexistence with limited reproductive space can be found in two closely related poison frogs (Dendrobatidae) from the eastern Andean versant of Peru: *Ranitomeya imitator* (SCHULTE, 1986) and *R. variabilis* (ZIMMERMANN & ZIMMERMANN, 1988) (Fig. 1). Neotropical poison frogs of the genus *Ranitomeya* show complex reproductive strategies including parental care (SUMMERS & SYMULA 2001, SUMMERS & MCKEON 2004, POELMAN & DICKE 2007, BROWN et al. 2008a,b). Both *R. imitator* and *R. variabilis* transport their larvae singly into phytotelmata, such as small water bodies in plant axils (LÖTTTERS et al. 2007, BROWN et al. 2008a,b). Another phytotelm-breeding species coexisting with *R. imitator* and *R. variabilis* is *R. fantastica* (BOULENGER, 1883), but its abundance is lower relative to its congeners (BROWN et al. 2008a, pers. observation L.M.S.). Besides tadpoles, *R. variabilis* also deposits its clutches in phytotelmata (at the water surface), while *R. imitator* lays its eggs on leaves or within phytotelmata away from water (LÖTTTERS et al. 2007, BROWN et al. 2008b).

Tadpoles developing in phytotelmata, as in the *Ranitomeya* species previously mentioned, are adapted to a life

with spatial and nutritive limitations (LANNON et al. 1987, CALDWELL & DE ARAÚJO 1998, MCDIARMID & ALTIG 1999, LEHTINEN et al. 2004, TEIXEIRA et al. 2006). Because of their small size, phytotelmata commonly cannot sustain more than one tadpole (BRUST 1993, SUMMERS 1999). As a consequence, they are often used by dendrobatid species (but also those of several other lineages including the hylid genus *Osteocephalus*) with extremely competitive and predatory larvae (BRUST 1993, PRAMUK & HILER 1999, SUMMERS 1999, POELMAN & DICKE 2007), which have often adopted cannibalistic tendencies. In addition to the elimination of competitors, cannibalism also compensates for the limited food availability in phytotelmata (SUMMERS 1990, CALDWELL 1993, WELLS 2007).

Many dendrobatid tadpoles are cannibalistic and cannot develop in the same phytotelm. As a result, parent frogs need to locate unoccupied pools for each of their tadpoles. Accordingly, phytotelmata represent a limited resource for reproduction (JUNGFER & WEYGOLDT 1999). The evolution of trophic egg-feeding is considered, in part, a result of this competition, and species that exhibit egg-feeding are able to use considerably smaller, nutrient-deficient reproductive resources, which few other species are able to successfully utilize (BROWN et al. 2010). Egg-feeding behaviour is known in *R. imitator* which feeds its tadpoles with trophic eggs, but is absent in *R. variabilis* (LÖTTTERS et al. 2007, BROWN et al. 2008a,b). Accordingly, larvae of *R. imitator* are freed from the nutritive constraints imposed by small phytotelmata and are able to use smaller pools than larvae of *R. variabilis* (BROWN et al. 2008a,b). Moreover, *R. imitator* prefers phytotelmata of the genera *Dieffenbachia*, *Xanthosoma* and *Heliconia* plants, while *R. variabilis* mainly uses bromeliad plants of the genera *Aechmea* and *Guzmania* (BROWN et al. 2008b). The latter are predominantly epiphytes growing on trees (MERCIER & KERBAUY 1997, CRAYN et al. 2004) and are usually higher above the ground than those phytotelmata preferred by *R. imitator*. Because the phytotelmata used by both species overlap somewhat in volume (*R. imitator*: 9–44 ml water, mean 24 ml; *R. variabilis*: 29–172 ml, mean 112 ml; BROWN et al. 2008b) we hy-



Figure 1. *Ranitomeya imitator* (A) and *R. variabilis* (B) can be distinguished by the presence of paired spots versus a single spot on the dorsal snout.

pothesize that the species may also show preferences for either 'high' (*R. variabilis*) or 'low' phytotelmata (*R. imitator*). The goal of the present study is to investigate by using field experiments whether there is more than one mode of



Figure 2. Tree with five artificial phytotelmata (bottles) in a vertical line. Bottles are fixed on the tree at 0 m, 0.5 m, 1.0 m, 1.5 m and 2.0 m high.

breeding resource partitioning between the two syntopic *Ranitomeya* species.

