

Strange parental decisions: fathers of the dyeing poison frog deposit their tadpoles in pools occupied by large cannibals

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Abstract Parents may increase the probability of offspring survival by choosing suitable rearing sites where risks are as low as possible. Predation and competition are major selective pressures influencing the evolution of rearing site selection. Poison frogs look after their clutches and deposit the newly hatched tadpoles in bodies of water where they remain until metamorphosis. In some species, cannibalism occurs, so parents deposit their tadpoles singly in very small pools. However, cannibalism also occurs in species that deposit tadpoles in larger pools already occupied by heterospecific or conspecific larvae that could be either potential predators or competitors. Here, I test the hypothesis that, given the choice, males of *Dendrobates tinctorius* would deposit their newly hatched tadpoles in low-risk sites for their offspring. I characterised the pools used by *D. tinctorius* for tadpole deposition, conducted experiments to determine the larval traits that predict the occurrence of and latency to cannibalism, and tested whether parents deposit their tadpoles in low-risk pools. I found that (1) neither pool capacity nor the presence of other larvae predict the presence/absence or number of tadpoles; (2) cannibalism occurs often, and how quickly it occurs depends on the difference in size between the tadpoles involved; and (3) the likelihood of males depositing their tadpoles in occupied pools increases with the size of the resident tadpole. I suggest that predation/cannibalism is not the only factor that parents

assess when choosing deposition sites, and that the presence of larger conspecifics may instead provide information about pool quality and stability.

Keywords Parental care · Rearing sites · Phytotelmata · Cannibalism · Competition · Poison frog

Introduction

Decisions made by parents about where to raise their offspring may have great fitness consequences. Selection, therefore, is expected to favour mechanisms that enable parents to assess the quality of such sites and select those that seem to maximise offspring growth and survival (Thompson and Pellmyr 1991). Predation, competition, and habitat desiccation, the main risks faced by the offspring of species that breed in temporary aquatic environments, have been identified as major selective pressures shaping the evolution of rearing-site selection by parents (Resetarits and Wilbur 1989; Fincke 1992a; Kats and Sih 1992; Blaustein and Kotler 1993; Murphy 2003; Blaustein et al. 2004; Rieger et al. 2004). Oviposition site selection may involve similar consideration of risks as selection of tadpole deposition sites. Patterns of selection of oviposition sites in relation to predator avoidance have been shown for mosquitoes (Mokany and Shine 2002; Blaustein et al. 2004; Silberbush and Blaustein 2011; Kershenbaum et al. 2012), frogs (Resetarits and Wilbur 1989; Rieger et al. 2004), and salamanders (Sadeh et al. 2009). Similarly, some frog species avoid intraspecific competitors of their offspring (Resetarits and Wilbur 1989; Crump 1991). Choices can be made too on the basis of environmental cues that are relevant for offspring development, such as temperature (Robertson 2009b), moisture (Brown and Shine 2005), or water presence (Rudolf and Rödel 2005), as it is necessary to prevent offspring death by desiccation of the rearing site. Likewise, choices can be

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influenced by food availability (Blaustein and Kotler 1993; Robertson 2009a) or previous successful experiences, for example by choosing places where there was a high hatching success in a previous reproductive event (Brown and Shine 2004).

Poison frogs (Grant et al. 2006) display a diversity of parental care modes, including no care (for example those species with endotrophic tadpoles), clutch attendance (one of the parents either stays constantly near the eggs or checks them a few times a day), tadpole transport, and, in some species, tadpole feeding (Grant et al. 2006; Lötters et al. 2007). Tadpoles are transported to bodies of water of varying size (Summers 1990; Brust 1993; Crump 1996; Poelman and Dicke 2007) where, in most cases, they remain unattended until metamorphosis. Some species deposit their tadpoles in large bodies of water, such as streams or permanent ponds, places at which anuran larvae seem to be under great predation risk by invertebrate larvae (Alford 1999); some others deposit their tadpoles individually in bromeliad axils and other small phytotelmata as a strategy to avoid larval cannibalism (Summers 1999; Summers and McKeon 2004). Individual deposition seems to be related to further parental care such as trophic egg provisioning (Brust 1993; Poelman and Dicke 2007; Brown et al. 2009), and the assessment of pool suitability prior to tadpole deposition (Schulte et al. 2011).

