Phytotelm size in relation to parental care and mating strategies in two species of Peruvian poison frogs

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Summary

Factors contributing to the evolution of reproductive strategies have been of great interest to evolutionary biologists. In tropical amphibians predation and competition have been suggested to play a major role. Poison frogs of the family Dendrobatidae display a trend towards the use of very small pools and increased parental care, particularly in the genus *Dendrobates.* Some species with female parental care, asymmetrical biparental care and biparental care, have evolved novel behaviors in association with the use very small phytotelmata. It has been hypothesized that selection pressure imposed by predation and competition favored the use of small phytotelmata, and this, in turn, produced selection for trophic egg provisioning to ameliorate the lack of available nutrients. To elucidate the ecological factors associated with the transition from uniparental male care to biparental care and associated changes in social behaviors, we evaluated key behavioral and ecological differences between *Dendrobates imitator* and *D. variabilis*. *Dendrobates imitator* used significantly smaller phytotelmata in different plant species than *D. variabilis* for tadpole and embryo deposition. The parental strategy of *D. variabilis* was limited to male parental care, whereas *D. imitator* exhibited biparental care. Males and females of *D. variabilis* were observed to have a promiscuous mating system with little mate fidelity. This contrasted with *D. imitator*, where paired males and females were observed interacting daily and were never observed courting additional mates. Our results are consistent with the hypothesis that a key ecological difference between these species, involving the size of pools typically used for reproduction, is strongly associated with the evolution of biparental care and monogamy in *D. imitator.*

Keywords: biparental care, Dendrobatidae, male-parental care, monogamy, phytotelmata, promiscuity, reproduction.

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Introduction

Factors that lead to the evolution of biparental care in ectotherms are diverse and not well understood, and the occurrence is relatively rare. One possible reason is that two parents are usually only slightly more effective than one parent at caring for offspring (Clutton-Brock, 1991). The evolution of biparental care is favored when the provisioning of care from two parents substantially increases the probability of survival in offspring and the chances of remating (for males) remains high (Maynard Smith, 1977). In species where selection favors guarding or provisioning offspring, parental care is more likely to be depreciable and biparental care is relatively common (Clutton-Brock, 1991). This is widely observed in cichlid fishes, where provisioning of care from two parents is critical in order to brood large clutches (Barlow, 1974; Wisenden & Keenleyside, 1995; Morley & Balshine, 2002). Other factors that may influence the evolution of biparental care include circumstances in which females can only spawn once in the same season (Blumer, 1982) or pair formation causes a high male mortality rate (Schachak et al., 1976; Linsenmair & Linsenmair, 1997). Offspring feeding competition might also play an important role in the evolution of biparental care and is observed in many biparental care species (Milne & Milne, 1976; Talamy, 1984; Scott, 1990). In these systems parents feed their young, competition for food is intense and the benefits of parental care are depreciable.

It has been repeatedly suggested that the need for biparental care led to socially monogamous pairs (Lack, 1968; Ligon, 1999; Reichard & Boesch, 2003). When the female (or the male) cannot rear the young successfully without help from a mate, social monogamy is likely to maximize male and female fitness (Wittenberger & Tilson, 1980; Kleiman & Malcolm, 1981; Birkhead & Møller, 1992). In anurans, social monogamy is rare and there is little evidence in favor of the parental care hypothesis (Caldwell & de Oliveira, 1999; Gillette et al., 2000). In most cases monogamy is likely to be the result of mate defense or short reproductive periods (Wittenberger & Tilson, 1980).

