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Competitive Interactions in Phytotelmata—Breeding Pools of Two Poison-Dart Frogs (Anura: Dendrobatidae) in Costa Rica

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ABSTRACT.—Competition and predation are two of the most important factors structuring communities, and these interactions may be exaggerated when two closely related species share similar resource requirements. We studied size-based habitat selection of artificial phytotelmata for deposition of tadpoles in two species of poison-dart frogs, *Dendrobates auratus* and *Oophaga granulifera*, in Costa Rica. *Dendrobates auratus* exhibits male parental care, and its tadpoles are predaceous, whereas *O. granulifera* exhibits biparental care, and its tadpoles are obligatory trophic egg eaters. These behavioral traits are integral factors in habitat selection for these two species. We found that the predaceous *D. auratus* selected large- and medium-sized pools, whereas *O. granulifera* selected all pool sizes but had a preference for small pools. *Oophaga granulifera* paid a high cost for exploiting large pools experiencing 100% mortality when sharing a pool with *D. auratus*. The use of small versus large pools in these species is rooted in each species' divergent parental care strategies and tadpole feeding behaviors.

Community organization is affected by two synergistic factors, predation and interspecific competition, where as predation represents interactions between trophic levels, and competition represents interactions within trophic levels (Connell, 1975). Predation is considered to have a major impact on competitive interactions via consumption of some or all individuals of a competing species (Chase et al., 2002). Interspecific competition occurs when two or more species require common resources and is often asymmetrical where one species exerts a stronger per capita effect over another species (Morin, 1999). Competition can lead to the exploitation and depletion of suitable resources, thus pushing individuals to habitat patches of lesser quality (Fretwell, 1972). Predation also can affect habitat selection, for example when prey species avoid sites occupied by potential predators (Resetarits and Wilbur, 1989) to decrease mortality.

Habitat selection is an important factor in structuring how species partition resource space, especially when the habitat in question is small and discrete (Fincke, 1999; Kitching, 2001). The coevolution of habitat selection strategies among closely related, competing and syntopic species is a fundamental aspect of the spatial and temporal dynamics of such species (Morris, 2003). Frog species that place tadpoles in small discrete pools such as phytotelmata provide an excellent model for understanding the spatial mechanisms of habitat selection, niche segregation (Hoff et al., 1999; Pfennig and Murphy, 2003), and community structure (Heyer, 1976; Duellman and Trueb, 1986; Wilbur, 1987). Species interactions are accentuated in phytotelmata because of the competition for limiting resources and the inability of tadpoles to disperse to competitor-free microhabitats (Summers and McKeon, 2004; Brown et al., 2008a,b). Poison-dart frogs (Dendrobatidae) that breed in phytotelmata provide such a system where closely related species interact in a limited breeding resource.

Phytotelmata are the most abundant source of standing water in tropical wet forests (Yanoviak, 2001). They are inaccessible to large predators of tadpoles such as fish, crabs, and crayfish but are inhabited by small invertebrate predators such as mosquito, odonate, and dipteran larvae as well as cannibalistic and predatory frog tadpoles (Fincke, 1999; Kitching, 2001). Phytotelmata offer additional challenges to the organisms that inhabit them such as susceptibility to drying, uneven distribution in a complex spatial environment, and unpredictable food availability (Fincke, 1999; Kitching, 2001; Lehtinen et al., 2004). Because of their small size and

dearth of resources, phytotelmata typically do not support multiple tadpoles, and the larvae of some species that use them are competitive and predatory (Summers, 1999; Wells, 2007) or feed on unfertilized eggs provided by a parent (Van Wijngaarden and Bolaños, 1992; Brust, 1993).

The use of phytotelmata for tadpole rearing sites is an evolutionary innovation in poison-dart frogs (Summers and McKeon, 2004; Grant et al., 2006). It has been hypothesized that the use of phytotelmata as tadpole-rearing sites has influenced the evolution of parental care and the social system in poison-dart frogs (Crump, 1974; Wells, 2007). There is evidence that phytotelmata breeding evolved once in the most recent ancestor of the Dendrobatidae, subfamily Dendrobatinae (*Phylllobates*, *Minyobates*, *Ranitomeya*, *Adelphobates*, *Oophaga*, *Dendrobates*; Grant et al., 2006), with a trend toward smaller pools and increased parental care over evolutionary time (Brown et al., 2008b, 2010).

