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The effects of cannibalism on Amazonian poison frog egg and tadpole deposition and survivorship in *Heliconia* axil pools

Abstract This study investigated the influence of cannibalism on egg and larval mortality, and on the deposition strategies of adults, in a tropical anuran breeding in very small leaf axil pools. Patterns of egg and tadpole deposition and mortality in the Amazonian poison frog, *Dendrobates ventrimaculatus*, were monitored in rainforest near Pompeya in Sucumbios Province, Ecuador. Oviposition and tadpole deposition typically ocurred in leaf axils of *Heliconia* plants. Pools typically received more than one oviposition. Egg survivorship was low, and significantly lower when eggs were deposited in pools with large tadpoles, indicating that cannibalism is an important source of mortality. Tadpole survivorship was also associated with the presence of other tadpoles: most pools ended with only one surviving tadpole, regardless of the number of tadpoles deposited in the pool. Egg deposition was signifcantly less likely for pools that had a tadpole in them, suggesting that adults can detect the presence of tadpoles and avoid ovipositing in pools that contain them. This hypothesis was tested with a series of pool choice experiments, which revealed that *D. ventrimaculatus* avoid placing either eggs or tadpoles into a pool which contains a large tadpole. Several hypotheses which could explain multiple deposition in this species are discussed.

Key words Cannibalism · Frogs · *Dendrobates* · Reproduction · Tadpole

Introduction

Research on anuran amphibian larvae has revealed complex behavioral and ecological interactions both within and between species (Wilbur 1984). While the roles of density-independent factors (e.g., weather) and density-dependent factors (e.g., predation, parasitism, and competition) on tadpole growth and survival have been well studied in temperate species (e.g., Morin 1983; Wilbur 1987; Skelly and Werner 1990), there has been less work done on the relative importance of these factors in tropical anurans (e.g., Gascon 1995).

Cannibalism has been found to be an important source of mortality in odonates which breed in small pools and leaf axils (Fincke 1994). Cannibalism is also believed to be an important source of mortality for tadpoles in the small leaf axil and treehole pools exploited by a variety of tropical frogs (Crump 1992), but data are limited. In this paper, I investigate egg and larval mortality, and strategies of egg and tadpol deposition, in the Amazonian poison frog, *Dendrobates ventrimaculatus*, a tropical anuran which breeds in extremely small pools, such as those that form in the leaf axils of *Heliconia* plants.

Toxic members of the family Dendrobatidae (referred to as "poison frogs": Caldwell 1997) all have parental care, in which one parent attends the eggs, and carries the tadpoles to small bodies of water. The sex of the parent which attends the eggs, and which carries the tadpoles, varies from species to species in the genus *Dendrobates*, whereas it is typically the male in other genera (Weygoldt 1987). Some species (e.g., *Epidpedobates*) carry the entire clutch at one time to small pools in streams, whereas others (e.g., *Dendrobates*) carry tadpoles one at a time to small pools of water that form in stem or leaf axils, treeholes or large seed husks (e.g., Summers 1989; Brust 1993; Caldwell and Araujo 1998).

D. ventrimaculatus lives in Amazonian Ecuador, Peru, and Brazil. Originally this species was part of a wide-ranging species complex under the name *D. quinquevittatus*. That name has since been restricted to refer to some Brazilian populations of this species complex (Caldwell and Myers 1990). The name *D. ventrimaculatus* was assigned to other populations (particularly in Peru in Ecuador) that were previously

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considered part of *D. quinquevittatus*. *D. ventrimaculatus* may in turn be a complex of species in need of further subdivision. The population of *D. ventrimaculatus* discussed in this paper is from Sucumbios Province, Amazonian Ecuador.

In a study of captive peruvian *D. ventrimaculatus*, Zimmermann and Zimmermann (1984) observed that both parents attend the clutch (1–3 eggs per clutch, each egg 1.5–2.0 mm in diameter), which is oviposited just above the water in a pool in the leaf axil of a bromeliad. The embryos reach the tadpole stage after approximately 10 days. The male carries the tadpoles (which average 10 mm in length) to a different pool and returns periodically to that pool to call, thus attracting his mate who lays eggs at the surface of the pool, which the tadpoles consume.

Recent field research on *D. ventrimaculatus* in Amazonian Ecuador suggests that this population (or species; see above) has male care, rather than biparental care. Briefly, the mating system is promiscuous, unrelated individuals oviposit in the same axil, and females do not return to pools to feed tadpoles (Summers and Amos 1997; K. Summers, unpublished work). Tadpoles are deposited in the pools by males, who carry them on their back from the pool over which they were oviposited (some are simply placed in the pool over which they were oviposited). The tadpoles grow and develop in the pool until metamorphosis, which can require several months in captivity (Zimmermann and Zimmermann 1984), and in closely related species (e.g., Caldwell and Araujo 1998).