The intermediate situation, in which males carry tadpoles to large phytotelmata, such as tree holes, either previously or subsequently occupied by conspecific or heterospecific (anuran or insect) larvae, has received less attention. Food variety and availability in these pools are very low, and the predation risk is posed mainly by other tadpoles and invertebrate larvae, such as odonate naiads (Summers and McKeon 2004). Field studies on *Dendrobates auratus* (Summers 1990), *Dendrobates castaneouticus* (Caldwell and De Araújo 1998), and *Dendrobates truncatus* (BR, J. Gómez and A. Amézquita, unpublished data) indicate that larval cannibalism is common in large phytotelmata, and suggest that it could be the result of indiscriminate predatory behaviour of tadpoles as a way to eliminate potential predators and competitors (Caldwell and De Araújo 1998; Summers and McKeon 2004). These species, therefore, constitute a great study system to assess the implications of parental decision-making.

The cost of choosing the wrong sites to deposit tadpoles can be very high in terms of increased offspring mortality, and in turn decreased fitness for the parent. Given that larvae are unable to leave the sites where their parents deposit them (Rudolf and Rödel 2005), selection should favour mechanisms by which parents can assess the danger in their young's rearing environment prior to depositing their tadpoles and choose the sites that minimize risks, such as predation and desiccation and maximise survival. Here, I test the hypothesis that parents choose rearing sites without potential predators/competitors that threaten offspring's survival. This was done in a population of the poison frog *Dendrobates tinctorius* in

French Guiana by (1) characterising the sites where tadpoles are deposited, (2) assessing whether cannibalism occurs and determining the intrinsic traits of tadpoles that predict its occurrence, and (3) testing whether, given the choice, parents deposit their tadpoles in sites without large conspecifics.

Materials and methods

Study site and species

D. tinctorius is a diurnal, large (37–53 mm at the study site (Rojas and Endler 2013)) frog of the Neotropical family Dendrobatidae. It occurs around canopy gaps in primary forests in the Eastern Guiana Shield, at elevations from 0 to 600 m (Noonan and Gaucher 2006; Born et al. 2010). In the field, pairs lay clutches of four to five eggs that hatch after approximately 2 weeks (BR, personal observation). Tadpoles are then carried by the male, one or two at a time (Fig. 1), to tree holes either in standing trunks or fallen trees, or to palm bracts (hereon referred to as pools) at variable heights (P. Gaucher, personal communication; this study). Such pools may contain nonpredaceous larvae of other frog species such as *Ameerega hahneli*, *Rhinella castaneotica*, *Allobates femoralis*, *Trachycephalus resinifictrix* and *Trachycephalus hadroceps* (P. Gaucher, personal communication; this study). Once at their rearing site, tadpoles remain unattended until metamorphosis, which occurs after approximately 2 months (BR, unpublished data). At present, not much about the behavioural ecology of the species is known, although there is preliminary evidence (BR, unpublished data) that males may move up to a few hundreds of metres from the area where they live (as per mark-capture-recapture data) during tadpole transport. More than one male can be seen depositing tadpoles in a given pool (BR, personal observation), which indicates that tadpoles found in the same pool could be unrelated or only partially related (for example if they were offspring of different males but the same female). Males carrying two tadpoles



Fig. 1 A male *Dendrobates tinctorius* transporting two tadpoles on his back

can deposit one tadpole at a given pool and leave with the second one still attached to their back until another suitable deposition site is chosen, or deposit both tadpoles in the same pool, at the same time (BR, personal observation).

This study was done at Camp Pararé, Les Nouragues Reserve, French Guiana (3°59'N, 52°35'W) in a low-land forest where there is a large population of *D. tinctorius* (Courtois et al. 2013). The average annual temperature and precipitation at the study site are 26 °C and 2,990 mm, respectively (Grimaldi and Riéra 2001).