The presence of disparate parental care strategies in syntopic species of poison-dart frogs can lead to complex interactions involving interspecific and intraspecific competition within breeding pools (Summers, 1990; Crump, 1992). For example, two closely related, syntopic Peruvian poison-dart frogs partition breeding pools based on pool size and differing parental care and mating strategies. The species with predaceous tadpoles (*Ranitomeya variabilis*) uses larger pools and the species that provisions its tadpoles with trophic eggs (*Ranitomeya imitator*) uses smaller pools (Brown et al., 2008a,b).

In southern Central America, poison-dart frogs are abundant components of the leaf litter community (Scott, 1976; Toft, 1981; Savage, 2002). Four species of poison-dart frogs occur along the central and southwest Pacific coast of Costa Rica, and at many localities, all four species occur sympatrically (MJR, unpubl. data). Two species breed in streams (*Silverstoneia flator* and *Phylllobates vittatus*), and two breed in phytotelmata (*D. auratus* and *O. granulifera*). The latter two species occur syntopically throughout the region and breed in the wet season. These two species are ideal organisms to study tadpole-rearing habitat selection and larval competitive interactions because of their syntopy and differing parental care strategies and tadpole feeding behaviors (Crump, 1994; Wells, 2007; Brown et al., 2008a).

Dendrobates auratus is polygynous and exhibits uniparental male care for clutches of 5–13 eggs from up to four different females (Summers, 1989; Savage, 2002). Tadpoles of *D. auratus* are indiscriminate predators, preying on invertebrates and conspecific and heterospecific tadpoles (Gray et al., 2009). Once the tadpoles are placed into the pool, the male no longer

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provides care, but Summers (1989) found that males frequently deposit more than one tadpole per pool and that *D. auratus* tadpoles cannibalize dead tadpoles and kill other species in the same pool.

Oophaga granulifera has biparental care that involves male egg attendance of clutch sizes of 2–4 eggs laid in the leaf-litter and female tadpole transportation and feeding. After a tadpole hatches, it crawls onto the back of the female and she transports it to a small phytotelmata, such as leaf-axils of *Dieffenbachia* spp. or bromeliads (Van Wijngaarden and Bolaños, 1992). Females return to the pool periodically to deposit unfertilized trophic eggs for the obligatory oophagous tadpoles to feed on until they metamorphose (Savage, 2002; Wells, 2007).

We examined breeding site interactions in these two distantly related species of poison-dart frogs in Central America to test whether these species have converged on the same ecological interactions observed in closely related species from South America (Grant et al., 2006; Brown et al., 2008a). We tested how these two syntopic poison-dart frog species select and interact within tadpole-rearing habitats (i.e., phytotelmata) in a natural field experiment. We created artificial breeding pool habitats of three different sizes (small, medium, and large) in a lowland moist forest in southwest Costa Rica. After the pools were placed in the forest, colonization of the pools occurred naturally. We expected that habitat selection (tadpole-rearing sites) would be driven by pool size without direct competitive interactions between *D. auratus* and *O. granulifera*. Thus, our first prediction was that the obligate egg-eating *O. granulifera* would preferentially select small breeding pools and that the predaceous *D. auratus* would preferentially select medium and large breeding pools. Because of the predatory and aggressive nature of *D. auratus* tadpoles, we expected that these two species could not coexist in the same pool long enough for *O. granulifera* to complete tadpole development. Thus, our second prediction was that, when *D. auratus* encountered *O. granulifera* in the same pool, the result would be that the latter species would be excluded from the pool via predation.

MATERIALS AND METHODS

Study Site.—We conducted this study at Tropical Forestry Initiative, Tres Piedras, Costa Rica (09°19'30"N, 83°52'0"W, 95 m elev.). This area is located at the northern edge of the Golfo Dulce region and is in the Pacific Lowland Tropical Moist Forest life zone and receives 2,500–4,000 mm of annual rainfall with a dry season from late December through April (Campbell, 1999).