Tadpoles of this species have been observed to cannibalize both fertile eggs and other tadpoles (Zimmermann and Zimmermann 1984; Summers and Amos 1997). Summers and Amos (1997) carried out experiments on cannibalism using large tadpoles only. Zimmermann and Zimmermann (1984) reported that young tadpoles would consume infertile eggs in captivity, but this has not been investigated in the field.

Materials and methods

This research was conducted in rainforest between the villages of Limoncocha and Pompeya, in the province of Sucumbios, in Amazonian Ecuador. The study site was established in an area in which *Heliconia* plants (mainly *H. stricta*) occur at high population densities. The stem and leaf axils of these plants provide pools which are used by *D. ventrimaculatus* for egg and tadpole depostion. These pools form when leaves start to pull away from the main stem of the plant.

We established a 40 × 85 m grid in an the area of high *Heliconia* density, with orange plastic flagging on wire stakes placed at 5-m intervals. We established lines with a Suntoo sighting compass, and trails in a pattern that traversed the entire study area. During the first several weeks of the research, the study site was partially inundated by flooding associated with heavy rains and river overflow. During the course of the study the flood water gradually subsided. The flooding inundated some pools in part of the study area. These were later uncovered by the receding water, and became available for egg and tadpole deposition.

We searched the study site every other day for *Heliconia* pools, and marked all pools with plastic flagging tape. We regularly monitored pools found to contain eggs or tadpoles (every other day). Qualitative estimates (based on perceived similarity to pools for which volume had been measured by removal of all water) of pool size were made as follows: small (less than 20 ml), medium/small (20–50 ml), medium (50–100 ml), medium/large (150–200 ml), large (>200 ml).

We marked and monitored a total of 241 pools with some evidence of breeding (eggs, embryos, tadpoles, or adults seen in the pool) on and just off the main study site, for varying amounts of time during the course of this study. Embryos were distinguished from eggs when the formation of the neural tube was clearly visible (stage 15–16). We examined pools with a small halogen flashlight for the presence of eggs, embryos, and tadpoles. Eggs and embryos that had not sunk to the bottom of the pool could be easily seen and counted. Tadpoles, on the other hand, could not always be seen. We also examined pools for the presence of other residents, such as earwigs (order Dermaptera), ants and other insects, mosquito and other insect larvae, spiders, and other species of frogs and tadpoles.

We estimated egg survivorship as follows. The total number of eggs that were known to survive to the tadpole stage (when they can be carried to a pool) was divided by the total number of eggs deposited. We removed eggs that might have matured and been transported during long gaps between samples (>3 days) from the survivorship calculations. We considered tadpoles not observed for three consecutive samples (and not observed later in the study) to be absent (dead). We could usually detect metamorphosing tadpoles because they tend to sit at the surface of the pool for several days while their tail is being completely resorbed.

For comparative purposes, we divided observations on pools into categories based on the presence or absence of tadpoles as follows:

1. B: before a tadpole was observed: at least two samples before tadpole was seen
2. DA: during and after the period that a tadpole was first observed in the pool
3. T: the total of all samples of a pool, regardless of the presence or absence of a tadpole

For survivorship comparisons, all clutches compared on the without-tadpole ledger had to reach maturity before or at the same sample as that in which the tadpole was first seen. Clutches compared on the DA ledger had to have still been in the egg stage when first seen with the tadpole, and we judged them to have survived if they were still present on the last sample that the tadpole was observed in, and they survived to the tadpole stage (if they were still alive after the tadpole disappeared, but did not survive, we did not count them in the survivorship calculations for DA). The number of clutches and eggs inferred to have been deposited was the minimum necessary to reasonably explain the numbers observed during the samples.

We carried out deposition experiments by placing matching long shot glasses (approximately 50 ml) inside *Heliconia* leaf axils, placing one on each side of a *Heliconia* pool, and securing them with wire. We checked the pools twice daily for the presence of eggs or tadpoles, except during absences. We recorded results only if the pool had been checked within the previous 24 h. We found oviposition in ten trials and tadpole deposition in nine trials.

It might be argued that the results could be biased towards not counting depositions in the pool containing a tadpole if those eggs or tadpoles that were deposited in the pool with the tadpole were quickly consumed. This criticism lacks force for oviposition, because the egg capsules are not consumed, and hence oviposition can still be detected. However, the possibility remains that the results concerning tadpole deposition could be biased. In order to test this, we carried out an experiment out in which a newly hatched tadpole was placed in the pool with the large tadpoles in four of the experimental pools, and left for 24 h. In each case the small tadpole survived for 24 h and was readily observed the next day (small tadpoles tend to remain near the surface when there is a large tadpole in the pool). Hence it is unlikely that tadpoles placed in a pool with a large tadpole would not have been detected.

