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Perceived predation risk decreases movement and increases aggregation of Amazon milk frog (Anura, Hylidae) tadpoles throughout ontogeny

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Abstract In order to maximize escaping success, prey may change their predator avoidance behaviors according to their susceptibility. Morphological development during ontogeny may lead to different susceptibility to predators. Consequently, prey may exhibit different predator avoidance strategies according to the ontogenetic state. In this study, we used tadpoles of the Amazon milk frog *Trachycephalus resinifictrix* (Anura, Hylidae) to evaluate how variation in the ability to actively escape owed to the mobility acquired through ontogeny affects the adoption of predator avoidance strategies. We sampled tadpoles ($N = 384$) in temporary ponds and divided them in four consecutive developmental stages according to body size and mobility capacity. Subsequently, we measured their movement and spatial distribution when subjected to chemical cues of predators or control solutions. We found that they spent less time moving and increased spatial aggregation after receiving solutions with predator cues, independent of their developmental stage. These results indicate that the variation in escape capacity through larval ontogeny does not determine their antipredator strategy. Since tadpoles of *T. resinifictrix* typically grow in environments with reduced space for active escaping, such as tree holes and bromeliads, it may be that the ability to flee from predators is absent, even when this behavior increases the survival chances.

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Introduction

Predation risk is an important selective force shaping the evolution of many different animal life-history traits (Lima & Dill, 1990; Sih, 1992; Langerhans, 2007; De Block et al., 2008). Characteristics that reduce predation risk may be favored because they reduce the encounter rate with predators (Sih, 1992;

Sansom et al., 2009) or because they increase the chances of escaping after being detected (Langerhans, 2007). For example, camouflage seems to have evolved in multiple prey species as a strategy to reduce detectability (Thery & Casas, 2002). In the same way, a reduction in foraging activity when predators are nearby may decrease the chances of detection (Sih et al., 2004). On the other hand, prey may increase apparent size (Peckarsky, 1980; Williams et al., 2000; Toledo et al., 2011), or rely on fast-moving abilities to escape from predators after being detected (Bauwens & Thoen, 1981; Irschick & Losos, 1998).

Among species that live in groups, spatial aggregation of individuals may also work as an antipredator strategy (Watt et al., 1997; Spieler & Linsenmair, 1999; Gallie et al., 2001; Spieler, 2003). Aggregations (situation in which individuals remain in close proximity) may decrease predation risk by intimidating predators through coordinated movements, increasing the vigilance efficiency, or reducing the probability of individual detection due to the dilution effect (Davies et al., 2012). The dilution effect is particularly intriguing because this strategy is evolutionary stable only if the increased detection risk of groups of prey is offset by the reduced individual risk of predation (Wrona & Dixon, 1991).

Although aggregation reduces the individual chances of predation, its relative benefits may be surpassed by alternative escaping behaviors. For example, for species with fast-moving abilities, active escape from predators might be more effective to avoid predation than remaining in groups (Lima & Dill, 1990). Besides varying among species, escape behaviors may also vary throughout ontogeny, especially in organisms that experience extreme morphological and physiological transformations (Johnson & Sih, 2007; Langerhans, 2007; Hossie & Murray, 2012). During relatively slow-moving developmental stages, strategies related to low detectability may be used, such as remaining static. However, with the development of morphological and physiological traits associated with an increase in movement capacity, active escape behaviors after detection of predators should be favored (Martín & López, 2003).

Anurans experience dramatic changes during ontogeny (Fabrezi et al., 2014). Furthermore, the kinematics of swimming tadpoles is closely paired to their size and shape (Liu et al., 1997). On the initial stages, tadpoles usually have incipient swimming capacity and they often live in groups (McDiarmid & Altig, 1999). As their ontogenetic stage advances, the swimming and breathing structures develop, increasing their mobility, swimming speed, and maneuverability (Wassersug & Sperry, 1977; Huey, 1980). Thus, the morphological variation through ontogenetic stages on tadpoles may lead to different susceptibility to predators (Azevedo-Ramos & Magnusson, 1999) and to the adoption of different predator avoidance strategies (Crump, 1984; Dayton et al., 2005; Jara & Perotti, 2009).