In amphibians, much research has focused on the influence of ecological factors on reproductive modes in the context of complex life cycles (e.g., Crump, 1974; Wells, 1977; Duellman, 1985; Duellman & Trueb, 1986; Wilbur, 1987). In temperate systems, complex life cycles have been viewed as strategies designed to capitalize on transient opportunities for growth and dispersal (Wilbur, 1980). In these systems, reproductive periods are relatively short and larvae are adapted to exploit the springtime pulse in primary productivity (Wilbur, 1997). In the tropics, ecological interactions are more diverse and complex, and the amphibian life cycle often includes additional elaborate reproductive strategies, such as the transport of tadpoles to small terrestrial pools. Predation and competition may play a major role in the evolution of these complex reproductive strategies (Crump, 1974; Alford, 1999), although relevant evidence is scarce (but see Heyer et al., 1975; Harris, 1999).

In temperate pond systems, a positive relationship has been demonstrated between pond size and factors that affect tadpole survival, such as the density of predators and competitors and the abundance of food (e.g., Sih et al., 1985; Pearman, 1993, 1995; Gurevitch et al., 2000; Snodgrass et al., 2000). These factors have been shown to affect tadpole survival in the tropics as well (Gascon, 1995). As bodies of water change in size, the primary factors that affect tadpole survival are also likely to change. In larger, more permanent pools, predation is likely to be a key factor limiting larval anuran population densities. As pools decrease in size, predators decrease in number and diversity (Menge & Sutherland, 1976, 1987; Post et al., 2000), and inter- and intraspecific competition become primary constraints (Menge & Sutherland, 1976, 1987). In very small pools, such as phytotelmata (small arboreal pools of water in axils of plants and tree holes), the constraints of predation and competition are reduced (or absent), but so is food availability (Brust, 1993; Pramuk & Hiler, 1999; Summers, 1999). Although a considerable amount of research has been conducted to evaluate the relationships between pond size and predators, competitors and food resources in larval amphibians (see above), few studies have explicitly investigated these factors in relation to species that utilize smaller bodies of water for reproduction.

Pool size may have important effects on the evolution of strategies of parental care and mating systems in frogs (e.g., Crump, 1974; Summers & McKeon, 2004). More specifically, the use of small pools may necessitate offspring provisioning due to low nutrient availability (Weygoldt, 1987; Brust, 1993; Caldwell & de Oliveira, 1999). In turn, biparental care may evolve if care by two parents provides a significant benefit to offspring survival relative to care by a single parent (Maynard Smith, 1977; Weygoldt, 1987). The importance of cooperation and coordination for the effective delivery of parental care may produce selection in favor of pair-bonding, monogamy and mutual territorial defense (Wittenberger & Tilson, 1980; Whiteman & Cote, 2004).

Poison frogs of the family Dendrobatidae (the authors could not agree upon a working taxonomy (see Grant et al., 2006); therefore, we have chosen to be conservative and use the previously established taxonomy until the matter is further reviewed) display a trend towards increased parental care and the use of smaller pools, particularly in the genus *Dendrobates* (Summers & McKeon, 2004). In all species of this genus, egg clutches are guarded by a parent, and tadpoles are transported after hatching by one parent to a suitable phytotelm. This genus displays a diverse range of parental care strategies (Table 1), the most common being uniparental male care, in which clutch-attendance and tadpole transport are done by the male. In some species, these duties can be split by both sexes (asymmetrical biparental care or biparental care), or taken over by the female entirely (uniparental female care). Species with female parental care, asymmetrical biparental care and biparental care, have evolved novel behaviors to utilize very small phytotelmata (such as bromeliad axils); for example, in many species, adult females provide trophic eggs to their larvae (Weygoldt, 1987; Brust, 1993; Caldwell & de Oliveira, 1999). It has been hypothesized that selection pressure imposed by predation and competition favored the use of small phytotelmata (Summers & McKeon, 2004), and this consequently produced selection for trophic provisioning to ameliorate the lack of available nutrients in small pools (Summers & Earn, 1999).

Within the genus *Dendrobates* there have been at least two evolutionary transitions from uniparental male-care: one in the *histrionicus* group, where

Table 1. Generalized reproductive behaviors exhibited in poison frogs of the genus *Dendrobates* (see Summers & McKeon, 2004).