We destructively sampled a series of 31 axil pools off of the main study site on 8 June 1997 and 9 June 1997, in order to estimate the standing occupancy of pools at any one point in time. We inspected all pools encountered during two searches for eggs and embryos, then removed the water and measured for total volume. We removed the axil from the plant and counted the number of tadpoles (if any). We also inspected the pools for partially eaten eggs.

We carried out the feeding experiments as follows. Water was removed from pairs of pools of approximately the same volume (within 10 ml), along with any eggs or tadpoles in the pools. To obtain tadpoles for the experiments, we obtained clutches from *Heliconia* axils off the main study site, and raised them indoors to the tadpole stage (stage 25). We mixed the water from the two pools to ensure an even distribution of nutrients for the two tadpoles, and then placed them back in the pools. We placed pairs of tadpoles of approximately the same weight (within 2 mg) in the *Heliconia* pools. We assigned tadpoles haphazardly to one of two treatments: "feeding-treatment" tadpoles were fed an egg or embryo periodically over the duration of the experiment (3 or 4 eggs total), "non-feeding-treatment" tadpoles were not fed. We kept water levels in the pools relatively constant by refilling pools that lost water. After 11 days we destroyed the pools and collected, weighed and measured the tadpoles. Unfortunately, 6 of the 16 pools (three in each treatment category) did not produce results, because of either tadpole mortality or pool leakage and drying. This reduced the sample size considerably and made it impossible to used paired comparisons in the statistical analysis. There was no significant difference between the final pools in terms of average pool volume [t-test, $n = 5$ (fed), $n = 5$ (not fed), $t = 0.692$, $P = 0.509$]. There was also no significant difference among tadpoles in initial weight [t-test, $n = 5$ (fed), $n = 5$ (not fed), $t = -0.517$, $P = 0.619$].

Statistical analyses were carried out using the software programs StatView (Abacus Concepts 1992) and SuperAnova (Abacus Concepts 1989). I analyzed the data to determine whether they met the assumptions of parametric statistical tests, such as normality of the distribution (Kolmogorov-Smirnov normality test), and homogeneity of the variances (Bartlett's test). I transformed data that did not meet these requirements to fit the assumptions of the parametric tests, or used nonparametric tests if transformation was not successful.

Results

An average of 2.6 clutches (SE = 0.141, range 1–10) and 6.7 eggs (SE = 0.386, range 1–28) were deposited in each axil where we observed oviposition ($n = 166$). An average of 1.25 tadpoles (SE = 0.054, range 1–6) were deposited in each pool where we observed tadpole deposition ($n = 172$).

Tadpole survivorship declined significantly as a function of the number of tadpoles deposited in a pool (Spearman rank correlation, $n = 115$, $\rho = -0.345$, $Z = -3.700$, $P < 0.0005$). Out of 25 pools with more than one tadpole deposition, only 5 had two surviving tadpoles, and no pools had more than two.

A quantitative measure of tadpole survivorship as a function of the number of tadpoles in a pool can be estimated as $s(t)$, where $s(t) = a - bs$, which is equal to the probability that a tadpole in a pool with t tadpoles will survive to metamorphosis. In this study, $a = 0.749$ and $b = 0.176$. Hence $ts(t)$ is a measure of reproductive success from a pool: if a tadpole is placed in a pool with t_0 unrelated tadpoles, then the reproductive success achieved by that parent would be $s(t_0)$. For example, the expected reproductive success from placing a tadpole in a pool with two unrelated tadpoles would be 0.397. This assumes that each tadpole in a pool has an equal chance of survival.

There was a nonsignificant trend toward increasing tadpole survivorship with increasing number of eggs deposited in the pool (Spearman rank correlation, $n = 115$, $\rho = 0.155$, $Z = 1.658$, $P = 0.097$). There was a significant positive correlation between the number of ovipositions observed in an axil and the survivorship of eggs in that axil (Spearman rank correlation, $n = 115$, $\rho = 0.318$, $Z = 3.400$, $P < 0.001$). There was no significant effect of pool size on egg survivorship [Welch's test, (a one-way ANOVA robust to unequal variances), $n = 88$, $P = 0.275$].

Although water level fluctuations were not tracked precisely, observations of the pools indicated that they fluctuated with the recency of precipitation, yet gradually lost water as they aged. This process was highly variable in duration, and pools could lose water quite suddenly for no obvious reason (possibly from the formation of small leaks). Nevertheless, pool size had a significant effect on pool duration. Larger pools tended to last longer, independent of when the pool was first marked (ANCOVA, using date pool was first marked as a covariate; $n = 139$, $df = 4$, $F = 4.901$, $P = 0.001$, for effect of pool size). However, all pools lost water, and there was no significant effect of original pool size on final pool volume (ANCOVA, using date pool was first marked as a covariate; $n = 81$, $df = 4$, $F = 0.422$, $P = 0.793$, for effect of pool size).

