

Offering offspring as food to cannibals: oviposition strategies of Amazonian poison frogs (*Dendrobates ventrimaculatus*)

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Abstract Species utilizing distinct resources for offspring production often show plasticity in reproductive strategies as a function of resource quality. For species using ephemeral pools, strategies are mainly shaped by a time constraint related to pool stability, resource availability and the colonizing community. We studied reproductive strategies in Amazonian poison frogs (*Dendrobates ventrimaculatus*) that are characterized by oviposition in distinct, small and resource-limited water bodies in leaf axils of plants and the transport of newly hatched tadpoles on the back of males to similar water bodies. Cannibalism of eggs by tadpoles was found to be the main cause of egg mortality. Typically, at the end of the rainy season new clutches of eggs were deposited in water bodies already containing a tadpole. Manipulation of the available number of water bodies showed that this observation did not result from resource limitation. We conclude that *D. ventrimaculatus* has a plastic reproductive strategy that includes provisioning its tadpoles with fertilized eggs as a function of desiccation risk of water bodies housing its offspring. Provisioning behavior is expected to increase developmental rate and, therefore, chances of metamorphosis for tadpoles that hatched towards the end of the rainy season. The plastic food provisioning strategy may be an important evolutionary link to bi-parental and female care with development of obligate unfertilized egg provisioning in the genus *Dendrobates*.

Keywords Reproductive strategy · Resource manipulation · Egg feeding · Cannibalism · Parental care

Introduction

Many animal species utilize spatially, structurally and temporally distinct resources for the development of their progeny (Mock and Parker 1997), which includes for

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example butterflies that oviposit on plants, parasitoid wasps that lay eggs in caterpillars, or amphibians that use ephemeral pools for oviposition. As a consequence, their offspring have limited chances to move to new resources, and therefore might compete locally for limited resources (Stephens and Krebs 1986; Mayhew 1997; Mock and Parker 1997). The direct relationship between resource quality—in terms of food availability, stability, risk of predation and competition—and the number and quality of offspring implies that there is strong selection on resource-selection behavior of parents (Godfray 1994; Mayhew 1997; Alford 1999; Álvarez and Nieceza 2002; Altwegg and Reyer 2003; Lehtinen 2004). The “oviposition-preference—offspring-performance” hypothesis therefore predicts that female oviposition decisions are selected to maximize fitness by maximizing larval performance (Thompson 1988; Mayhew 1997). This hypothesis has been supported by many studies on insect parasitoids (Waage and Godfray 1985; Godfray 1987; Vet et al. 1993; Brodeur et al. 1998) and phytophagous insects (Hopkins and Ekbohm 1999). However, there is growing evidence that, although female oviposition decisions are made to maximize their net fitness, female decisions may not match maximal performance of some or any offspring (Mayhew 1997). For example, females may produce a large number of low quality offspring by increased oviposition in high-quality resources (Nufio and Papaj 2004) or females may allocate their investment differently over offspring to match resource quality (Ekbohm and Popov 2004). Furthermore, these decisions might look suboptimal when not considered in the total reproductive strategy. Oviposition on/in apparent suboptimal resources may be caused by other factors that affect female fitness, such as maximization of female performance (Scheirs et al. 2000) including female survival probability (Weisser et al. 1994; Mattiacci and Dicke 1995) or may result from avoiding competitors occupying high quality patches (Murphy 2003), including offspring of conspecifics that may have cannibalistic traits (Fincke 1994; Crump 1983), that kill or suppress competitors (Godfray 1994). Reproductive resources are often affected temporally by abiotic and biotic conditions (Wellborn et al. 1996; Wilbur 1997; van Zandt and Agrawal 2004; Rudolf and Rödel 2005) and, therefore, decisions that may be optimal for one offspring might not benefit any other of a female’s offspring (reviewed by Mayhew 1997). Parents confronted with variability of resources over time should be able to monitor the quality changes in their reproductive resources and should display plastic responses to these conditional changes as components of their reproductive strategy to maximize their fitness (Gross 1996). A laboratory study on solitary endoparasitoid wasps, for example, showed that these wasps usually lay a single egg per host, but competition for a limited number of hosts can result in an adaptive oviposition strategy in which females lay multiple eggs per host or oviposit in hosts containing competitors (van Alphen and Visser 1990; Visser 1993). However, examples of plastic responses as components of reproductive strategies in response to changes in environmental conditions during a reproductive season in the field are scarce.