Characterisation of tadpole deposition sites

In order to identify the kind of pools that *D. tinctorius* uses for tadpole deposition, I did an extensive search for available water-filled pools on both fallen logs and standing trees along a 1.5 km transect. Every pool found was measured in its length, width, depth, and height above the ground. A stable indicator of pool water-holding capacity was calculated using the formula for the volume of an ellipse ($\frac{4}{3} \pi \times \text{length}/2 \times \text{width}/2 \times \text{depth}$) divided by two; actual water volume of a given pool varied visibly with changes in precipitation and temperature (BR, personal observation). For every pool, I recorded the presence or absence, and number of *D. tinctorius* tadpoles. The occurrence of eggs or larvae of other frog species, as well as the presence/absence of odonate naiads were also recorded as binary variables in both cases. In order to estimate the characteristics of preferred sites for tadpole deposition, I compared the characteristics of available pools with no tadpoles of *D. tinctorius* to those of pools occupied by the species by means of a logistic regression. The measured characteristics were used as predictor variables and the presence (1) and absence (0) of *D. tinctorius* tadpoles was entered as a binary variable. The characteristics of the subset of pools where *D. tinctorius* tadpoles were found were tested as predictors of the number of tadpoles found at a given time by means of a regression analysis. A pool was considered unused only if tadpoles were never seen there during the regular surveys done throughout the nearly 5 months of the duration of the study. I tested for the effect of the presence of larvae of odonates and of other frog species on the presence of *D. tinctorius* larvae by means of Chi-square analyses. The characterisation of deposition sites was done throughout the whole field season in 2011.

Experiment 1. Determinants of tadpole cannibalism

Twenty pairs of tadpoles were formed in order to test for the occurrence of cannibalism. Pairs were formed randomly from tadpoles coming from different natural pools placed simultaneously in an opaque plastic container with approximately 200 ml of rainwater and crushed leaf litter. Both tadpoles of each pair were photographed prior to

beginning the experiment in order to measure their body length (from the tip of the snout to the base of the tail) with the software ImageJ. The containers were left in the field, covered in order to avoid additional tadpole depositions, and checked twice a day until cannibalism occurred in order to record the “latency to cannibalism”. I tested for the effect of the absolute difference in size between the tadpoles in each pair (length of the largest–length of the smallest) on the probability of cannibalism within the first 24 h, and on the latency to cannibalism, by means of logistic regression and logarithmic regression, respectively.

Experiment 2. Tadpole deposition site choice

Because cannibalism seems to occur often (this study), it would be expected that fathers choose to deposit their tadpoles in pools without larger conspecifics if given the choice. To test this, I ran a second experiment by setting up 35 pairs of opaque plastic containers scattered in the forest in places where *D. tinctorius* adults had been seen. Five tadpoles were held individually in the containers for a week prior to the beginning of the experiments in order to detect negative effects of the plastic on the survival of larvae, if any, but no effects were noted. All tadpoles survived, behaved normally and looked healthy, and were not included in the subsequent experiment. Each experimental pair consisted of two containers with approximately 200 ml of rainwater and crushed leaf litter in the bottom. One of the containers had a tadpole of *D. tinctorius* (resident) whereas the other one was unoccupied. Resident tadpoles were collected from pools located at least 400 m away from the experimental setup where they were used. Paired containers were 15–30 cm apart. Each pair of containers was checked twice a day for the presence of newly deposited tadpoles. The father's choice was recorded as a binary variable: 1 for tadpoles deposited in the occupied container and 0 for depositions in the unoccupied container. When a newly deposited tadpole was found in either container (newcomer), both the resident tadpole and the newcomer were photographed in order to measure their body length and calculate the difference in size between them. Additionally, residence time (the number of days since each pair of containers was set up until a tadpole was deposited in either container) was recorded. The difference in size between the two tadpoles (length of the resident–length of the newcomer) was tested as a predictor variable of the father's choice with a logistic regression (Rudolf and Rödel 2005), with residence time as a covariate, using a stepwise procedure (backward: LR (Menard 2001)). These and all statistic analyses were done with the software SPSS 20.0 for

Mac. Both experiments were carried out between March 22 and May 31, 2011.

Results

Characterisation of tadpole deposition sites

Among the 30 pools found and surveyed regularly during the study, neither pool capacity nor height were good predictors of the presence of *D. tinctorius* larvae, which were found in only 16 of them (logistic regression; height—Wald $\chi^2=0.565$, $P=0.452$; capacity—Wald $\chi^2=0.814$, $P=0.367$; $N=30$). In various cases, more than one pool that seemed suitable for *D. tinctorius* tadpole deposition was found on the same treefall, but not all pools were used. On a few occasions, I observed males without tadpoles visiting used pools, and coming back a few days later with tadpoles attached to their back; other times, I saw also tadpole-carrying males visiting used pools, and leaving with the tadpoles still attached to their back. Interestingly, on at least three occasions, tadpole-carrying males arrived to never-used pools, stayed there for longer than 15 min, and left without depositing any tadpoles.