The frequency of egg and tadpole deposition in each pool declined over time (Fig. 1). However, the total frequency of deposition fluctuated over the course of the study (Fig. 2). There was no significant relationship between the amount of rainfall and the frequency of egg deposition (linear regression, $n = 34$, $r^2 = 0.001$, $F = 0.032$, $P = 0.858$), but there was a significant relationship between rainfall and tadpole deposition (linear regression, $n = 34$, $r^2 = 0.249$, $F = 10.632$, $P < 0.01$).

Total egg to tadpole survivorship, calculated across pools regardless of the presence or absence of tadpoles, was 19% ($n = 114$, SE = 2.8%). An average of 33% ($n = 106$, SE = 3.6%) of the eggs in each pool were observed to stop developing, possibly as a result of fungal infection. I calculated the effect of tadpoles on egg survivorship in three ways. First, comparisons were made within pools which had eggs deposited both before and after the deposition of a tadpole, so that each pool served as its own control. Second, comparisons were made across eggs in all pools, between pools in which a tadpole was observed at anytime and those in which they were not. Finally, comparisons were made between eggs in all pools or pool periods without a tadpole (i.e., before a tadpole was deposited) and eggs deposited in a pool containing a large tadpole (i.e., a tadpole that had been in the pool for at least 2 weeks).

There was no significant difference between egg survivorship in the presence or absence of tadpoles in the

Fig. 1 The number of egg
clutch and tadpole depositions
observed in *Heliconia* axils as a
function of the pool sample
(1st, 2nd, 3rd, and so on).
Clutches seen on the first sam-
ple of a pool were only counted
if they were in an early stage of
development (within a few days
of oviposition). Hence the esti-
mate for the number of clutches
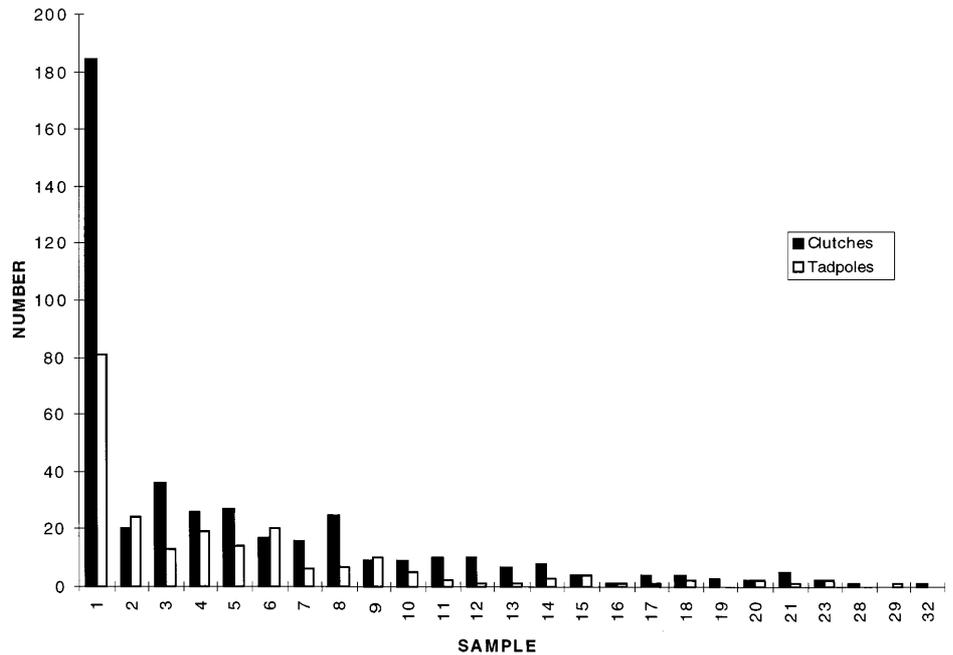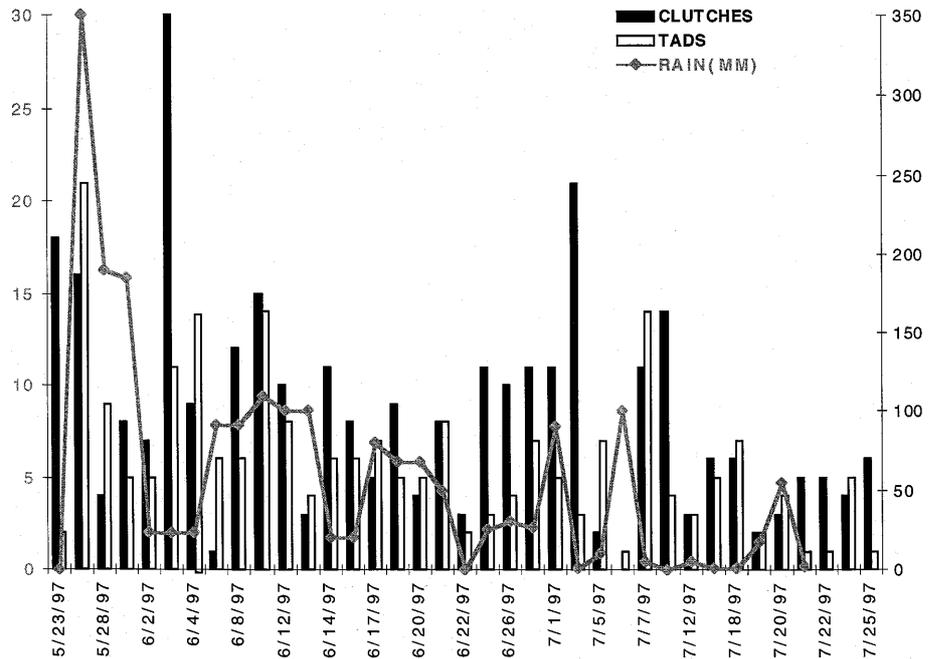found in pools on the first
sample is conservative