Neotropical poison frogs of the genus *Dendrobates* are good candidates for the study of this phenomenon. Characteristically they lay terrestrial eggs and newly hatched tadpoles are transported on the back of one of the parents to distinct plant-held water bodies including tree holes, seed husks and the leaf axils of aroids, heliconias and bromeliads (Myers and Daly 1983; hereafter referred to as phytotelmata). These frogs display a variation of reproductive strategies associated with the use of small resource-limited ephemeral pools in which they deposit their offspring (Weygoldt 1987; Summers and McKeon 2004). Parental care of eggs and

tadpoles in the different species can be provided either by the male, the female or by both parents. In some species females deposit unfertilized trophic eggs in phytotelmata containing their own offspring (Weygoldt 1987; Summers and McKeon 2004) that obligatorily feed on these eggs (Brust 1993; Pramuk and Hiler 1999).

A complex of closely related species affiliated with *D. ventrimaculatus* (Symula et al. 2003; Brown et al. 2006; Noonan and Wray 2006) uses water bodies in leaf axils for both tadpole and egg deposition. The reproductive season in these species may last for several months during the rainy season, up to the entire year when phytotelmata do not desiccate, and females produce multiple clutches per reproductive season. Males care for eggs and transport tadpoles, one or two at a time, on their back to other phytotelmata. Typically egg clutches are deposited on the edge of the phytotelm partly submerged below the water line (Bechter and Lescure 1982; Summers and Amos 1997). Larger tadpoles may cannibalize conspecific eggs and tadpoles regardless of relatedness when sharing a phytotelm (Summers and Symula 2001) with the result that a single water body normally yields only a single frog at a time (Summers and Amos 1997). However, multiple depositions of tadpoles and eggs in the same phytotelm do occur and molecular studies have shown that these may originate from several parents (Summers and Amos 1997). Tadpole development in these small resource-limited pools requires 2–3 months until metamorphosis (Caldwell and Araujo 1998). Towards the end of the reproductive season the quality of many phytotelmata decreases dramatically either by increased desiccation risk, changes in chemical composition of the solution or by the presence of a conspecific tadpole from previous clutches (Kam et al. 2001). It is therefore expected that parents respond to these changes in reproductive resources by changing their reproductive strategy. In the present field study we addressed three questions: first, we investigated whether parents avoid deposition of offspring in phytotelmata containing a conspecific tadpole, and compared success of egg development in absence or presence of tadpoles. Secondly, we experimentally studied whether the availability of reproductive resources, by manipulating the availability of phytotelmata, influences the parents in resource use; e.g., does oviposition in phytotelmata containing a tadpole result from limitation in availability of unoccupied phytotelmata? Third, we investigated whether oviposition decisions are dependent on seasonal variation in desiccation risk of phytotelmata by correlating rainfall in the study area with oviposition strategies of frogs. Furthermore, we made detailed observations on the behavior of Amazonian poison frogs involved in oviposition and tadpole deposition to support interpretation of the findings. Finally, we discuss the implications of these findings in the context of poison frog reproductive strategies and variation in reproductive strategies in general.

Methods

Study area

This study was carried out on a population of Amazonian poison frogs (*Dendrobates ventrimaculatus* Shreve 1935) on a rocky outcrop (411 m above sea level) in the rainforest of Nouragues reserve of French Guiana (4°5' N, 52°41' W). Frog habitat consisted of small patches of vegetation with maximal height of 3 m above the forest floor. These patches of vegetation included the epiphytic *Catopsis berteroniana*

bromeliads and two terrestrial bromeliads (*Pitcairnia geykessi* and *Aechmea aquilega*) (see Sarthou 2001 for a detailed description of the study area). Vegetation patches were separated by at least 2 m of granite rock. We studied reproductive activity of individual frogs on nine of these patches from 10 April 2002 to 27 July 2002.