Experimental Design.—We established seven 10 m × 10 m quadrats within a 25-ha remnant of primary forest. The quadrats were used to draw arbitrary limits so that we could easily locate our artificial pools for subsequent surveys. The sizes of the three artificial pools were small = 35 mm film canisters (32 mL); medium = shallow plastic dishes (295 mL); and large = plastic cups (473 mL). The artificial pools were attached to trees, saplings, and buttresses with thumbtacks and distributed within the plots haphazardly. All pools were placed between 25 cm and 175 cm above the ground. Pools were then filled about half full with water and a small amount of leaf litter. We did not manipulate water levels after the initial input; no pools dried out during the course of the study. After the quadrats were established, we placed 12 artificial pools of the three size classes in each quadrat for a total of 84 pools for trials 1 and 2. For trial 3, we used four quadrats with 15 pools per quadrat for a total of 60 pools, 20 of each size.

We ran the experiment during three time periods: 10 July to 31 August 2001 (52 days); 12 September to 25 October 2001 (45 days); 20 June to 1 August 2005 (43 days). We observed tadpoles within 48 h after the pools were filled with water. The

time interval between surveys varied from 1–16 days with an average of 8.5 days for trial 1, 3.8 days for trial 2, and 2.9 days for trial 3 (overall average = 5 days). During each survey, we recorded the pool size, presence/absence of tadpoles, species identity, and number of tadpoles. We used a small flashlight to look into the pools to count tadpoles and a small probe to move leaf-litter.

Tadpole Identification.—All members of the genus *Oophaga* (9 species) have tadpoles with similar mouth morphology that are specialized to feed on trophic eggs (Weygoldt, 1980; Grant et al., 2006). The tadpoles of *D. auratus* are dietary generalists, and this ecology is reflected in their mouth morphology (Lannoo et al., 1987; Summers, 1990; Caldwell, 1993).

We identified tadpoles to species based on body shape and oral morphology. Tadpoles were placed in small glass vials, and we used a 10 × hand lens to observe the mouthparts. The two species were identified using the following characters: *D. auratus* has two rows of labial teeth on the upper labium and three rows on the lower labium, a more robust, rounded body and a moderate tail fin; *O. granulifera* has large jaw sheaths, zero and one tooth rows below and above the mouth, respectively, and a very low tail fin (Van Wijngaarden and Bolaños, 1992; Lips and Savage, 1996; Savage, 2002). We identified a tadpole the first time it was observed in a pool or whenever the number of tadpoles in a pool changed. This was done to minimize handling and potential damage to tadpoles.

Analyses.—To determine whether pool size use differed between *D. auratus* and *O. granulifera* we used a 2 × 3 (species by small, medium, or large pools) likelihood χ^2 contingency analysis (Krebs, 1999; Manly et al., 2002). We also used a χ^2 -test for each species separately to determine whether each individual species showed a preference for a particular pool size. We used a nonparametric Kruskal-Wallis test to compare the mean number of tadpoles per pool in *O. granulifera* and *D. auratus* because these data did not have a normal distribution. Finally, we also used a likelihood χ^2 contingency analysis to test whether *D. auratus* placed more tadpoles in unoccupied pools versus pools already inhabited by *O. granulifera*.

The exact number of days to exclusion and cannibalism was unknown because we did not survey pools daily. Thus, the data we provide for this question is approximate. In cases where *D. auratus* invaded pools of *O. granulifera*, we recorded the initial number of *O. granulifera* tadpoles and days before invasion and the number of invading *D. auratus* tadpoles and days to exclusion (i.e., killing of the resident tadpole). We omitted one of the exclusion events because 14 days passed between surveys, and this datum was an obvious outlier caused by uneven sampling. All other events were recorded on our normal survey schedule of 1–5 days. We used one-way ANOVA to test whether there was a difference in days to exclusion of *O. granulifera* by *D. auratus* between large- and medium-sized pools.