Odonate larvae were found in 10 (33 %) of the pools and tadpoles of other frog species (namely *R. castaneotica*, *A. femoralis* and *A. hahneli*) were found at some point in 29 (97 %) of the pools. Neither the presence of naiads ($\chi^2=0.068$, $df=1$, $P=0.794$, $N=30$), nor the presence of eggs or larvae of other frog species ($\chi^2=0.851$, $df=1$, $P=0.356$, $N=30$) were related to the presence of *D. tinctorius* tadpoles in the pools examined. *D. tinctorius* deposit their tadpoles in pools of small to medium capacity (median=254.78 ml; min=11.8 ml; max=1684.7 ml; Fig. 2) at observed heights between 0 and 65 cm (mean \pm SD=29.44 \pm 17.90 cm; median=30.50 cm), although there are anecdotal reports of tadpoles of this species in tree holes over 20 m above the ground (P. Gaucher, personal communication). I found between 1 and 10 tadpoles (mean \pm SD=3.29 \pm 2.33; median=3.00) of *D. tinctorius* at once in 16 pools, 14 water-filled cavities found in fallen trees (tree holes) and two fallen palm bracts. Pool capacity was not found to be a good predictor of the maximum number of tadpoles found in each pool at once (linear regression (on Log₁₀-transformed variables): $R^2=0.126$, $F_{1,15}=2.025$, $P=0.177$). Tadpoles of *D. tinctorius* were often deposited in pools already occupied by both conspecifics and heterospecifics. The larvae of other anuran or insect species ended up, in most cases, being eaten by the predaceous larvae of *D. tinctorius*. Likewise, tadpoles of *D. tinctorius* could precede tadpole deposition or egg laying by other species of frogs or odonates. Those tadpoles and eggs (or embryos) also ended up, invariably, being eaten by *D. tinctorius* larvae. Interestingly, some of the pools that were never found to have tadpoles of *D. tinctorius* had a high

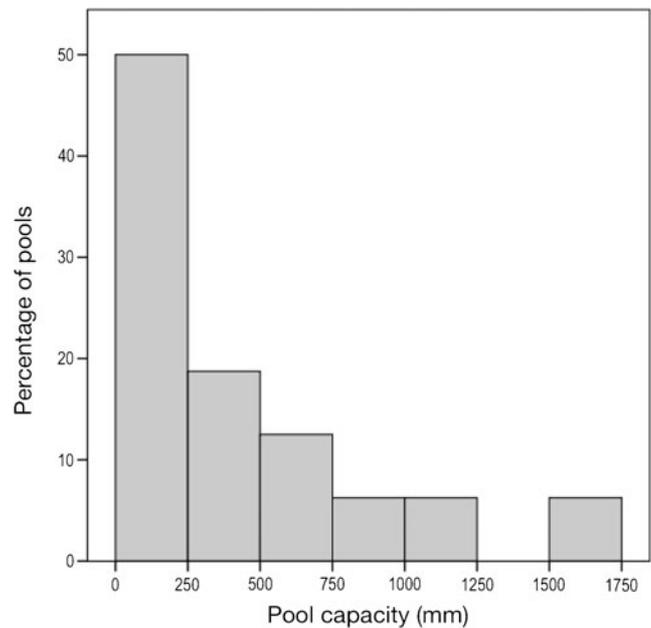


Fig. 2 Distribution of capacity among the pools where tadpoles of *Dendrobates tinctorius* were found

number of tadpoles of *A. femoralis* or *A. hahneli*, sometimes more than 20.

Experiment 1. Determinants of tadpole cannibalism

Cannibalism occurred in 100 % of the experiments within 2 weeks, with the larger tadpole always eating the smaller one. Difference in length between the two tadpoles had a significant effect on the latency to cannibalism (logarithmic regression: $R^2=0.23$, $F_{1,20}=5.35$, $P=0.033$; Fig. 3). Pairs of tadpoles with similar sizes showed the greatest variation in latency to cannibalism (Fig. 3). In 50 % of the cases, cannibalism occurred within the first 24 h. Cannibalism was observed in natural circumstances (i.e., in the natural pools chosen by the species for tadpole deposition) on 12 occasions in 5 out of 16 used pools.