Care type	Clutch attendance	Tadpole transport	Egg feeding	Taxonomic groups
Uniparental male care	Male	Male	None	Most members of *Dendrobates* (36 species)
Uniparental female care	Female	Female	Female only	*Histrionicus* group (4 species)
Asymmetric biparental care	Male	Female	Female only	*Histrionicus* group (4 species)
Biparental care (symmetric)	Male	Male	Female, but directed by Male	*Vanzolinii* group (5 species)

species exhibit both asymmetrical biparental care (where parental care is performed mainly by females, but males attend clutches) and uniparental female-care, and the other within the *vanzolinii* group, which is thought to exhibit primarily biparental care (Caldwell, 1997; Caldwell & de Oliveira, 1999), although this has only been confirmed in the field in *D. vanzolinii* (Caldwell, 1997). Phylogenetic analyses (Symula et al., 2003; Roberts et al., 2006) suggest that biparental care may also characterize the four other members of the *vanzolinii* group (*D. imitator*, *D. biolat*, *D. lamasi* and *D. flavovittatus*), but this remains speculative. *Dendrobates imitator* have been observed to exhibit biparental care in captivity (JLB, personal observations), but this has not been confirmed in the field.

To elucidate the ecological factors associated with the transition from uniparental male care to biparental care and related changes in social behaviors (i.e., monogamy), we evaluated key behavioral and ecological differences between *D. imitator* (a member of the *vanzolinii* group with putative biparental care) and *D. variabilis* (a member of the *ventrimaculatus* group with male parental care) (Summers & Amos, 1997; Summers & Clough, 2001; Poelman & Dicke, 2007). Confounding factors associated with phylogentic divergence and environmental conditions are reduced, because these two species are closely related (Symula et al., 2001; Noonan & Wray, 2006) and occur sympatrically in north-eastern Peru in the Province of San Martin (Schulte, 1999; Roberts et al., 2006). These factors provide a unique opportunity to evaluate the association between reproductive resources and parental care/mating strategies. In this manuscript we report observations on phytotelmata use, parental care, courtship, mating behavior, aggression, and territoriality in *D. imitator* and *D. variabilis*. On the basis of preliminary observations on captive specimens, we predicted that *D. imitator* would display biparental care, whereas *D. variabilis* would not. We further predicted that *D. imitator* would show social monogamy, whereas *D. variabilis* would exhibit a promiscuous mating system. We return to these predictions in the discussion.

Methods

The study area was located in the Cainarachi valley, northeast of Tarapoto, Departamento San Martín, Perú, on the road to Yurimaguas (km 34). In May

2005 we set up two field sites in the Cainarachi valley which we monitored daily from 19 May to 28 July 2005, 15 May to 27 July 2006, and 25 May to 1 August 2007. Site one was located to the east of Rio Cainarachi (6°25′25.60″S, 76°18′25.52″W) at 597 m above sea level. The area surveyed was 36 × 26 m (936 m^2). Site one and a majority of the land above and adjacent was dense secondary forest. Much of the land below site one was cleared or being used for agriculture. The eastern edge of the site (the lower edge) was fifty meters from the edge of a plantain plantation. Site two was located to the west of Rio Cainarachi (6°24′57.74″S, 76°17′41.05″W) at 612 m above sea level, approximately 4 km NW from site one. The area surveyed at site two was 24 × 40 m (960 m^2). With the exception of agricultural plots adjacent to the southern margins of our test site, the surrounding (dense secondary growth) remained relatively intact. Both sites contained populations of both species (*D. imitator* and *D. variabilis*) and lie within premontane rainforest (fide Holdridge, 1967). Average annual rainfall is 2500 mm, with reduced amounts between June and September. Seasonal air temperatures within the valley range 16–32°C in clearings, with seasonal cooler periods during July and August.