Fig. 2 The number of egg
clutch and tadpole depositions
observed over the course of the
study, with rainfall data in
millimeters (right side axis)

pool for comparisons of surivorship before and after
deposition (Mann-Whitney U-test, $n = 45$ (no tadpole),
$n = 20$ (tadpole), $Z = -1.173$, $P = 0.241$), or com-
parisons across all pools (Mann-Whitney U-test, $n = 29$
(no tadpole), $n = 86$ (tadpole), $Z = -0.688$, $P =
0.491$). Egg survivorship was significantly lower for eggs
deposited in pools that contained large tadpoles (tad-
poles that had been in the pool for at least 2 weeks):
no eggs survived when placed in axils containing
large tadpoles [Fig. 3; Mann-Whitney U-test, $n = 74$
(no tadpole), $n = 11$ (large tadpole), $Z = -2.474$, $P <
0.05$].

The reason for this discrepancy may have been in-
advertently revealed by the feeding experiments. The
feeding experiments were designed to investigate the
effect of cannibalism on growth rates in the field. Pre-
vious experiments under laboratory conditions had re-
vealed a significant effect of cannibalism on growth
rates, but these experiments were done with medium- to
large-sized tadpoles (Summers and Amos 1997). The
field experiments in this study were done with newly
hatched, small tadpoles. The experiments did not reveal
any significant difference in growth rates between the fed
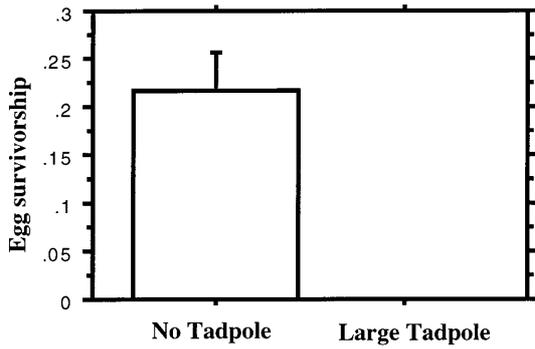and unfed tadpoles, although there was a trend toward

Fig. 3 Average egg survivorship in pools or pool periods without a tadpole, compared with egg survivorship in pools with a large tadpole
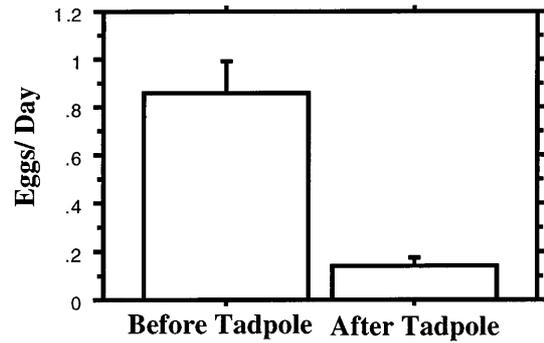

Fig. 5 The average number of eggs deposited in pools per day, before and after tadpoles were placed in the pool
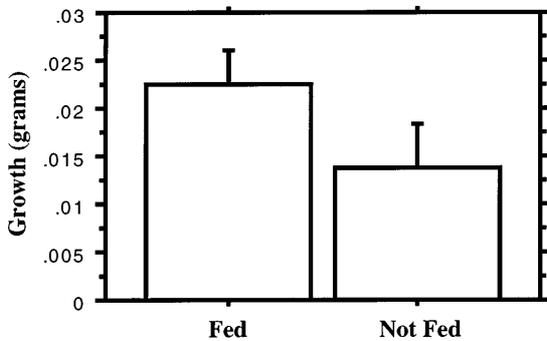

Fig. 4 Average growth rates over 11 days for fed and unfed tadpoles from the feeding experiment

higher growth rates in tadpoles that were fed [Fig. 4; Mann-Whitney U-test, $n = 5$ (fed), $n = 5$ (not fed), $Z = -1.358$, $P = 0.175$]. One reason for the lack of significance may have been the small sample size. However, a careful investigation of the pools after the experiment revealed that many of the eggs fed to the tadpoles had not been eaten. This suggests that small

tadpoles may be less effective cannibals, and hence pose less of a threat to eggs and embryos than medium- and large-sized tadpoles.