In this study, we used tadpoles of Amazon milk frog *Trachycephalus resinifictrix* (Goeldi, 1907) to evaluate how variation in mobility capacity through ontogeny affects the adoption of different predator avoidance strategies. This species has been previously reported to occur in phytotelmata, such as ground bromeliads (Hero, 1990) and tree holes (Schiesari et al., 2003). Tree holes, in particular, have been identified as calling, breeding, and developmental sites for this frog. In this habitat, they apparently face a low predation pressure and, probably due to the low nutrient availability, tadpoles usually feed on eggs from subsequent clutches (Schiesari et al., 2003). However, different from these descriptions, we recently found populations of this species occurring in temporary ponds in Central Amazon Forest. Such places often present greater area and higher predation pressure than the previously reported habitats for this species. Because predators in temporary ponds are often sit-and-wait invertebrates, tadpoles with better mobility capacity located in these areas should be likely to show active responses to predatory attempts (Wellborn et al., 1996).

Because the swimming ability of tadpoles increases during their development (Landberg & Azizi, 2010) and because tadpoles present in temporary ponds may face greater predation pressure than in tree holes, we hypothesized that individuals in early developmental stages preferentially aggregate under predation risk, but change to active escape in the latter stages of development. If this hypothesis is true, we expect that recently hatched tadpoles will reduce their distance to conspecifics and their movement after receiving cues of predator presence, while individuals near the adult stage will increase their distance to conspecifics and their movement after perceiving predation risk.

Materials and methods

Study area

We carried out the experiment in November 2014, in Reserva 1501 (Km 41) (02°24′S; 59°43′W), ARIE-PDBFF (Biological Dynamics of Forest Fragments Project), in the Central Amazon Forest, approximately 80 km north from Manaus, Amazonas, Brazil. It is a primary tropical rainforest characterized by annual average temperatures of 27°C and annual average precipitation of 1900–2500 mm (Bierregaard Jr. et al., 1992).

We collected tadpoles of the Amazon milk frog *T. resinifictrix* from temporary ponds located at a sandy road that gives access to the reserve (ponds size ranged from 1 × 0.3 to 7 × 3 m). Each pond contained a high density group of tadpoles organized in polarized schools in similar developmental stage, suggesting that they may belong to a single clutch. Species confirmation was performed by (1) examination of specific larval traits such as the larval tooth formula; and (2) morphological observation of nearly metamorphosed individuals (Gosner stage 44; Gosner, 1960). All traits were compared with the known tadpoles from amazon region (see Hero, 1990). Usually, tadpoles of this species develop until metamorphosis in tree holes and bromeliad water (Hero, 1990), making this the first report of clutching of this species on temporary ponds. Our initial observations on natural ponds indicated that individuals in the first developmental stages remained aggregated and motionless. After any disturbance, they scattered, aggregated back, and remained motionless again. Nevertheless, individuals in later stages remained scattered and active, increasing the movement immediately after any disturbance. There were abundant predators in these ponds, such as giant water bugs, odonata larvae, and water spiders.

Data collection

We sampled tadpoles of *T. resinifictrix* ($N = 384$) in four consecutive ontogenetic stages indicated by increasing body size (stage 1: 0.27 ± 0.05 cm, stage 2: 0.73 ± 0.07 cm, stage 3: 0.92 ± 0.15, and stage 4: 2.03 ± 0.39 cm; average $\pm$ SD length) with a sieve of 2 mm net in four temporary ponds. Despite using arbitrary classifications for ontogenetic stages, the differences in body size were clearly related to different developmental stages in regards to morphological structures and swimming behavior. After the experiments, we returned the tadpoles to the sampling ponds.

To evaluate if predation risk affects the movement and aggregation behaviors of tadpoles at different ontogenetic stages, we established experimental arenas in the field near the ponds for each stage. Each arena consisted of 16 plastic plates of 20 cm diameter and 2 cm deep with approximately 100 ml of pond water. Before placing the tadpoles in the plastic plates, we mixed the clutches to remove parental effects on tadpole behavior. Afterwards, we simultaneously placed six larvae of similar sizes and same developmental stage (according to our classification) in the same plate and allowed them to acclimate for 30 min. After acclimation, we recorded the tadpoles' behavior using a camera Fujifilm Finepix S2800 for 30 s. At the end of the recording, we took a snapshot of the tadpoles' positions in each plastic plate. Although the natural aggregations in ponds contained many more individuals than in our experimental setup, we noted that when using groups of six individuals in the plates, the tadpoles exhibited very similar behaviors to the ones observed in the ponds.