Grids and transects were established at each site. The transects consisted of a predetermined series of hairpin turns winding the width of the site; extending from one end to the other. Due to site abnormities, transects were not the same between sites, but the area surveyed at any section of transect were similar (ca. 3 m^2). The observers entered the site from a randomly determined side and transects were started from a corresponding predetermined point. Every other survey, transects were walked in reverse. Capture points were recorded at 0.5 m^2 resolution; this was done by visually subdividing each 2 m^2 grid into four 1 m^2 squares that were further subdivided into four 0.5 m^2 squares. These transects allowed us to begin to assess the ecological and behavioral differences between these species in the field. On 17 May 2005 we selected two plots for transect surveys: one ‘natural’ plot and one ‘artificial’ plot. The natural plot (site one), contained no artificial phytotelmata, whereas the ‘artificial’ plot (site two) contained a high density of artificial phytotelmata (plastic bottles fixed to trees ca. 1–2 m high). Artificial phytotelmata had been established in 1999. The artificial phytotelmata allowed us to easily observe reproductive behaviors, making detailed observations more feasible (Figure 1). The combination of sites with natural and artificial phytotelmata allowed us to obtain more data but also ensured that data

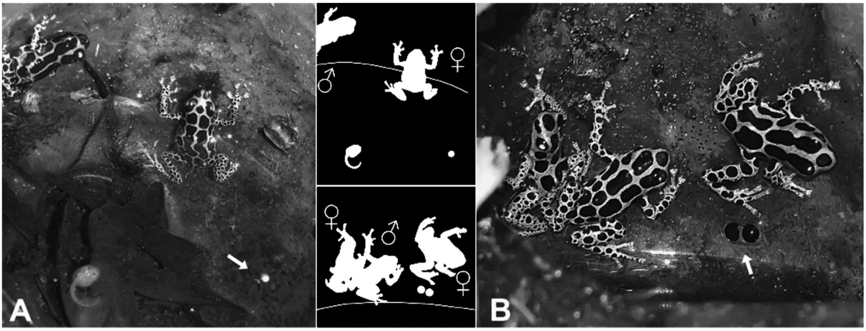

Figure 1. Photographs from focal observations. (A) A pair of *Dendrobates imitator* feeding their tadpole a trophic egg (highlighted with an arrow). This pair was observed together for over three months, feeding 3 other tadpoles during that period. This behavior was never observed in *D. variabilis*. (B) A breeding group of *D. variabilis* consisting of two females and a male (two embryos highlighted with arrow). Multiple *D. variabilis* males and females mating was not an uncommon observation, however this was never observed in *D. imitator*.

from the artificial pools are relevant to natural situations. All phytotelmata at both sites were identified and marked, then checked daily for the presence of tadpoles and/or eggs. Additional observations were gathered during this study at various sites throughout the Cainarachi valley, including sites where both species occur alone and additional natural and 'artificial' sites.

Monitoring of transects (ca. 40 min) involved two observers walking slowly, scanning the forest floor, emergent rocks, and vegetation for adult frogs. All individuals observed were captured and given a distinctive mark (toe-clip) that allowed individual identification. Individuals were sexed (if possible, based on calling and reproductive activity), photographed (for identification, if new capture), and, using calipers, measured snout-vent length (SVL). We recorded time of day, individual identification, location (grid number), capture height (only in 2005 at site one), air temperature, time required to walk transect, as well as any other notable observations.

We performed focal observations on both species on an ad libitum basis. These consisted primarily of paired males and females; however, we also observed tadpole transport/retrieval/deposition and adult aggression. During these surveys, we remained relatively motionless and were able to watch the subjects from a distance of 2–4 m. Throughout observations we never handled or caught individuals; however, at times, individuals were captured after focal observations were terminated to confirm identity. To aid data collection on behavioral observations, when possible, paired individuals in artificial pools were filmed using a remote activated Sony DCR-HC42 on a tripod, which was placed at the margins of pools. When using this method, after camera placement, we remained 6–10 m away (minimizing disturbance), using binoculars to view pairs. Focal observations were also gathered using two automated video cameras with infrared sensors (Sony DCR-HC42, modified Trail Master Active IR sensor: TM1050 Bat and TM700vRT, and remote IR light source). The cameras were placed at artificial pools, where pairs had previously been observed. The cameras were used for 35 days generating at total of 348 min of additional behavioral observations (i.e., pool use and tadpole deposition).