Comparing egg depositions within pools before and after tadpoles were deposited, eggs were significantly more likely to be deposited in pools when they did not contain tadpoles [Fig. 5; Mann-Whitney U-test, $n = 72$ (before), 65 (after), $Z = -7.714$, $P < 0.0001$].

For the destructively sampled pools, 12 out of 31 (39%) had some evidence of breeding in them (eggs or tadpoles or both). There was no significant correlation between the number of tadpoles deposited and pool volume (Spearman rank correlation, $n = 9$, $\rho = -0.239$, $Z = -0.675$, $P = 0.5$), nor between the number of eggs deposited and pool volume (Spearman rank correlation, $n = 5$, $\rho = 0.000$, $Z = 0.000$, $P = 1.000$). Pools with eggs or tadpoles were not significantly larger than empty pools, although there was a trend in that direction (t-test, $n = 28$, $t = -1.362$, $P = 0.185$).

Experiments on egg and tadpole deposition revealed a significant tendency to place eggs and tadpoles in pools that did not contain a large tadpole (Fig. 6, chi-square

Fig. 6 The observed and expected numbers of tadpoles and clutches of eggs deposited in pools with and without tadpoles during the deposition experiment
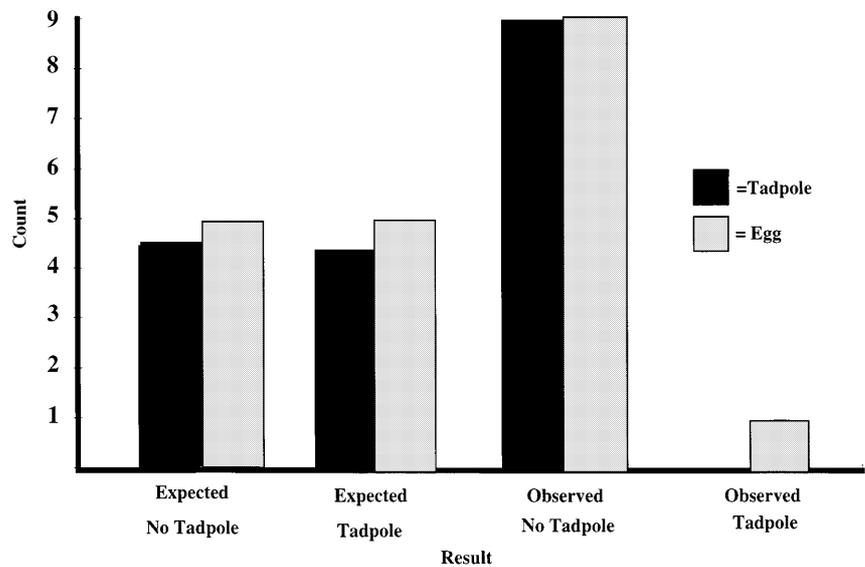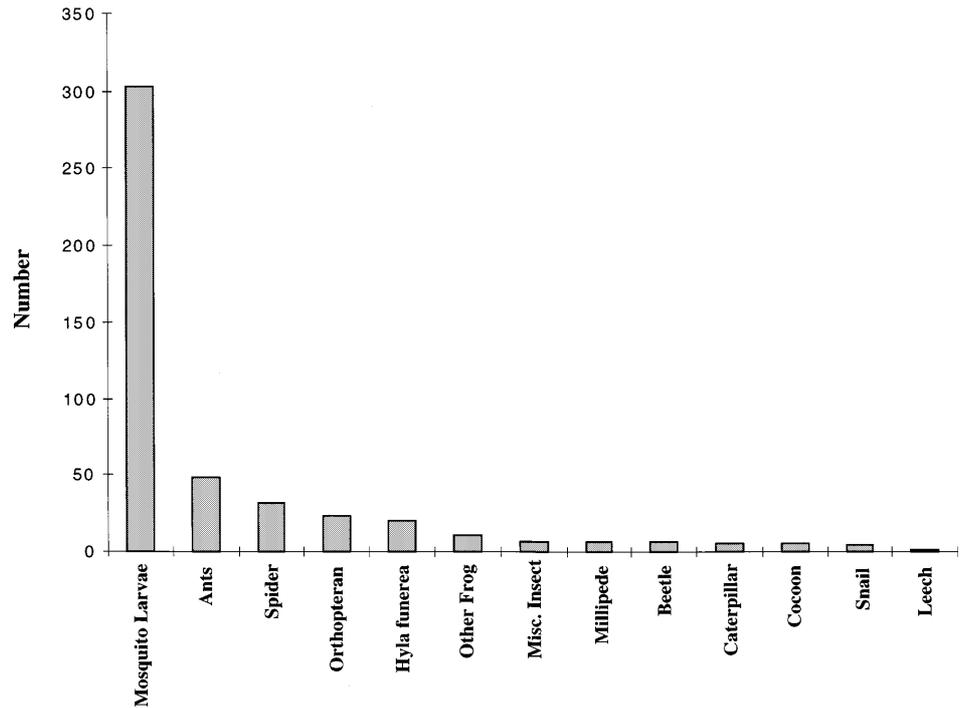
Fig. 7 The number of pool samples in which other vertebrates and invertebrates were found in *Heliconia* pools utlized by *Dendrobates ventrimaculatus* for breeding. *Other Frog* refers to species other than *Hyla funerea*; mostly species of *Eleutherodactylus*. *Misc. Insects* refers to unidentified insects