After the initial record and snapshot, we alternated the inoculation of different treatments simulating the presence of a predator or a control stimulus (just one treatment per plate). To simulate the presence of a predator, we produced a solution with chemical cues of giant water bugs (Belostomatidae), that is one of the most voracious predators of tadpoles in ponds (Toledo, 2005) and frequently found in the study area. To obtain this solution, we maintained ten giant water bugs in 250 ml of water for 24 h before the experiment. We considered treatment as the careful inoculation of 2.0 ml of predator solution on eight plates of each ontogenetic stage, and control as the inoculation of 2.0 ml of filtered water on the other eight plates of each stage. To avoid disturbance effects, we always inoculated the predator or control solutions in the corner of the plates and as far as possible from any tadpole. Immediately after each inoculation, we repeated the video recording and snapshot procedures. We considered each plate of six larvae as a single replicate (totaling eight replicates per treatment). We conducted all experiments in the afternoon (3 pm) on two consecutive days that had similar climatic

conditions, avoiding possible alterations in tadpoles activity associated with variations in temperature and circadian rhythms between samples. In addition, we never used individuals in more than one test.

Movement data

To quantify changes in movement of the tadpoles under predation risk, we measured the time spent in movement by at least one individual using the recordings taken before and after the inoculation of the solution (treatment or control). Then, we calculated the difference between the time spent in movement before and after the solution inoculation. In this way, positive values for the difference of the time spent in movement before and after treatment indicate that the larvae increased the movement after the inoculation.

Given that the tadpoles acquire higher mobility capacity along their development (Wassersug & Sperry, 1977; Huey, 1980) and that they are able to recognize predator chemical cues (Kiesecker et al., 1996), our expectation was that tadpoles in later developmental stages would mainly rely on active escape. Consequently, we expected that larvae in the initial developmental stages would show negative values for time spent in movement after the inoculation of the solution containing predator cues and no difference when the inoculation contained only water. This difference would turn to positive values for tadpoles in the latter developmental stages.

Distribution data

To assess changes in aggregation of the tadpoles under predation risk, we measured the area occupied by each tadpoles' group using the snapshots taken before and after inoculation of the treatment or control solutions. For each snapshot, we marked the position of each individual tadpole and then calculated the area of the minimum polygon formed by the six tadpoles in each plate using the Image J software (version 1.48v; Schneider et al., 2012). Then, we calculated the difference between the area of the polygons conformed by the position of the individuals before and after the inoculation of treatment or control solutions. Negative values for the difference between the areas of the polygons before and after treatment would indicate that the larvae decreased aggregation after solution

inoculation, while positive values would indicate that they increased aggregation.

Given that tadpoles acquire higher movement abilities throughout their development, our expectation was that tadpoles in the final developmental states would show decreased aggregation under predation risk. Consequently, we expected that the difference in polygons areas before and after the inoculation of the predation solution to be positive when compared to the control for tadpoles in the initial developmental stages. This difference should turn to negative for tadpoles at the final developmental stages (Fig. 1).

Statistical analysis

We investigated changes on movement and aggregation of the tadpoles in response to the risk of predation using factorial ANOVA. We considered the ontogenetic stage (3 levels), treatment (2 levels) and their interaction as the explanatory variables and time spent moving as the response variables. We did not include the first stage in the movement time analyses because at this stage the movement time was always 0. In order to discern the differences between stages that moved, we removed this stage for the statistical analysis to avoid significant results derived only to the effect of the first stage. For the second analysis, we considered the ontogenetic stage (4 levels), treatment (2 levels) and their interaction as the explanatory variables and the polygon area formed by tadpoles as the response variable. We considered the level of significance $\alpha \leq 0.05$, and performed all statistics analyses using R. According to the visual inspection of residuals, the data followed all test assumptions (Quinn & Keough, 2002).