The distinctive color patterns of these frogs allowed us to recognize specific individuals at a distance in most cases. Most individuals were identified by the use of ‘photocards’: cards with photos of all the previously caught individuals and their number. After each season the frogs’ toes usually regenerated (although scar tissue was present), and individuals between seasons were identified based on photo cards. If we were unsure of an ID, we took ventral photos and compared them to the individuals in question. In the Cainarachi valley, *D. imitator* and *D. variabilis* are Müllerian mimics (Symula et al., 2001) and display remarkable similarity in morphology but can be distinguished from each other using the following characteristics: trill-like call (audible from >4 m) with pauses between calls (*D. imitator*) vs. quiet short-buzz call (only audible from <4 m) which is repeated frequently (*D. variabilis*); presence of paired (*D. imitator*) or single (*D. variabilis*) nose spot(s); dorsal spotting ovoid and large (*D. variabilis*) vs. dense dorsal spots, irregular in shape and size (*D. imitator*); monotone dorsal coloration (*D. imitator*) vs. gradient (anterior-posterior) from yellow-green to blue-green (*D. variabilis*); presence of very fine green to yellow green netting and a black background (limbs are >50% black; *D. imitator*) vs. small-evenly spotted limbs on a black background (limbs typically <50% black; *D. variabilis*).

Field identification of tadpoles was done using the following characteristics: grey to dark pigmentation (*D. variabilis*) vs. transparent to cream pigmentation (*D. imitator*); if colored (>Gosner stage 30), single nose spot present (*D. variabilis*) vs. paired spots (*D. imitator*); head shape round and interorbital distance large (*D. imitator*). Questionable tadpoles were raised until the nose spot and patterns were evident.

During the 2005 field season we surveyed 100 artificial pools biweekly. Pools were constructed from 0.5–1.5 l soda bottles, halved and nailed to trees (mean water volume = 254 ml, range 60–740 ml). All surveyed pools were established, at latest, by 2003, and adult frogs were accustomed to their presence and used them regularly. Pools were emptied into buckets and contents were poured through mesh screening into another bucket. The filtered matter was explored by hand, searching for tadpoles. Tadpole presence/absence was recorded and the following tadpole measurements were taken: body length (length from tip of snot to base of tail), body width (at widest point), and total length (length from tip of snout to tip of tail).

In 2006, we surveyed canopy phytotelmata three times a week for three months using tree-climbing gear. These surveys evaluated vertical space use by both species. We surveyed six trees, all of which were greater than 12 m tall (range 12.5–40 m) and contained at least a dozen phytotelmata at varying heights (between 3 and 37 m). The survey areas were inhabited by both *D. imitator* and *D. variabilis*. Six artificial pools were placed within each tree at equidistant intervals. We recorded time, individual identification, species, capture/tadpole deposition height, air temperature, time of day, as well as any other notable observations.

Statistical Analyses were performed in SPSS 15.0 (SPSS, 2007). Independent Student's t-tests were used to test for significance between means of the two species. If the assumption of homogeneity of variance was not met, data were ln transformed. In one case (comparison of clutch sizes), ln transformed data did not meet the assumption of homogeneity of variance. In this case, a Mann–Whitney test was performed. Chi Square contingency tests were used to calculate significances between data composed of frequencies.

Results

Between 19 May 2005 and 1 August 2007, we walked transects ($N = 178$, site one = 65, site two = 113; totaling 7547 min) an average 8 times per week at varying hours. In total and we observed 15 paired *D. imitator* for a total of 2625 min (average observation 43.3 min, range 26–255 min) and 23 courting pairs of *D. variabilis* for a total of 1866 min (average 48.3 min, range 9–186 min) and 1202 min of observations of non-paired individuals of both species (average observation 12.1 min, range 1–56 min).