RESULTS

We monitored a total of 228 pools during all three experimental trials, and 166 (72%) pools were used as breeding sites (Table 1). Our likelihood χ^2 analysis showed that neither species selected differently sized pools in equal proportion to their availability ($\chi^2 = 67.870$; $P = 0.0001$; $N = 166$; $df = 2$). *Dendrobates auratus* did not use small pools and selected large and medium pools in almost equal proportions ($\chi^2 = 1.82$; $P = 0.17$; $df = 1$; Fig. 1). For all three trials, *D. auratus* placed a total of 159 tadpoles in 89 pools. Of these 159 tadpoles, 88 were placed in 43 medium pools ($\bar{x} = 2.0$, range 1–3 per pool) and 71 in 46 large pools ($\bar{x} = 1.5$; range 1–7; Fig. 2). In 41 cases, *D. auratus* placed more than two tadpoles in a pool, but we found no difference in the number of tadpoles placed in each size of pool (Kruskal-Wallis $\chi^2 = 1.9$; $P = 0.16$; $df = 1$).

TABLE 1. Number of pools of each size occupied over all three time periods combined for both species.

Species	Small pools	Medium pools	Large pools	Total
<i>Dendrobates auratus</i>	0/76 (0%)	43/76 (56%)	46/76 (60%)	89/228 (39%)
<i>Oophaga granulifera</i>	36/76 (47%)	23/76 (30%)	18/76 (23%)	77/228 (33%)
Occupied by both species	0/76 (0%)	10/76 (13%)	9/76 (11%)	19/228 (8%)

We found that *O. granulifera* were selecting small breeding pools over large- and medium-sized breeding pools ($\chi^2 = 23.8$; $P = 0.0001$; $df = 2$). For all three trials, *O. granulifera* placed a total of 97 tadpoles in 77 pools. A Kruskal-Wallis test showed that the mean number of tadpoles differed with pool size ($\chi^2 = 8.2$; $P = 0.016$; $df = 2$). Twenty-four tadpoles were placed in 18 large pools of 76 available ($\bar{x} = 1.3$, range 1–2), 33 tadpoles in 23 medium pools of 76 available ($\bar{x} = 1.4$, range 1–2), and 40 tadpoles in 36 small pools of 76 available ($\bar{x} = 1.1$ range 1–2; Fig. 1; Table 1).

We observed 19 cases where both species occupied the same pool simultaneously (nine large pools, 10 medium pools). In all of these cases, *O. granulifera* occupied the pool first and was subsequently invaded and predated by *D. auratus*. In these 19 cases, both species were syntopic for an average of 2.5 days before *D. auratus* excluded (i.e., predated) *O. granulifera* (Table 2). There was no effect of pool size on the number of days to exclusion by *D. auratus* over *O. granulifera* ($P = 0.2862$; $N = 18$; large pools $\bar{x} = 2.8$ days; medium pools $\bar{x} = 2.0$ days).

Dendrobates auratus placed tadpoles in 55% of the large pools and 39% of the medium pools occupied by *O. granulifera*. Twenty-one *O. granulifera* tadpoles were killed by the invading *D. auratus* tadpoles. *Oophaga granulifera* experienced 100% mortality via predation from *D. auratus* when sharing large- and medium-sized pools with *D. auratus*. In two cases, we observed *D. auratus* preying on stage 41 and 42 (Gosner, 1960) tadpoles of *O. granulifera* within 24 h after the addition of four and six early stage (i.e., not precisely staged) tadpoles. In these cases, the *D. auratus* tadpoles fed on the dead *O. granulifera* carcass, which was visible, for seven days. We observed seven other direct attacks by *D. auratus* tadpoles on *O. granulifera* tadpoles, and from these interactions, we inferred that the remaining 10 cases of co-occurrence ended via predation.