Study species

Dendrobatidae is a family of Neotropical terrestrial and diurnally active frogs with the exception of a single aquatic nocturnal species (*Aromobates nocturnus*) (Wells 1981; Myers and Daly 1983; Myers et al. 1991; Summers and McKeon 2004). Amazonian poison frogs (*D. ventrimaculatus*) are 15–18 mm in size, brightly colored and can be found in the entire Amazon basin (Symula et al. 2003). We used unique color patterns to recognize individuals. Patterns were drawn on identification cards to enable identification of frogs during subsequent visits in the field (Summers 1989, 1992). Since only males call, individuals could be recorded as males when they were observed calling, and as females when they were involved in courtship behavior typically following a calling male to a bromeliad leaf axil (Bechter and Lescure 1982). Other frogs were recorded as being of unknown sex.

Assessing egg and tadpole deposition strategies

Bromeliad distributions in the nine vegetation patches, each with a size of ca. 100 square meters, were mapped by dividing the patch into a grid of square meters. Subsequently, the positions of bromeliads were drawn inside these square meters to the closest decimeter. Over the study period of 4 months, the nine patches were monitored in series of three subsequent days followed by a day without observation. During each visit we recorded and mapped the locations of eggs and tadpoles, and marked leaf axils of bromeliads containing new depositions with small colored stickers for egg and tadpole presence. Phytotelmata that contained a clutch of eggs were monitored for the survival of eggs during subsequent visits. All encountered frogs were individually identified, and their location was mapped to the closest decimeter. The amount of rainfall was measured to the nearest tenth of a mm on a daily basis in the local Nouragues weather station and transposed into weekly amounts of rainfall.

Resource manipulation

In the eighth study week, 5 June 2002, the nine vegetation patches were randomly assigned to one of three resource manipulation treatments: removal, addition and control. For the removal treatment, the number of water bodies was decreased in three vegetation patches by puncturing half of all leaf axils, which drained water from the axils. For the addition treatment, a total of 362 plastic cups containing 15 ml of water was attached to bromeliads with wires, doubling the number of water bodies in three patches. The addition or removal of water bodies on individual bromeliads was executed in a way that did not change the spatial distribution of reproductive resource density. This was done to prevent the emergence of potential new territories by addition of resources on locations where they were previously

absent (Donnelly 1989a, b). The remaining three plots served as unmanipulated controls. We continued monitoring deposition of eggs and tadpoles as described above for the rest of the study period.

Parenthood discrimination

We tested the ability of males to discriminate between clutches of their own eggs and those of conspecifics (Sherman et al. 1997), because kin discrimination plays an important role in the trade-offs of the previously described reproductive strategies of poison frogs. Ten naturally deposited clutches were each replaced by another clutch. We matched clutches by age and clutch size. During subsequent visits, we monitored whether eggs of the replaced clutch developed into tadpoles normally and whether tadpoles were transported by the male caring for this clutch. We used tadpole transport by the male as an indication that males recognize the replaced clutches as own offspring. Recognition of parenthood of a clutch by a male may be based on the location of the eggs, thereby treating eggs in its territory or on the exact same place as its own offspring. To assess whether males used the location of a clutch as a factor to determine their parenthood we (1) relocated clutches to the nearest leaf axil of the same bromeliad ($n = 10$) to test for recognition of the exact oviposition site, and (2) relocated clutches to the nearest bromeliad plant within the male's territory, resulting in a movement of 1–2 m from their original site ($n = 3$, due to a limitation of available clutches for the experiment) to test whether males treat all clutches in their territory as own offspring. When tadpoles had hatched and disappeared without observation of transport by a male, we emptied the leaf axil to check for tadpoles. This was done to confirm that the male transported the tadpoles, as hatched tadpoles that are not transported slide into the pool of the leaf on which the eggs were oviposited.

Statistical analyses

Statistical tests were performed using SPSS 12.0.1 for Windows and GenStat 8th Edition. A comparison between egg survival within clutches in phytotelmata containing a tadpole and clutches in phytotelmata where tadpoles were absent was made, using a Mann–Whitney U test. Stepwise Logistic Regression was applied to analyze the frequency of egg deposition in tadpole-containing phytotelmata compared among different reproductive resource manipulation treatments. All newly deposited clutches were valued as 1 when they were deposited in a tadpole-containing phytotelm, as 0 when tadpoles were absent and included in the analysis as binomially distributed dependent variable. The dependent variable was modeled in a full model containing the effects of resource manipulation, assessment period (before or after resource manipulation) and vegetation patch. The final model, represented by a minimum adequate model, was reached by running a full model, including all effects and their interactions, and subsequently deleting non-significant effects using the maximum-likelihood method (Crawley 1993). The presented null model indicates the overall deviance in the dependent variable. None of the interactions between terms were significant and therefore not presented in the results. In a separate regression analysis, oviposition behavior was correlated with rainfall to measure temporal variation in reproductive strategies and reproductive activity.