Size

The mean (± SD) snout–vent length (SVL) of adults were 17.4 ± 1.2 mm for males (range 13.2–19.7 mm, $N = 64$) and 18.2 ± 1.1 mm for females (range 15.9–20.5 mm, $N = 35$) in *D. imitator*, and 17.4 ± 1.0 mm for males (range 15.6–19.5 mm, $N = 31$) and 18.0 ± 1.0 mm for females (range 14.8–19.6 mm, $N = 28$) in *D. variabilis*. Females were significantly larger than males in both species ($t = -3.25$, df $= 97$, $p < 0.001$; $t = -2.18$, df $= 55$, $p < 0.017$, respectively).

Habitat use

D. imitator: This species was found throughout early secondary to old growth forests where phytotelmata were abundant. All observed individuals occurred in the lower portion of canopy, with the highest observation at 4.5 m (mean = 0.9 m, $N = 115$). No frogs were heard calling from higher perches. Adult frogs were infrequently found on the leaf litter (13%, $N = 12$); a majority of sightings were above ground on vertical objects or the broad leaves of plants (87%, $N = 103$).

D. variabilis: This species was found throughout secondary to old growth forests where arboreal phytotelmata were present. Individuals were observed in the understory and the canopy, with the two highest observations at 8.4 and 7.0 m. No frogs were heard calling from higher perches. Adult frogs were infrequently found on the leaf litter and a majority of sightings were above ground on vertical objects.

Generalized reproduction

D. imitator: Reproduction typically occurred in early morning (0700 h–1000 h) or late afternoon (1500 h–1800 h). Reproduction was initiated by the male, who began calling from an elevated perch. The female slowly approached the calling male and, once she was visible, he called at a faster rate. Once the female was in very close proximity (ca.10 cm), the male continued walking in the direction of a suitable breeding site. The male paused approximately every minute to call in the direction of the following female. In most instances the breeding site was secluded within the leaf litter, dense foliage, or within the axil or basal sheathing leaf of a phytotelm-containing plant. Clutches were observed on the inner leaves and stems of *Heliconia* (52%,

$N = 26$), *Dieffenbachia* (22%, $N = 11$), *Xanthosoma* (24%, $N = 12$) and bromeliads (2%, $N = 1$). Upon arriving at the suitable breeding site, the male called at an increased rate (19.4 calls per min, $N = 4$) for an extended period (81 min, range 72–120 min, $N = 4$). Eventually the female became receptive and deposited 1–3 eggs (mean $= 1.6 \pm 0.5$ eggs, $N = 33$ clutches), usually a couple of minutes apart from each other. The male immediately fertilized the egg(s) by turning away from the female (both then facing opposite directions) and placing his vent against hers. Eggs were never laid in close proximity to water; if they were laid within a phytotelm they were at least 14 cm above the surface of the water.

D. variabilis: Reproduction occurred throughout the day and was initiated by the male, who called from an elevated perch usually in response to the presence of a female. The male approached the female and increased his call rate. When the female was in close proximity, the male led the female to the egg deposition site (as described for *D. imitator*). In most instances the breeding site was at the edge of the water, secluded within the axil of a bromeliad. Egg clutches were observed in water filled axils of *Heliconia* (9%, $N = 2$), *Dieffenbachia* (24%, $N = 5$) and bromeliads (67%, *Aechmea* spp., $N = 9$; *Guzmania* spp., $N = 3$; other, $N = 2$) near or below the water line. Upon arriving at the suitable breeding site, the male called for an extended period (mean 163 min, $N = 8$, range 71–424 min). Eventually the female laid 2–6 eggs (mean $= 3.7 \pm 0.6$ eggs, $N = 32$ clutches). The male immediately fertilized the eggs by facing away from the female and placing his vent against hers or walking over the egg after oviposition. Typically reproduction was done in pairs (77%, $N = 27$), although we have observed groups of two males and one female (17%, $N = 6$) and two females and one male (6%, $N = 2$) engaging in reproductive behaviors.