Experiment 2. Tadpole deposition site choice

Twenty-four out of 35 pairs of experimental containers (68.6 %) were used by adults to deposit their tadpoles. The size of the resident tadpoles at the time when the choice was made varied from 5.41 to 10.90 mm (mean \pm SD=7.46 \pm 1.25), whereas the newcomers' size ranged from 4.60 to 6.06 mm (mean \pm SD=5.29 \pm 0.42; the resident was always larger). None of the tadpoles used as residents showed hind limbs or other signs of being near metamorphosis, which is reached at 11.06–15.26 mm (mean \pm SD=13.330 \pm 1.09) in this species (BR, unpublished data). Thus, resident tadpoles represented a real threat of cannibalism for newcomers.

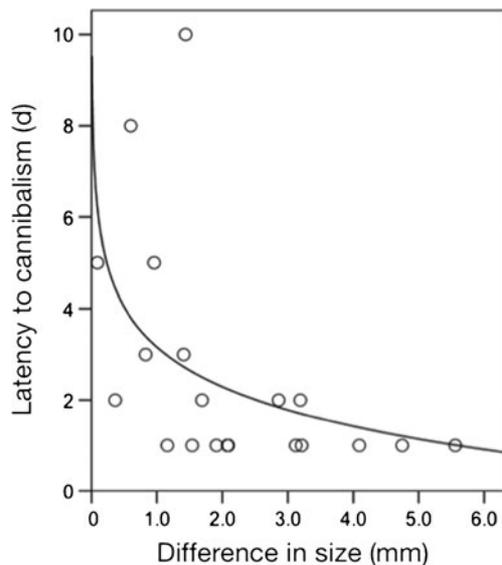


Fig. 3 Relationship between difference in size (body length; from the tip of the snout to the base of the tail) between two tadpoles and the latency to cannibalism. Line shows predicted values from a logarithmic regression

Tadpole deposition seemed to occur at similar rates in occupied and unoccupied containers (11 unoccupied (45.9 %), 13 occupied (54.1 %); binomial test statistic=13.00, $P=0.838$, $N=24$). However, the difference in size between resident and newcomer was found to be a good predictor of parental choice: the larger the size difference between the two, the more likely it was for fathers to deposit their tadpoles in the occupied container (logistic regression; residence time: $B=-0.085$, Wald $X^2=1.813$, $P=0.178$; difference in size: $B=1.709$, Wald $X^2=5.515$, $P=0.019$; $N=21$; Fig. 4). Residence

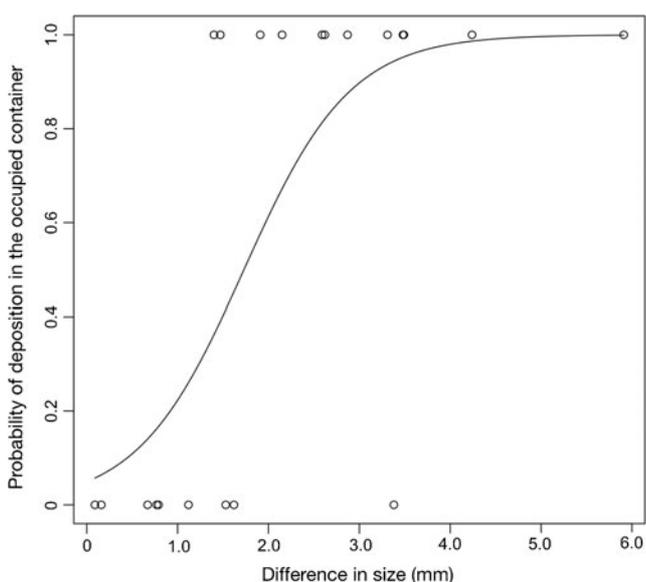


Fig. 4 Effect of the difference in size between a resident tadpole and a newcomer, on the probability that the father deposits his tadpole in a pool already occupied by a conspecific. Circles denote observed data; the line shows predicted probabilities from a binomial logistic regression

time had no influence on the parental decision. Three pairs of tadpoles could not be photographed because of extreme rain, so are not included in the logistic regression; in two cases, the father chose the unoccupied container, and in the third case, he chose the occupied one. The difference in size between one pair of tadpoles was an outlier; removing that data point did not change the conclusion.