Results

In the nine vegetation patches we observed a total of 72 individual frogs during the study period of 112 days. A total of 35 individuals, distributed over the study area with 3.9 ± 1.8 (SD) individuals per patch (ca. 100 square meters), could be identified as males, another 33 individuals, 3.7 ± 1.3 (SD) per patch, as females. Four individuals were neither observed vocalizing nor in courtship and could, therefore, not be sexed. Males were seldomly observed on more than one patch and aggressively defended territories over the entire study period. Defense consisted of chasing, calling and physical combat directed towards intruding males. The intruding males we observed (22 occasions), were males of neighboring territories in the same patch either carrying a tadpole ($n = 9$) or approaching the resident male that was in courtship with a female ($n = 8$). In contrast, individual females were typically observed in more than one patch and were never observed in agonistic interactions.

Oviposition and tadpole deposition preference

We observed 132 clutches of 1–6 eggs with an average of 2.6 ± 0.98 (SD) eggs per clutch all attached to the leaf just below the water surface in the phytotelmata of bromeliads. Eggs hatched after 10–15 days, on average after 12.4 ± 1.72 (SD) days. Tadpole transport was observed 35 times; in two of these cases a female transported the tadpoles. Tadpole deposition was observed in 21 of these cases, of which 16 occurred in phytotelmata inside the territory of the transporting male. In 30 cases phytotelmata contained both eggs and a tadpole. In 28 (93%) of the cases, oviposition occurred in phytotelmata already containing a tadpole. Egg mortality within a clutch was significantly higher when a conspecific tadpole occupied the phytotelm compared to when there was no tadpole present (Mann–Whitney U test, $Z = -7.997$, $n = 132$, $P < 0.001$) (Fig. 1), which indicates that tadpoles consumed eggs. This is supported by several observations of tadpoles actually consuming eggs ($n = 7$) by biting into the eggs and aggressively moving the tail to generate force required to break the jelly of the egg mass apart. Clutch size was not different between clutches that were deposited in phytotelmata containing a tadpole (2.63 ± 1.05 (SD)) and clutches deposited in unoccupied phytotelmata (2.62 ± 0.96 (SD)) (Mann–Whitney U test, $Z = -0.052$, $n = 132$, $P = 0.96$).

Courtship behavior was observed 103 times (28 different males and 33 females). Individual males were observed courting on 1–9 occasions (3.7 ± 2.3 (SD)) and males that were observed in courtship on more than three occasions were found

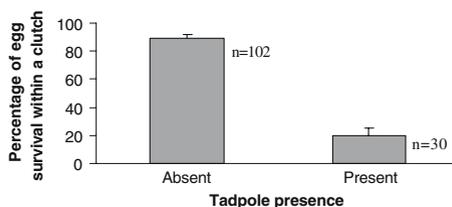


Fig. 1 Survival of eggs in clutches deposited in phytotelmata with a conspecific tadpole present or absent. Bars represent averages with SE of the percentage of eggs that survive within a clutch. Presence of tadpoles decreases the survival of eggs (Mann–Whitney U test, 251.000, $Z = -7.997$, $n = 132$, $P < 0.001$)

courting the same female in $74\% \pm 19.8\%$ (SD) of the cases. However, all individual males courted at least two different females during the reproductive season. The courtship behavior of 34 pairs could be followed until oviposition. Males led their females always to a phytotelm inside their territories and in six cases these phytotelmata already contained a tadpole. We observed one male engaged in courtship while transporting a tadpole. During courtship the tadpole slid off the back of the male into the phytotelm and the following day a clutch of eggs was observed in the same phytotelm.