In reproductive bouts with two males present, the males wrestled with each other while the female remained close by, appearing to observe the male–male aggressive interactions ($N = 4$). Between wrestling bouts, either male would court the female. Eventually, one male conceded and left the pool ($N = 2$) or the female laid an egg in the presence of both males and the more aggressive male would have first access to the egg (appearing to fertilize them). Shortly after (ca. 1 min), the subordinate male attempted to fertilize the egg(s) while the dominant male continued courting the female ($N = 4$). This cycle of courting and egg deposition was repeated for each egg deposited and continued until it became dark. In the instances of two females and one male, the male courted both females, alternating his efforts between each female every couple of minutes. In both observations, only one of the females deposited eggs. Reproduction peaked after rain, especially if it came after a dry period (unpublished data). Males only called when attempting to court a female or during courtship.

Generalized behaviors of paired males and females

D. imitator: In multiple cases, a particular female and male pair occupied the same territory ($N = 15$). The male vocalized toward the female throughout the day, even in the absence of other males. Although pairs remained within the same area for an extended period, they rarely interacted physically except when egg feeding or reproducing. Females foraged throughout the day, but other behaviors are poorly known because females were infrequently encountered. Males were observed 2.1 times more frequently than females. Pair bonds were maintained for the duration of each field season ($N = 13$, maximum of 4 months). No pairs were observed to remain intact for successive field seasons and known individuals were observed without their partner from previous seasons ($N = 2$). Paired individuals were observed together, egg feeding, as many as 8 times (mean = 2.9, $N = 44$).

D. variabilis: There is no evidence of pair bonding in this species and reproductive pairs were not observed to interact after reproduction. On several occasions, over a period of less than 30 d, paired individuals were observed breeding with different mates ($N = 4$).

Generalized egg feeding behaviors

D. imitator: Resident males were frequently observed within their territory near pools that contained tadpoles ($N = 26$). At times, tadpoles became active and approached the surface of the water near the adult. Males surveyed pools in their territory as frequently as every other day. Every 6–10 days (mean = 7.3, 7 observations) the male initiated egg feeding by calling at the site of pool that contained a tadpole. The male continued to call until the resident female arrived. Once she arrived, the male called from the edge of the pool, changing calling sites every couple of minutes. Occasionally the tadpole approached the surface of the water and vibrated violently against one of the adults. In some instances the tadpole appeared to be nibbling at the limbs of either adult. Eventually the female dove underneath the water and released a trophic egg. The successful egg deposition usually was preceded by several similar episodes in which the female did not deposit a trophic egg. In several instances more than one trophic egg was released ($N = 9$); in these cases the male continued to call after the deposition of the first trophic egg, and the female entered the pool and released another trophic egg. During the entire process the male continued to call and rarely entered the water before or after trophic egg deposition. Pairs were observed to feed trophic eggs to as many as four tadpoles at various developmental stages. None of the trophic eggs were observed to begin development, and hence were not likely to be fertilized.

D. variabilis: We have never observed trophic eggs in pools containing *D. variabilis* tadpoles, nor have we observed any behaviors which resemble trophic egg feeding.

Relative size of territories and maintenance of boundaries

D. imitator: This species occupied small territories (approximately 10 m^2, minimum convex polygons (unpublished data) defined by repeated recaptures within an area) and were observed to stay in the same territories for extended periods of time (over 4 months). Resident males called frequently, usually in response to nearby calling males. Vocal bouts occurred throughout the day, but peaked in early morning between 0800 h and 0900 h (mean = 9.6 calls per min, $N = 7$) and in late afternoon, 1400 h to 1600 h (mean = 4.6 calls per min, $N = 24$). Vocal bouts involved as many as 6 males; each positioned about 3 m apart. These territorial calls were loud and could be heard by humans from up to 20 m; during vocal bouts males positioned themselves on a perch (typically 1 meter off the ground) facing the direction of the closest calling male. If an approaching male intruded into the territory of a calling male, the defending male approached the male, began to call at a faster rate, and then attacked the intruder. The attack usually consisted of one male grasping the other near the inguinal region, similar to inguinal amplexus, and wrestling ($N = 8$). Individuals continued to wrestle until one of the two retreated (injury was never observed in any of the participants). In captivity we have observed similar male–male aggression and additionally female–female aggression. The female–female wrestling was similar to male–male aggression (described above); however, in addition, the resident male called nearby throughout the duration of the interactions ($N = 2$, ca. 4 h each).