Discussion

Males of *D. tinctorius* make what seem to be strange decisions regarding where to deposit their tadpoles. In a choice experiment between an unoccupied pool and a pool already occupied by a conspecific, fathers preferred to deposit their newly hatched tadpole with a large conspecific, but in an unoccupied pool if the conspecific in the alternative site was similar in size to its own tadpole. These results are interestingly counterintuitive given how often larval cannibalism takes place in natural pools. Cannibalism may be favoured in situations where resources are scarce and competition is high, as seems to be the case in phytotelmata (Lehtinen et al. 2004). During the course of this study, cannibalism occurred in all of the experimental setups (experiment 1) and was seen on numerous occasions in natural pools, which is an indication of its prevalence in natural conditions. In all cases, cannibalism involved a large tadpole eating a smaller one. Surveys of the natural pools used by *D. tinctorius* males for tadpole deposition (i.e., tree holes and palm bracts) revealed that the probability of finding tadpoles of *D. tinctorius* in a given pool does not depend on its capacity or height, or on the presence of potential heterospecific predators (odonate naiads) or prey (small naiads or larvae of other frog species). The number of tadpoles in a pool is also not related to its overall capacity.

Parents can lessen the risk of mortality to their larvae by avoiding competitors and potential predators. Some species of dendrobatids seem to inspect pools prior to depositing tadpoles, and use visual and/or chemical, and possibly mechanosensory, cues to avoid depositing in pools that are already occupied by conspecifics (Summers 1990; Caldwell and de Oliveira 1999; Poelman and Dicke 2007; Brown et al. 2008b; Schulte et al. 2011). This does not seem to be the case for *D. tinctorius*: the present study provides experimental evidence that, regardless of the high risk of cannibalism, fathers do not avoid depositing newly hatched tadpoles in pools already occupied by conspecific larvae. If only the occupancy of the pool is taken into account, there is a slight tendency towards preferring occupied pools. Some deposition events may have been missed due to cannibalism by the resident tadpole, which was free in the container rather than isolated as in other studies (Schulte et al. 2011; Schulte and Lötters 2013). However, this would produce a bias favouring the detection of deposition events in unoccupied containers,

counter to the trend. Selection would be expected to favour parental choices that maximise offspring survival. Therefore, given that cannibalism is common and heavily dependent on size differences between the tadpoles involved, male *D. tinctorius* should avoid depositing newly hatched tadpoles in pools already occupied by conspecifics, especially if they are large. This study shows the opposite and is, to my knowledge, the first to consider not only the presence but also the size of conspecifics, as a factor influencing parental decision-making in the context of offspring rearing site selection.

There are at least four possible explanations for this strange parental choice, whereby males deposit their tadpoles in pools occupied by large cannibals. First, despite the high risk of cannibalism, males might choose to deposit a newly hatched tadpole in an occupied pool because the presence of a larger conspecific tadpole indicates that other important requirements for larval development are met in that pool. Considering the ephemeral nature of most phytotelmata the presence of a large conspecific might, for example, give fathers an indication of habitat permanence (i.e., water-holding ability of a pool (Edgerly et al. 1998)). Cues of habitat permanence have been shown to influence oviposition site choice by some insects (Edgerly et al. 1998; Mokany and Shine 2003) and other frog species, which are capable of timing oviposition in a given site according to its water-holding capacity and water presence in the future (Rudolf and Rödel 2005). Habitat desiccation is a major cause of mortality among species that develop in ephemeral habitats (Aspbury and Juliano 1998; Altermatt et al. 2009). A recent study, in which chemical cues were used to simulate the presence of conspecific tadpoles, showed that males of *Ranitomeya variabilis* deposit their tadpoles in occupied pools during the dry season, when the risk of pool desiccation is very high (Schulte and Lötters 2013). Poelman and Dicke (2007) also reported oviposition in occupied pools by *Ranitomeya ventrimaculata* towards the dry season, whereas Rudolf and Rödel (2005) demonstrated that in the tree hole-breeding frog *Phrynobatrachus guineensis* the presence of conspecifics in a tree hole could be used by parents as a cue of habitat permanence. Females of *Oophaga pumilio*, which deposit their tadpoles in phytotelmata of very small capacity, consistently chose among the available deposition sites those with the greatest water volume. This choice would give their offspring a better chance to reach metamorphosis before the pools dry (Maple 2002), and highlights how different strategies could be employed by parents to prevent offspring death by dehydration. During the course of this study, water volume varied greatly over time, with both used and unused pools being totally full 1 day and less than a half full a few days later. In fact, at least seven pools were completely dry after a couple of days with temperatures over 30 °C and virtually

no rain (BR, personal observation). A few tadpoles, usually the largest ones, managed to survive in these conditions by remaining buried in the mud at the bottom of the pool, but many of them died (BR, personal observation).