test on combined data, $n = 19$, $\chi^2 = 9.630$, $P < 0.005$). All nine tadpoles deposited were placed in the empty pool, and nine out of ten clutches of eggs were as well. The results for egg deposition only were also marginally significant (chi-square test, $n = 10$, $\chi^2 = 3.810$, $P = 0.051$). The sample size for tadpole deposition was too small for chi-square analysis, but given that the number of depositions in pools without tadpoles was equal to the number of ovipositions in such pools, and there were no tadpole depositions in pools with tadpoles, it seems clear that the frogs tend to avoid placing tadpoles in pools with larger tadpoles.

A variety of invertebrates were found in the *Heliconia* axils (Fig. 7). Particularly common were earwigs (order Demaptera), ants (formicidae) and mosquito larvae. Several species of frogs (*Hyla funerea*, *Eleutherodactylus acuminatus*, and other *Eleutherodactylus* species) were also found in the axils (Fig. 7). There was a significant difference in the number of observations in which mosquito larvae were seen in a pool between pools with and without tadpoles (Mann-Whitney *U*-test, $n = 36$ (without tadpole), 155 (with tadpole), $Z = -3.222$, $P < 0.002$). There were no significant correlations between egg or tadpole survivorship and the presence of any of the other vertebrates or invertebrates observed in the pools, with the exception of the presence of spiders, which had a significantly positive effect on egg survivorship (Spearman rank correlation, $n = 115$, $\rho = 0.314$, $Z = 3.352$, $P < 0.001$). The reason for this positive correlation is unknown. The number of eggs deposited in a pool was negatively related to the frequency with which earwigs were observed in the pool

(Spearman rank correlation, $n = 189$, $\rho = -0.234$, $Z = -3.202$, $P < 0.005$).

Discussion

Patterns of egg and tadpole mortality

Egg mortality is quite high in *D. ventrimaculatus* clutches. Mortality tends to decline with increasing numbers of ovipositions, but the reason for this correlation is unknown. It may simply be because more adults attempt to breed in higher quality pools, but experiments on pool quality are necessary to evaluate this hypothesis.

The lack of a strong effect of the presence of tadpoles on egg survivorship was surprising. However, the results from the feeding experiment, suggesting that small tadpoles are inefficient cannibals, may explain why the overall effect of all tadpoles on egg survivorship was not significant. The high and highly variable proportion of eggs which failed to develop may also have reduced the significance of the association between the presence of tadpoles and egg mortality. Nevertheless, the strong negative association between the presence of large tadpoles and egg survivorship indicates that cannibalism does have an important effect on egg mortality.

Cannibalism also appears to have a strong effect on tadpole survivorship, as few pools produce more than one surviving tadpole at a time, and there is a strong negative association between the number of tadpoles in a pool and tadpole survivorship.

Egg and tadpole deposition strategies

Why do *D. ventrimaculatus* adults tend to place tadpoles at the surface of the water in the axil pools, rather than higher up where they will not be exposed to tadpoles? The answer to this question is presently uncertain, but it seems likely that the frogs face a tradeoff between the risk of cannibalism and the risk of desiccation. Eggs placed high above the water will be increasingly subject to desiccation as the water level gradually lowers. This can lead to embryo mortality, and one embryo was found high above the water's surface that had desiccated before it could reach the tadpole stage and be carried to a pool.