We found that the frequency of oviposition in tadpole-containing phytotelmata was related to a temporal effect when comparing egg deposition strategy before and after the reproductive resource manipulation treatment, i.e., assessment period, of the vegetation patches. After resource manipulation a larger fraction of clutches was deposited in phytotelmata containing a tadpole (Stepwise Logistic Regression, *assessment period* deviance = 12.58, *df* = 1, $P < 0.001$; Full model deviance = 120.17, *df* = 114; Null model deviance = 141.49, *df* = 131; Final model deviance = 128.92, *df* = 130) (Fig. 2). The plastic cups that were added in three plots were used for both oviposition and tadpole deposition. Oviposition decisions were not influenced by either treatment (i.e., increased number of oviposition sites, decreased number or no change in number of oviposition sites) or patch (Stepwise Logistic Regression; *treatment*: *df* = 2, $P = 0.87$, *patch*: *df* = 8, $P = 0.90$). Daily rainfall varied from 0 to a maximum of 52.6 mm. The amount of rain reached a maximum in the 8th week of the study, the first week of June 2002, and decreased rapidly towards the end of the experimental period. We found that the number of clutches deposited per observation week was positively related to the amount of rainfall (linear regression, $r = 0.096$, $R^2 = 0.44$, $F = 11.026$, $n = 16$, $P < 0.01$). The number of clutches decreased when the amount of rainfall decreased. As a result the percentage of clutches deposited in phytotelmata containing a tadpole was negatively related to the amount of rainfall (linear regression, $r = -0.61$, $R^2 = 0.47$, $F = 10.524$, $n = 14$, $P < 0.01$) (Fig. 3). The data presented in Figs. 2 and 3 therefore show that during the season, the decrease in amount of rainfall is correlated with an increase in the number of clutches deposited at tadpole sites.

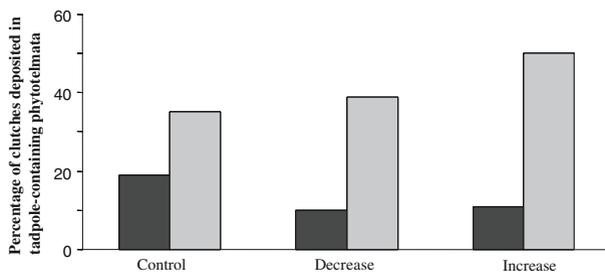


Fig. 2 Percentage of clutches deposited in water bodies containing a tadpole before and after resource manipulation. The black bars represent the percentage of clutches deposited before resource manipulation (total $n = 85$), the grey bars that of the subsequent period in which resources are manipulated (control, decrease or increase of the number of water bodies) (total $n = 47$). Egg deposition frequency at tadpole-containing phytotelmata was significantly different between the study period before and after resource manipulation (Stepwise Logistic Regression, *assessment period* deviance = 12.58, *df* = 1, $P < 0.001$). Oviposition decisions were not influenced by either treatment or patch (Stepwise Logistic Regression; *treatment*: deviance = 0.28, *df* = 2, $P = 0.87$, *patch*: deviance = 3.49, *df* = 8, $P = 0.90$)

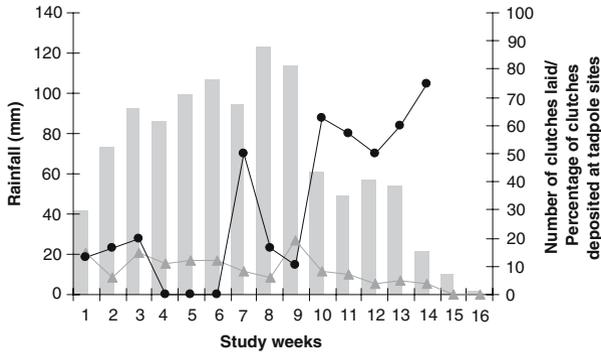


Fig. 3 Rainfall and oviposition strategies over the study period. Total amount of rainfall per week is plotted on the primary axis and presented in grey bars. The number of clutches over the study period, starting on the 10th of April (week 1), are plotted in grey triangles against the secondary axis representing actual numbers of clutches found. The black dots plotted against the secondary axis represent percentages of clutches deposited during the respective weeks in phytotelmata already containing a tadpole. A significant correlation with rainfall was found for both the number of clutches produced (linear regression, $F = 11.026$, $n = 16$, $P < 0.01$) and the percentage deposited in phytotelmata containing a tadpole (linear regression, $F = 10.524$, $n = 14$, $P < 0.01$)

Parenthood discrimination

All males ($n = 10$) that sired a clutch of eggs, which had been replaced by a clutch from a conspecific male, transported the entire number of hatched tadpoles and thus accepted them as their own offspring. Actual tadpole transport was observed in seven cases and none of the phytotelmata contained tadpoles when emptying the leaf axil to check for transport. The results were similar for the relocated clutches both to the nearest axil and to the nearest bromeliad (10 out of 10 and 3 out of 3, respectively). Males treated all clutches within their territory as their own offspring.