Second, tadpole deposition in pools occupied already by conspecifics, despite the occurrence of cannibalism, can be a consequence of suitable sites being a limited resource. Parents, therefore, may have no alternative. Previous studies where the density of adult *Oophaga pumilio* increased considerably after the addition of tadpole deposition sites (bromeliads), suggest that these are indeed a limited resource (Donnelly 1989). Additionally, although mothers of *Oophaga pumilio* prevent larval cannibalism by depositing their tadpoles individually, multiple depositions in a single axil can occur when the availability of sites for tadpole deposition is limited (Brust 1990). *D. tinctorius* males readily utilise newly available natural and artificial deposition sites (BR, unpublished data), which could indicate that for this species the resource is limited, as is the case for *A. femoralis* (Ringler et al. 2013), *R. ventrimaculata* (Poelman and Dicke 2007) and some species of odonates (Fincke 1992b). However, of the 30 pools that were measured and checked for tadpoles throughout the study, only 16 ever had *D. tinctorius* larvae and neither the pool capacity nor the presence of larvae of odonates or other frogs was a good predictor of *D. tinctorius* presence. It thus seems that pool traits not considered in this study might influence fathers' choices, and that not every water-holding hole may be suitable for tadpole deposition. Abiotic factors such as temperature and chemical properties of the water (pH, conductivity, etc.) should be included in further attempts to elucidate those pool traits that determine their use by parents as tadpole-rearing sites. However, the abundance of unused pools does not support the idea that the "strange parental choice" of *D. tinctorius* is due to limitation in rearing-site availability.

Third, tadpole deposition in occupied pools might be a feeding strategy that speeds growth rates of residents. Carnivorous diets are known to increase growth rate (Wildy et al. 1998; Summers 1999; Alvarez and Nicieza 2002), which could in turn shorten the time until metamorphosis allowing individuals to leave desiccation-prone pools sooner (Alford 1999). Furthermore, increasing growth rates could also improve fitness because rapid growth allows tadpoles to more quickly reach a size at which they are safer from particular predators, and to attain a larger size at metamorphosis, which might enhance terrestrial survival and fecundity (Alford 1999; Harris 1999). This could make sense if, for example, the new tadpole were related to the resident, because the probability of survival of the latter would be increased with the consumption of the newcomer. Such is the case of species, such as *R. ventrimaculata*, which lay egg clutches in phytotelmata already occupied by a related conspecific tadpole, presumably as a feeding strategy; this occurs especially during the dry

season, when speeding up growth might reduce the risk of death by desiccation (Poelman and Dicke 2007). However, this scenario is unlikely in *D. tinctorius*. Several times more than one male was seen depositing tadpoles in the same pool, and “resident” tadpoles for the choice experiment were collected more than 400 m away from where they were used, making it highly unlikely that they were related to the males making the choice. To my knowledge, there is no evidence of parents deliberately feeding young tadpoles to older ones. Cases of what has been called “reproductive parasitism” are known, in which tadpoles are deposited in places where there are conspecific eggs or embryos (Brown et al. 2008b), so that the newly deposited tadpole has a size advantage over the “residents”. In an Ecuadorian population of *R. ventrimaculata*, for example, embryos may slip down the axil where they were laid as eggs. Males (either related or unrelated to the embryos) can use those same axils to deposit new tadpoles, which have a size advantage over the embryos and will feed on them (Summers and Amos 1997). Because the new tadpoles are not necessarily related to those already occupying the axil, this behaviour does not entail a feeding strategy either. These cases do not resemble what happens in *D. tinctorius*, in which resident tadpoles are larger than the newly deposited ones. Therefore, the “feeding strategy” hypothesis is the least plausible explanation for the choice made by male *D. tinctorius* of depositing newly hatched tadpoles in pools with large cannibals. Nonetheless, it should not be entirely discarded until more is known about the abilities of fathers to identify a tadpole in a pool within their spatial range as their own.

Fourth, these “strange decisions” could be a mistake made by fathers, which might be unable to detect the presence of a conspecific tadpole during their visit to potential deposition sites, or the product of a random choice. This, however, is highly unlikely given the growing body of evidence regarding site assessment prior to tadpole deposition (Brust 1993; Summers 1999; Brown et al. 2008a, b; Stynoski 2009; Schulte et al. 2011). Furthermore, recent findings indicate that even poison frogs with a low level of parental care are capable of deciding strategically, rather than randomly, where to deposit their tadpoles (Ringler et al. 2013).