We observed directly four cases where large tadpoles of *D. auratus* ate smaller conspecifics and 20 cases where there was a decrease in the number of *D. auratus* tadpoles from the number observed initially. The estimated number of days to the absence of a *D. auratus* tadpole ranged from 2–24 days ($\bar{x} = 9.0 \pm 6.7$ days) when conspecifics were present. We observed 19 cases where a cohort of *D. auratus* tadpoles was placed in a pool with established conspecifics of varying sizes and each time the number of tadpoles decreased (Table 2). In a subset, nine cases, we observed the addition of new, small tadpoles to pools that already had large resident tadpoles. In these cases, the newly added tadpoles were apparently eaten by established, resident tadpoles within 15.5 ± 6.9 days (range 5–24 days). We did not stage or measure tadpoles, and tadpole sizes were estimated by comparing relative sizes, with longer and rounder tadpoles considered to be older.

DISCUSSION

We found that breeding pool size and predation determined habitat use in tadpoles of *D. auratus* and *O. granulifera*, and we further documented how these two syntopic species compete for and interact within breeding pools. Pool size was a significant predictor of habitat use for both species. Thus, our first prediction of the selection of habitat by pool size is supported. In the 19 cases when both species occupied the same pool at the same time, *D. auratus* preyed on and excluded *O. granulifera*, supporting our second prediction of predation by *D. auratus* on *O. granulifera*. However, in cases of interspecific occurrence, *O. granulifera* never survived to metamorphosis; thus, our second prediction was supported.

Although there was a significant preference for small breeding pools over large and medium pools in *O. granulifera*,

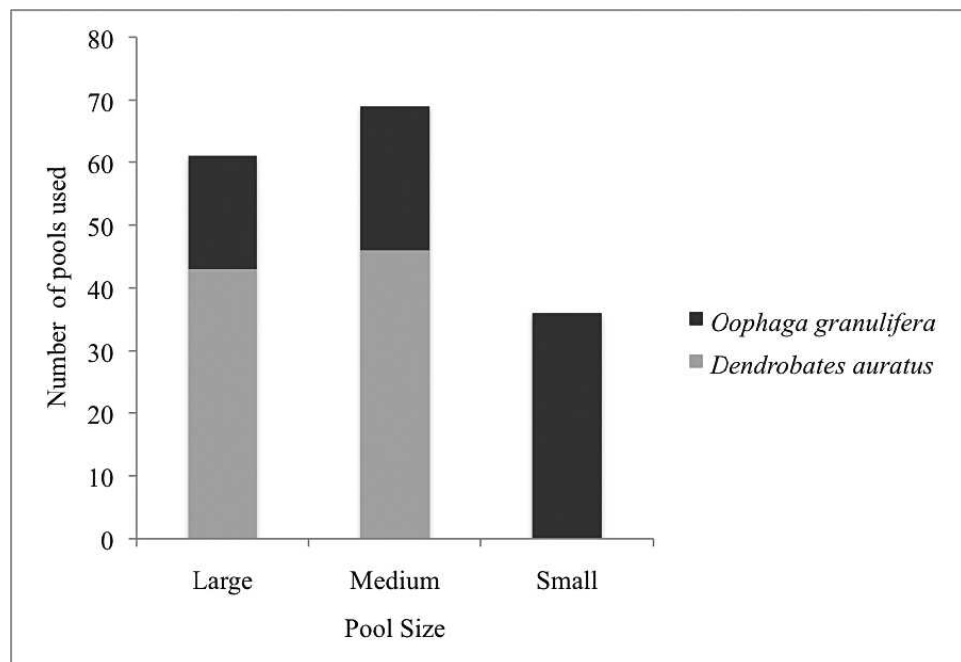


FIG. 1. Number of breeding pools by size used by each species with all three sampling periods pooled.