Our study was performed in a premontane, late-stage secondary forest near Tarapoto in the upper Cainarachi

Valley, Departamento San Martín, Peru, between 22 July and 17 November 2008. A site of approximately 1000 m² was chosen, containing populations of both *R. imitator* and *R. variabilis*. A total number of 125 artificial phytotelmata (i.e., halves of transparent plastic bottles), with each containing 500 ml of water, were attached to 25 trees distributed throughout the study site. On each tree, five of these pools were fixed in a vertical line one upon the other spaced at approximately 0.5 m. As such, the lowest pool was fixed at ground level, and the highest at 2.0 m above the ground (Fig. 2). Small holes were made in the sides of the bottles to maintain constant water levels. The large size of the bottles was chosen with the goal to guarantee that the frogs could easily see all pools in the line if they entered the tree. The disadvantage of the chosen size was that the water volume exceeded the observed range of both *R. imitator* and *R. variabilis* (compare BROWN et al. 2008b).

Pools were checked weekly for tadpoles and eggs. Occupied pools were not replaced because of collateral experiments. Since *Ranitomeya* species avoid occupied phytotelmata (SUMMERS 1999, POELMAN & DICKE 2007, BROWN et al. 2008a), such pools had to be excluded from subsequent analyses. Consequently, the number of free phytotelmata was not necessarily five per tree throughout the entire study period. Therefore we differentiated between only two categories instead: preference for 'high' or 'low' pool positions, focusing on the remaining possibilities. When, for instance, on any given tree a frog only had the choice between four pools (instead of five because one was occupied) and it chose one of the two higher ones, its choice was categorized as a preference for 'high' pool positions. When there was an unequal number of empty pools and a frog chose the pool in the middle, this was categorized as indifferent and was excluded from our analysis (Fig. 3).

Frequencies of clutch and tadpole depositions in 'high' versus 'low' pool positions were compared using a G-test (WOOLF 1957). The comparison was calculated under the null hypothesis that the frequency of deposition events was random (0.5 in either 'high' and 'low' pool positions).

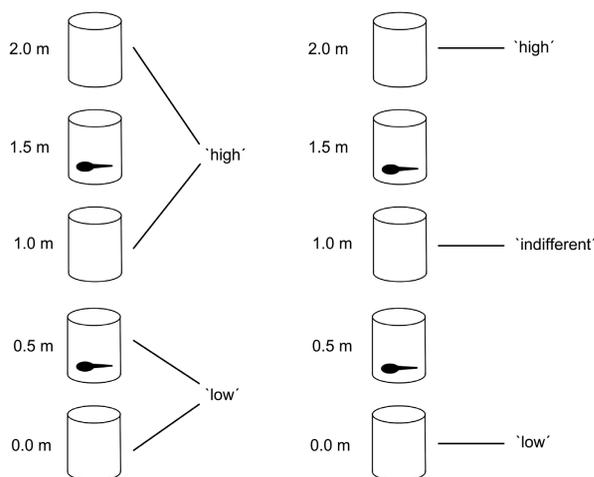


Figure 3. Categorization of pool positions. If one of the five pools was occupied, the remaining four pools were split in two high and two low pools. When there were an unequal number of empty pools, the pool in the middle was categorized as indifferent.

The G-test was preferred over a chi-square test as it is the more exact method when the number of observations is limited (SACHS 1974, GOTELLI & ELLISON 2004). The G-test was adjusted in the manner of WILLIAMS (1976) as the total number of observations was less than 200. To compare depositions of tadpoles in *R. imitator* and tadpoles and eggs in *R. variabilis*, contingency tables were calculated using a Fisher's exact test (FISHER 1922, TOWNEND 2002).

Both *R. imitator* and *R. variabilis* did not show any preference for 'high' versus 'low' pool positions with regard to tadpole deposition. *Ranitomeya variabilis* chose the 'high' 13 times and the 'low' pool position 14 times for its larvae (G-test: $G_1 = 0.037$, $P = 0.847$), and *R. imitator* chose the 'high' six times and the 'low' pool position four times (G-test: $G_1 = 0.384$, $P = 0.536$). A comparison of both species shows no difference in the preference of 'high' versus 'low' pool positions ($P = 0.714$, Fisher's exact test). Our study of egg deposition in *R. variabilis* revealed a trend towards 'high' pool positions, as 30 clutches were laid in 'high' and

Table 1. Numbers of deposition decisions of *Ranitomeya variabilis* for its tadpoles in relation to the relative height of the artificial phytotelmata.