Besides cannibalistic conspecifics, tadpoles also face heterospecific predators and both conspecific and heterospecific competitors (Alford and Wilbur 1985; Twomey et al. 2008). Males of *D. tinctorius* do not seem to avoid either predators or competitors for their offspring when choosing sites for tadpole deposition, as they can be deposited either before or after other species bring tadpoles to or lay eggs in the same pool. Rather, *D. tinctorius* tadpoles seem to be a good example of intraguild predators (Polis et al. 1989; von May et al. 2009) partially governed by priority effects (Fincke 1999). Early arrivals may have access to more abundant resources and not only become better competitors but also become predators rather than prey. Thus, the order of arrival may affect not only the outcome but

also the nature of interspecific interactions (Blaustein and Margalit 1996), determining who will be a better competitor (Alford and Wilbur 1985; Lawler and Morin 1993; Knight et al. 2009; Hernandez and Chalcraft 2012) and whether the interaction will be competition or predation (Fincke 1999; Eitam et al. 2005).

Odonate naiads are major predators of anuran tadpoles (Alford 1999). Naiads were found simultaneously with tadpoles of *D. tinctorius* in 33 % of the pools examined in this study, but naiads large enough to kill a co-occurring large *D. tinctorius* tadpole were found only in one pool (two naiads at once). In a subsequent visit, that tadpole had disappeared but the naiads were still alive, which strongly suggests that one of them ate the tadpole. On several occasions, adult odonates were seen ovipositing in pools containing *D. tinctorius* tadpoles and the tadpoles subsequently seen preying on the hatching odonate larvae. Thus, if the odonate naiads arrive early enough they can prey on *D. tinctorius* tadpoles and vice versa.

The presence of larvae of other frog species (potential heterospecific competitors) did not seem to prevent *D. tinctorius* tadpole deposition, and either eggs or tadpoles of other species were found at some point in 97 % of the pools surveyed during this study. On the contrary, if heterospecifics do not represent strong competitors, pools with heterospecific eggs or tadpoles could be even preferred by fathers. In most cases, given favourable differences in size, both eggs and tadpoles of other frogs are quickly consumed by the voracious tadpoles of *D. tinctorius*, providing very nutritious meals. For example, tadpoles of *D. tinctorius* have been seen in tree holes where the hyloid frogs *T. resinifictrix* and *T. hadroiceps* breed (P. Gaucher, personal communication). Eggs, embryos and larvae of these two species are readily consumed by *D. tinctorius* larvae (P. Gaucher, personal communication), which in turn experience considerably higher growth rates than when fed only with detritus (BR, P. Gaucher and T. Legagne, unpublished data). Similarly, tadpoles of *A. femoralis* deposited in a pool already occupied by *D. tinctorius* do not survive for long (BR, personal observation). This is also the case of the closely related *D. auratus*, which preys on tadpoles of *Oophaga granulifera* whenever the two co-occur (Ryan and Barry 2011).

Future work combining behavioural ecology and molecular techniques may elucidate the reasons why frogs in the *D. tinctorius* group (Grant et al. 2006) did not evolve the strategy of single tadpole deposition despite their high levels of cannibalism. So far, however, it seems that *D. tinctorius* larvae have the ability to successfully outcompete both conspecifics (provided a minimum difference in size) and heterospecifics co-occurring in their pools via predation. Further research is needed in order to assess the effect of large noncarnivorous larvae on the growth of newly deposited tadpoles of *D. tinctorius*.

Choosing good places for tadpole deposition has direct effects on fitness because the conditions experienced by larvae affect their survival as well as other important life history traits such as time to and size at metamorphosis (BR, J. Gómez and A. Amézquita, unpublished data), and size at maturity (Mokany and Shine 2003). Apparently, strange parental decisions, such as depositing offspring with large cannibals, may ultimately not be that strange if they entail the consideration of factors that influence the survival of offspring not only immediately (i.e., predation) but also over the longer term (e.g., competition, habitat desiccation, and food availability). The results presented here raise questions regarding those benefits that would compensate for the loss of offspring to cannibalism, and those abiotic traits that ultimately make a pool suitable for tadpole deposition. The answers to these questions would represent an important step forward in our current understanding of parental decision making. Finally, this study emphasises the importance of rearing site selection and priority effects in shaping the dynamics of temporary pool communities.

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