Results

In the experimental arenas, tadpoles behaved in a similar way that we observed in natural ponds. After acclimation, tadpoles became motionless in the bottom of the plates. In this position, they sometimes moved the end of their tails, but without any evident displacement. No individual showed any signs of injury or oxygen depletion like putting their mouths outside the water. After the inoculation of predator solution, the time spent moving by tadpoles was reduced independently of their developmental stage

Fig. 1 Schematic representation of the methods used to experimentally measure the variation in the movement (using footage) and aggregation (using photographs) of *Trachycephalus resinifictrix* tadpoles in the presence or absence of predation risk
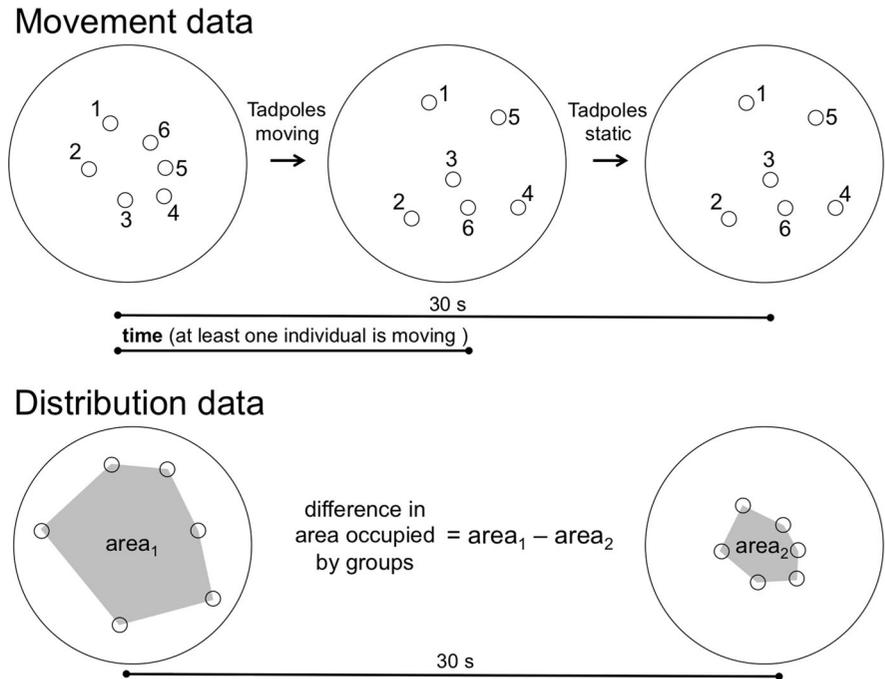

Table 1 ANOVA models showing the effects of ontogenetic stage (four ontogenetic classes) and treatment (control, predation risk) on aggregation and movement time of tadpoles of *Trachycephalus resinifictrix*

Effect	d.f.	F	P
Δ aggregation area			
Ontogenetic stage (O)	3	0.471	0.703
Treatment (Tr)	1	3.843	0.054
Interaction ($Tr \times O$)	3	0.377	0.769
Residual	66		
Δ movement time			
Ontogenetic stage (O)	2	2.525	0.093
Treatment (Tr)	1	9.407	0.004
Interaction ($Tr \times O$)	2	0.259	0.773
Residual	40		

(Table 1). Pooling all stages together, individuals spent 6.73 ± 6.46 s (mean $\pm$ SE) less time moving after receiving a solution with predator cue, while they spent 0.29 ± 9.74 s more after receiving the control treatment. In the same way, independent of their developmental stage, the reduction in the area of the positional polygon formed by tadpoles groups was greater after receiving a predator cue (12.4 ± 27.5 cm^2), in comparison to the area reduction observed after receiving the control solution (0.52 ± 23.2 cm^2) (Table 1).

Discussion

We found that tadpoles of *T. resinifictrix* spent less time moving and reduced the distance among individuals after receiving a solution containing predator cues. These results indicate that tadpoles of Amazon milk frog are, in fact, able to detect chemical cues of predators in the water and choose to aggregate and remain motionless. This pattern occurred even among individuals in advanced developmental stages that presented higher swimming capacity. Consequently, the improvement in alternative predator escaping behaviors was insufficient to trigger changes in the antipredator strategy.