Height	Total	high	low	indifferent
0.0 m	4	0	4	0
0.5 m	9	0	6	3
1.0 m	12	2	3	7
1.5 m	5	4	0	1
2.0 m	8	8	0	0
Total:	38	14	13	11

Table 2. Numbers of deposition decisions of *Ranitomeya variabilis* for its clutches in relation to the relative height of the artificial phytotelmata.

Height	Total	high	low	indifferent
0.0 m	11	0	11	0
0.5 m	6	0	5	1
1.0 m	8	4	2	2
1.5 m	22	19	0	3
2.0 m	7	7	0	0
Total:	54	30	18	6

Table 3. Numbers of deposition decisions of *Ranitomeya imitator* for its tadpoles in relation to the relative height of the artificial phytotelmata.

Height	Total	high	low	indifferent
0.0 m	1	0	1	0
0.5 m	3	1	2	0
1.0 m	2	0	1	1
1.5 m	4	4	0	0
2.0 m	1	1	0	0
Total:	10	6	4	1

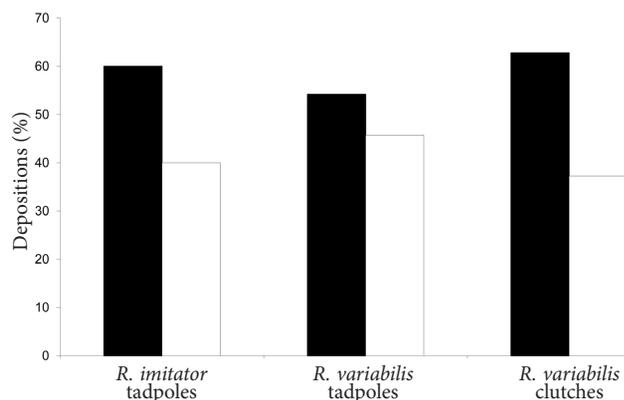


Figure 4. Relative tadpole and egg deposition frequencies of *Ranitomeya imitator* and *R. variabilis*. Black bars show depositions in higher and white bars in lower pools.

18 in 'low' pool positions (G-test: $G_1 = 3.032$, $P = 0.082$) (Fig. 4). The possible preference of a 'high' pool position for eggs could be explained by a higher presence of potential terrestrial predators close to the ground, as the clutches of *R. variabilis* are deposited above the water surface (BROWN et al. 2008b). However, comparing the egg deposition with the tadpole deposition patterns in the same species contradicts this hypothesis as no significant differences were detected ($P = 0.331$, Fisher's exact test).

We were unable to detect evidence of vertical partitioning of pools in these two species. One reason for this finding could be the limitation of the vertical range caused by the study design. In its natural habitat without artificial pools but many bromeliads it is rare to find *R. variabilis* below 2 m above the ground. They can be observed at heights of up to 7 m, which is where their breeding plants grow (BROWN et al. 2008a). Another reason might be the choice of the large pool size as the volume of 500 ml exceeds both the observed pool size ranges of *R. imitator* (9–44 ml) and *R. variabilis* (29–172 ml; BROWN et al. 2008b).

It may be hypothesized that phytotelmata size is not the only factor leading to spatial segregation of reproductive resources. It is likely that, due to the biology of the breeding plants, phytotelmata size and height are autocorrelated since plants used by *R. imitator* grow typically at lower heights than those used by *R. variabilis*, which are typically higher up on a tree (MERCIER & KERBAUY 1997, CRAYN et al. 2004, BROWN et al. 2008b). However, comparing our study with the results of BROWN et al. (2008b) shows that pool size seems to be the more important factor. Therefore, it may be suggested that an adaptation of phytotelmata-breeding species to particular plants may not be related to the location of phytotelmata, but rather their water-holding capacity. Our results are in concert with those of MAY et al. (2009). They reported that *Ranitomeya biolat* was using bamboo internodes as breeding sites and showed a significant preference for a certain volume of water, but no preference for a particular vertical position of the pools.

Since resource partitioning is a necessary requirement for the coexistence of two species using limited resources, one main difference between *R. variabilis* and *R. imitator* should be the use of different phytotelmata (HARDIN 1960,

INDERMAUR et al. 2009). In our study we were able to show that niche partitioning along a single niche axis, i.e., the size of breeding pools (shown by BROWN et al. 2008a,b), may already act as a sufficient niche differentiation to avoid competition between two closely related syntopic species and that a niche segregation of the vertical position of the breeding systems may not be as important.

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