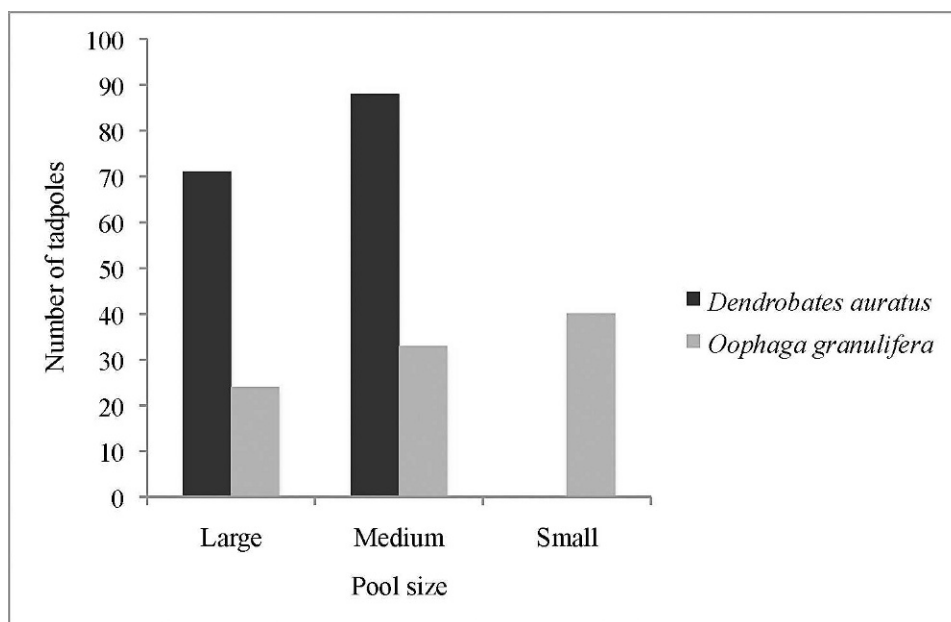


FIG. 2. Number of tadpoles placed in each pool by size with all three sampling periods pooled.

the use of all three pool sizes by *O. granulifera* suggests that pool size was not a critical determinant of habitat selection in this species (Fig. 2). Because of the variable timing of surveys and potentially rapid time of predation, the large and medium pool use we observed may be an underestimate of actual use of these larger pools. If this were the case, then *O. granulifera* would have experienced greater predation than we observed as well. Females used large and medium pools 53% of the time, thus exposing tadpoles to potential predators (see below). The use of smaller breeding pools has been associated with increased parental care in the form of trophic egg provisioning to avoid predation and competition pressures from other frogs breeding in phytotelmata (Summers and McKeon, 2004; Brown et al., 2008a, 2010). *Oophaga granulifera* used 47% of the available small breeding pools and thereby avoided predation. The use of medium and large breeding pools came at a cost for *O. granulifera* because their tadpoles experienced a predation rate of 53% from *D. auratus* after 2–3 days of predator

colonization (Table 2). Van Wijngaarden and Bolaños (1992) found *O. granulifera* tadpoles in the axils of terrestrial aroids with small accumulations of water that apparently were too small for the predaceous tadpoles of *D. auratus*. To date, under natural field conditions, tadpoles of *O. granulifera* have only been found in leaf axils (Savage, 2002). It is unclear why we found *O. granulifera* using larger breeding pools in the face of predation. We speculate that the use of larger breeding pools by *O. granulifera* may be a form of bet-hedging of female reproductive success in the face of potential predation in a larger breeding pool versus the potential drying out in a smaller pool. Phytotelmata are susceptible to drying out (Kitching, 2001), and drying of breeding pools can be an important source of tadpole mortality (Caldwell and de Araújo, 2004). During the course of our study, no pools dried. However, years of low rain may result in small pools drying during the wet season leaving only large breeding pools for *O. granulifera* to use. This plasticity in pool size use suggests that

TABLE 2. Summary of the 19 cases where *Dendrobates auratus* invaded pool occupied by *Oophaga granulifera*. In all cases, *O. granulifera* tadpoles were killed. *denotes direct observation of *D. auratus* attacking or eating *O. granulifera*.