In some ways, the problems faced by poison frogs in deciding where to oviposit and where to deposit tadpoles parallel those faced by parasitoids in deciding where to oviposit larvae. There is ample evidence for host discrimination with respect to superparasitism in parasitoids (Godfray 1994), and we might expect similar abilities in poison frogs. Researchers have speculated that poison frogs might be able to determine whether or not a tadpole was already present in a pool, and use this information to decide whether or not to place a newly hatched tadpole in the pool. Until now this hypothesis has remained untested.

Comparisons of the average number of eggs deposited in pools per day before and after tadpole deposition suggest that *D. ventrimaculatus* adults can detect the presence of tadpoles in a pool, and avoid placing eggs in axils with tadpoles. The choice experiments presented here also provide experimental evidence for this hypothesis. Hence both observational and experimental data from this study indicate that Amazonian poison frogs are capable of detecting the presence of tadpoles in a pool, and attempt to avoid placing eggs or tadpoles in pools with large tadpoles.

Genetic analysis using microsatellites has demonstrated that eggs and tadpoles from different clutches in the same pool are frequently not full siblings (Summers and Amos 1997). Experiments using removable pools demonstrated that females do not return to pools to feed their offspring (K. Summers, unpublished work). The experiments on deposition reported here demonstrate that *D. ventrimaculatus* attempt to avoid placing tadpoles with large unrelated tadpoles. Nevertheless, eggs and tadpoles are sometimes deposited with large tadpoles in pools (eggs more frequently).

There are several possible explanations for this. First, it may be the case that high population density relative to the availability of empty pools makes deposition in pools with large tadpoles advantageous in spite of the cost. Again, this parallels circumstances in some parasitoids, where superparasitism can in some cases be advantageous to the secondary female in spite of lower survivorship of the clutch (van Alphen and Visser 1990). In order to accurately evaluate the possibility that multiple tadpole deposition (for example) is advantageous to the frog placing a tadpole in an already occu-

pied pool, it is desirable to have a quantitative measure of survivorship (see Results), to know the degree of relatedness among the tadpoles in a pool, the benefit of cannibalism to the cannibal, the time available for searching, the distribution of pools, the cost of tadpole production and the proportion of pools with and without tadpoles, in order to estimate the expected fitness gain from depositing a tadpole in a pool with one or more tadpole already in it. The high survivorship cost of placing tadpoles in the same pool, and the low tadpole occupancy rate found in the pool surveys (see Results) suggests that superparasitism should be rare in this population, but further research is needed.

Another possibility is that deposition of tadpoles with clutches of eggs or smaller tadpoles is a form of reproductive parasitism (Weygoldt 1987; Summers and Amos 1997; Summers and Earn 1999). Such parasitism could take a variety of forms, including parasitism of the reproductive effort of females by polygynous males, or parasitism of the reproductive effort of one pair by an unrelated pair. In each case, it will be critical for the parasite to ensure that its tadpole is positioned to cannibalize rather than be cannibalized (e.g., by depositing a mature tadpole in a pool with smaller tadpoles or eggs).

Finally, some of these cases are likely to be self-superparasitism, or deposition of full siblings in the same pool. Deposition of eggs or small tadpoles with large tadpoles may be a form of feeding (although feeding is not obligatory in this population: K. Summers, unpublished work). Self-superparasitism involving tadpoles could also conform to the "lunchbox hypothesis" (Mock and Parker 1997): small tadpoles would be available as a substitute if the large tadpole dies for some reason, but could serve as food if the large tadpole is healthy and survives.

Heliconia pool communities

A diverse community of adult and larval vertebrates and invertebrates inhabits the *Heliconia* pools, and yet predators on *D. ventrimaculatus* eggs or tadpoles seem to be rare, since there was no association between egg or tadpole mortality and the presence of any of the other pool denizens. Perhaps most surprising was the absence of any odonate larvae, which are known predators of poison frog tadpoles (Fincke 1994). One dead odonate larva was found in an axil pool during the course of the study, whereas well over 500 pools were searched on and off the study site. The reason for this low prevalence is unknown, although it may be associated with the small size and generally low nutrient quality of the *Heliconia* pools.

The most common denizens of the *Heliconia* pools, other than *D. ventrimaculatus* eggs and larvae, were mosquito larvae. The significant lack of mosquito larvae in pools containing tadpoles indicates that *D. ventrimaculatus* tadpoles eat mosquito larvae. This result is consistent with work on other dendrobatids, such as *D. auratus* from Central America and *D. castaneoticus*,

from Brazil (Caldwell and Araujo 1998). Caldwell and Araujo (1998) suggested that predation on mosquito larvae by *Dendrobates* tadpoles evolved as a mechanism to kill organisms that could potentially become predators on the tadpoles, such as larvae of the large mosquito *Toxorhynchites*. This is possibly the case for *D. ventrimaculatus*, although very large mosquito larvae were not seen in any of the pools, even those without *D. ventrimaculatus* tadpoles.

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