Discussion

Our study shows that the cannibalistic tendencies of tadpoles of Amazonian poison frogs play an important role in the outcome of reproductive resource use by parents. Females that deposit eggs in phytotelmata containing a tadpole suffer a fitness cost through cannibalism of these eggs. We found eggs to be deposited away from tadpoles at the beginning of the rainy season, showing that the frogs avoid oviposition at sites with high risk of egg cannibalism. Towards the end of the rainy season, however, a large percentage of clutches was deposited in phytotelmata containing a tadpole. This oviposition at tadpole deposition sites towards the end of the rainy season may have several explanations.

First, parents may be constrained by a limited number of phytotelmata that get occupied by tadpoles from previous reproductive efforts, forcing parents into using phytotelmata containing cannibalistic offspring for egg deposition (Summers 1999). Males of *D. ventrimaculatus* in our study defended territories containing several bromeliads with many phytotelmata that were not used during the reproductive season. Use of a limited number of phytotelmata per bromeliad only, may be caused by a low percentage of suitable phytotelmata within these bromeliads. Our

manipulation experiment, in which water-holding plastic cups were added or the number of phytotelmata was halved, showed that on all three patches where reproductive resource availability was increased, plastic cups were used for both egg and tadpole deposition and some plastic cups received oviposition when containing a tadpole. However, on most patches the number of clutches deposited at phytotelmata containing tadpoles increased, regardless of treatment. Manipulation of the number of resources in opposite directions resulted in a significant effect of oviposition strategy in the same direction, indicating that an effect of treatment is overruled by an effect of time. Therefore, phytotelm number *per se* cannot explain the observation that, towards the end of the study period, frogs increasingly lay eggs in phytotelmata that contain a tadpole.

Second, selection of already-occupied phytotelmata may be based on preferred abiotic characteristics that overrule the negative consequences of the presence of conspecifics (Resetarits and Wilbur 1989; Spieler and Linsenmair 1997; Downie et al. 2001; Marsh and Borrell 2001) or previous depositions of conspecifics may function as an indication of resource quality (Downie et al. 2001; Rudolf and Rödel 2005). However, in species with cannibalistic or siblicidal larvae costs of cannibalism overrule any cost or benefit of other biotic or abiotic conditions of a pool. Such species typically deposit a single offspring per resource when sufficient resources are available (Waage and Godfray 1985; Godfray 1994) and may display plasticity in reproductive strategies as a function of host depletion with offspring of previous depositions and that of conspecifics (van Alphen and Visser 1990; Visser 1993). Frog parents might, however, not be able to discriminate between occupied and unoccupied phytotelmata constraining them in displaying plastic responses towards previous depositions. This possibility is not supported by the literature. Amphibians, including dendrobatid frogs (Downie et al. 2001), have been shown to be selective for pools with respect to resource composition and abiotic quality (Wilbur 1997; Murphy 2003; Rudolf and Rödel 2005) and presence of predators and competitors (Resetarits and Wilbur 1989; Spieler and Linsenmair 1997). In a choice test consisting of pairs of long shot glasses placed in *Heliconia* axil sheets to mimic natural *Heliconia* phytotelmata, one glass containing a tadpole and the other lacking a tadpole, Summers (1999) showed that Ecuadorian *D. ventrimaculatus*, oviposit less in glasses holding a conspecific tadpole. Although the French Guianan population studied here may represent a distinct species from the Ecuadorian population (Brown et al. 2006; Noonan and Wray 2006), the close phylogenetic relationship may indicate that the species we studied (*D. ventrimaculatus s.l.*) is well able to detect conspecifics and avoid oviposition near tadpoles. In the related species *D. pumilio* females have been observed staring into the leaf axil and inspecting the phytotelm for tadpole presence before depositing the tadpole she was transporting on her back. When a conspecific tadpole had been observed occupying the phytotelm, the females moved to another phytotelm to oviposit. Tadpoles in this species display a conspicuous swimming behavior when conspecific frogs are sitting in the leaf axil (Weygoldt 1980). Males of *D. ventrimaculatus* in this study were observed staring into the leaf axil and occasionally during the observation a tadpole was observed swimming to the surface. However, we did not observe conspicuous behavior of the tadpole such as described by Weygoldt (1980).