Date of observation	Initial no. of <i>O. granulifera</i>	No. days before invasion by <i>D. auratus</i>	No. of invading <i>D. auratus</i>	No. days to absence of <i>O. granulifera</i>	Pool size
10 July 2001	1	7	2	3	Large
10 July 2001	1	12	1*	0	Medium
14 July 2001	1	3	2	3	Large
11 August 2001	1	?	7	14	Large
13 September 2001	1	28	1	5	Large
13 September 2001	2	32	4*	3	Medium
13 September 2001	1	14	2*	0	Medium
15 September 2001	1	31	2*	1	Large
15 September 2001	1	32	2	3	Large
15 September 2001	1	35	1*	2	Medium
20 September 2001	1	32	1	3	Large
20 September 2001	1	14	1	3	Large
2 October 2001	1	15	2*	1	Large
2 October 2001	1	14	1*	1	Medium
2 October 2001	1	9	1	5	Medium
11 October 2001	1	11	4	3	Medium
17 October 2001	1	5	1*	2	Large
5 July 2005	2	4	1*	2	Large
12 July 2005	1	17	2	5	Large

O. granulifera is not a size-dependent habitat specialist even though the use of larger breeding pools by *O. granulifera* leads to competition and predation by *D. auratus*.

Breeding pool size was a significant predictor of where *D. auratus* placed tadpoles, because this species occupied large- and medium-sized pools and never used small pools. Summers and McKeon (2004) found that *D. auratus* tadpoles had slower growth rates and shrank in size in smaller pools and inferred they would not survive to metamorphosis in small phytotelmata. The lack of available food resources for their predaceous tadpoles in small pools may be the driving force behind *D. auratus* selecting large pools over small pools (Summers and McKeon 2004). The trophic rank hypothesis predicts that species at higher trophic levels require greater area than do their prey, and a predator can only persist in a large patch that is already occupied by its prey (Holt et al., 1999; Srivastava et al., 2008). Larger phytotelmata collect more nutrients and harbor more prey species for *D. auratus* tadpoles to feed on than smaller phytotelmata (Sota, 1996; Yanoviak, 1999; Kitching, 2001).

Dendrobates auratus is an indiscriminate predator of mosquito larvae, giant damselfly larvae, and other small macroinvertebrates, as well as hetero- and conspecific tadpoles (Summers, 1990). Because of the restricted size and limited resources of phytotelmata, cannibalism may be beneficial to the older or stronger tadpoles by removing conspecific competitors in nutrient-poor pools (Crump, 1992; Caldwell and de Arajúo, 1998; Gray et al., 2009). Cannibalism was the only source of predation we observed on *D. auratus* (i.e., Summers, 1990; Caldwell and de Arajúo, 1998). The incidence of multiple *D. auratus* tadpoles per pool in our study most likely encouraged cannibalism. Summers (1999) reported that cannibalism was an important source of mortality in *Ranitomeya* (= *Dendrobates*) *ventrimaculatus* tadpoles and was associated with high densities of tadpoles per pool. Carnivorous tadpoles benefit from feeding on conspecifics by reducing competition for resources and increasing metabolic efficiency. Nagai et al. (1971) found that tadpoles of *Bufo japonicus* converted amino acids more efficiently when fed conspecifics, and Crump (1990) found tadpoles of *Hyla pseudopuma* grew larger when fed conspecifics over heterospecific tadpoles. The predatory nature of *D. auratus* tadpoles appears to be an important factor in larval competition and cannibalism and the structuring of habitat use in our study system.

Our findings on tadpole habitat use are similar to those of Brown et al. (2008a,b) who found that predaceous species selected large pools, and oophagous species selected small pools. Brown et al. (2008b) found that differences in parental care between *Ranitomeya imitator* (biparental care) and *Ranitomeya variabilis* (male parental care) resulted in *R. imitator* using smaller breeding pools than *R. variabilis*. Brown et al. (2008a) suggested that a transition from larger to smaller pools is associated with the evolution of biparental care. We note that their study occurred in Peru and focused on sister taxa, whereas our study occurred in Costa Rica on two more distantly related species (Grant et al., 2006; Roberts et al., 2006). All four species belong to the subfamily Dendrobatinae, but the interacting species pairs are in two clades, South American and Central American (Clough and Summers, 2000; Grant et al., 2006). The concordance of this study with that of Brown et al. (2008a,b) may be surprising considering the relatively distant phylogenetic relatedness of our taxa. The similarity of these systems across distinct phylogenetic scales suggests a common selective force shaping competition in these communities. Future work should track the evolution of syntopic tadpole interactions at additional phylogenetic levels.

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