The reduced movement after perceiving higher predation risk is widespread among anurans (Skelly, 1994; Nicieza, 1999; Laurila, 2000; Gallie et al., 2001; Bridges, 2002; Mathis et al., 2003). This behavioral strategy may decrease the detection rates because the tadpoles' predators are usually visually oriented (e.g., odonata larvae) or use water vibrations to perceive

prey, particularly for individuals that occur in temporary ponds (Persons, 1999). In fact, we observed many predator species that rely on visual (i.e., odonata larvae) or vibrational (i.e., aquatic spiders) cues to forage. In such environments, active escape from one predator may propagate water vibrations or increase the chance of visual detection by additional predators (Bleckmann & Lotz, 1987). Furthermore, temporary ponds are also more prone to desiccation, which shrinks water volume and limits the space available for escaping (Skelly, 1996; De Block et al., 2008).

The tendency to aggregate may explain why individuals reduced movement and indicated that individuals of *T. resinifictrix* may also benefit from the dilution effect. Aggregations may incur additional benefits such as increased vigilance or group defense (Davies et al., 2012). However, none of the other possible advantages of aggregation to avoid predation seem to explain aggregation of tadpoles in our studied system. Given that the water in ponds is highly turbid, the increased vigilance and the coordinated group movements may not decrease the predation risk to tadpoles (McDiarmid & Altig, 1999). Such prey strategies are effective when predators are able to see many preys together (Pritchard, 1965). Nevertheless, even the dragonfly larvae must be near tadpoles to detect them visually. Consequently, it is probable that the main advantage in the aggregation occurs because predators may attack any individual in the group. Consequently, the greater the group, the lower the probability of individual predation (Wrona & Dixon, 1991). If escape strategies that rely on rapid movement are less efficient due to low space available and the presence of different predator species with distinct hunting strategies (e.g., Relyea, 2001), aggregations may be the most profitable predator avoidance strategy throughout all ontogenetic development.

Because the efficiency of the dilution effect depends on the number of individuals that form the group, it may be less efficient for tadpoles in latter developmental stages. Probably, the aggregations of tadpoles in later stages of development are smaller in number in comparison to other ontogenetic stages due to a natural cumulative effect of mortality with increasing age (Kirkwood & Holliday, 1979). Furthermore, older tadpoles have a higher probability of detection due to their greater size. Consequently, unless greater size reduces the number of potential predators (Tejedo, 1993), older tadpoles may face

higher predation pressure than younger and smaller ones. Therefore, it seems intriguing that they exhibited the same predator avoidance strategies observed in individuals in early developmental stages. It is possible that their predator avoidance strategies are not flexible (Sih et al., 2004). If this is the case, the anti-predatory behaviors observed may be a unique strategy that has different efficiencies under distinct ontogenetic stages. Perhaps, it represents the option that maximizes survivorship at the end of the whole development, even if it is not the most profitable one for specific stages. Alternatively, it is important to note that *T. resinifictrix* tadpoles typically occur in tree holes (Hero, 1990), which represent areas with restricted space for active escaping and probably low predation pressure. In fact, tree holes seem to be the main reproductive site for this species and territorial adult males are often found defending these areas (Schiesari et al., 2003). Since males defend territories associated with tree holes, it is possible that tadpoles found in ponds were laid by females that mated with males that adopted an alternative mate-locating tactic. On the other hand, hylids females could also show plasticity in oviposition (Touchon & Warkentin, 2008), and temporary pounds could be the opportunity to nest in an alternative place when the preferred clutching site is limited. If one or both situations are true, tadpoles in ponds may lack the ability to change the behavior according to their swimming capacity because they are an example of a population that evolved in a habitat with low predation pressure.

One of the immediate consequences for individuals that reduce activity when predators are nearby is the concomitant reduction in foraging activity (Verdolin, 2006). Our results indicated that this might occur in *T. resinifictrix*. Consequently, individuals of this species may face a trade-off between foraging needs and predator avoidance. Such demand may be particularly important for individuals that occur in temporary ponds, since in this habitat they may suffer a higher rate of predation.

Conclusion

Tadpoles of the Amazon milk frog choose to aggregate and remain motionless under predation risk independent of their developmental stage. The improvement in swimming performance does not trigger any

alternative escaping behavior and the tendency of tadpoles to show a greater spatial aggregation after perceiving predator cues indicates that individuals of *T. resinifictrix* may benefit from the dilution effect. Perhaps, the adoption of active escaping increases the chances of detection by non-visual predators. Alternatively, it may be that tadpoles of this species lack the ability to change their behavior according to their developmental stages because they originally evolved in restricted habitats with low predation pressure.

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