Third, parents may be time-limited in resource selection caused by substantial amount of time that is invested in other behavior, for example defence of a territory, foraging or courtship, and therefore parents may be able to monitor a small number

of phytotelmata only (Summers and Earn 1999). Species using ephemeral reproductive resources are strongly selected for using stable phytotelmata for tadpole deposition as desiccation of phytotelmata is a common cause of tadpole mortality (Kam et al. 2001). Quality and stability of phytotelmata is most likely measured by repeatedly visiting the same pools to monitor changes in water level and water chemistry (Spieler and Linsenmair 1997; Lehtinen 2004; Rudolf and Rödel 2005). Monitoring the same resource repeatedly may further limit individuals in monitoring phytotelmata for their quality (Rudolf and Rödel 2005). Our manipulation experiment showed that frogs opportunistically used added water-holding plastic cups for egg and tadpole deposition. Furthermore, tadpoles from clutches that had been relocated, even up to meters away from their original site, were transported normally and on a few occasions transport of tadpoles to water bodies in territories of other males was observed (Summers and Amos 1997). These observations indicate that Amazonian poison frogs are not time-limited in monitoring reproductive resources.

Fourth, depositing eggs and tadpoles in the same water body may be part of a reproductive strategy. Parents may gain fitness when tadpoles are deposited in phytotelmata already containing eggs of other pairs on which their offspring can feed. Such cases of reproductive parasitism where tadpoles are added to phytotelmata containing eggs have been reported by Summers (1999) in a study on Ecuadorian *D. ventrimaculatus*. However, transported tadpoles are small, often not able to tear the jelly mass of eggs apart and have a low rate of egg consumption. Eggs may therefore escape cannibalism when tadpoles are deposited in phytotelmata containing eggs (Summers and Symula 2001). In contrast to observations of Summers (1999), in our study the presence of eggs and tadpoles in a single phytotelm was commonly a result of oviposition in phytotelmata already containing a large tadpole, rather than deposition of small tadpoles in phytotelmata containing eggs. Parents may, however, deliberately deposit eggs in a phytotelm containing their tadpole to increase survival chances and quality of some of their offspring at a cost of that of others. Towards the end of the rainy season many phytotelmata dry out and desiccation risk likely constrains the survival chances of many tadpoles. By providing a high nutritive food source, i.e., fertilized eggs, parents may be able to reduce the time to metamorphosis or may increase metamorphosis size of some of their offspring by sacrificing other offspring of their own. An increase in growth for tadpoles consuming eggs was shown for Ecuadorian *D. ventrimaculatus* by Summers and Amos (1997). This sacrifice is likely to be small as eggs that are laid during the final months of the rainy season are not likely to metamorphose successfully, because tadpole growth requires at least 3 months of phytotelm stability after oviposition and, thus, these eggs may only be of reproductive value when fed to other offspring. When males sacrifice eggs of multiple females by leading females in courtship to phytotelmata with his tadpoles, this behavior should still be regarded as reproductive parasitism as males increase their fitness at a cost of that of some females (Weygoldt 1987; Summers 1999; Heying 2001). Females themselves may, however, gain fitness when they provide a food source to their own offspring. This may be achieved by frequent mating with the same male, as was observed in this study, by pair bonding as was found in closely related frog species (Caldwell 1997) or by discriminating own offspring from non-kin to prevent provisioning to unrelated offspring. The latter is unlikely for Amazonian poison frogs as the present study shows that males, that are closest associated with tadpoles, do not discriminate between kin and non-kin. We

have shown that Amazonian poison frogs start increasing egg deposition in phytotelmata containing a tadpole when rainfall decreases towards the end of the rainy season. This strategy can be explained as plastic food provisioning, responding to the risk of phytotelm desiccation housing their offspring. Such environmentally induced trait expression affecting numerous individuals within a population (West-Eberhard 2003) may explain the evolution of unfertilized egg provisioning and the involvement of females in parental care found in multiple lineages of Dendrobatidae (Bourne et al. 2001; Summers and McKeon 2004). Experimental manipulation of pool stability and resource availability in pools together with a comparison of closely related species with different modes of parental care within *Dendrobates* is needed to further elucidate environmental causes of shifts in reproductive strategies.

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