D. variabilis: Most males were transient in terms of habitat use; few occupied the same area for more than a week. Individuals were frequently found more than 5 m from their previous observations. Occasionally males and females remained in the same area for an extended period of time. In these instances males never engaged in vocal bouts and did not appear to monitor or defend the margins of its home range. We never observed any physical aggression associated with territory maintenance.

Tadpole transportation behavior and deposition sites

D. imitator: In every observation of tadpole transportation in which the sex of the adult was identifiable, all were adult males ($N = 18$). Males retrieved embryos from the breeding site, typically removing the developing embryos from the egg. This was done by tearing the embryo sac open with its rear legs. The freed embryo then wriggled itself onto the back of the male ($N = 2$). In several instances, a male removed one embryo a couple days before the other ($N = 3$). Out of 18 instances when males were observed transporting larvae, in 16 cases (88%) a single larve was carried, and 2 cases (12%) 2 larvae were carried. Males traveled up to 5 m in their survey for pools to deposit their tadpoles within and spent considerable time looking for pools. During transportation, some males continue to forage, call and aggressively defend their territories ($N = 5$). However, a majority of males carrying larvae exhibited a greater degree of sensitivity to threat than do males (or even the same males) when not carrying a tadpole and have been observed to flee into the leaf litter once they detected our presence, an uncommon behavior among non-transporting males. *Dendrobates imitator* was found to use the following phytotelmata for tadpole deposition: *Dieffenbachia* (35%, $N = 42$), *Xanthosoma* (36%, $N = 43$), *Heliconia* (15%, $N = 18$), Marantaceae (9%, $N = 11$), Bromeliaceae (3%, $N = 4$) and tree holes (2%, $N = 3$). Average phytotelm size used was 24 ± 11 ml ($N = 26$, range 9–44 ml).

D. variabilis: In every observation of tadpole transportation in which the sex of the adult was identifiable, all were adult males ($N = 25$). Males retrieved developing tadpoles from the breeding site, removing them from the egg ($N = 9$) or retrieving the tadpoles from the phytotelmata which they hatched into ($N = 1$). The embryo was removed from the embryo sac by the adult male, who tore the sac open with his rear legs. The freed tadpole then wriggled onto the back of the male ($N = 9$). At times the male used his back legs to push the tadpole onto his lower back ($N = 3$). In the single observation of a male retrieving the tadpoles from the water, he entered the water and manipulated the tadpole onto his back (as described above) until all 3 tadpoles present were placed on his back. We observed males transporting tadpoles 25 times, and males carried between 1 and 6 tadpoles (mean = 2.7), depositing the individuals communally or individually. If tadpoles were deposited communally, the male transported and deposited the entire clutch into the pool. Typically he returned and retrieved each tadpole individually and place them in separate pools, usually in close proximity to the communal deposition site ($N = 3$). In many instances the male did not transport tadpoles at all, allowing all the embryos to hatch into the pool in which the eggs were laid ($N = 17$). In the following weeks, the male did not return to retrieve the tadpoles. *Dendrobates variabilis* was found to use primarily Bromeliaceae (81%, *Aechmea* spp., $N = 9$; *Guzmania* spp., $N = 4$), *Heliconia* (13%, $N = 2$) and *Dieffenbachia* (6%, $N = 1$) for tadpole deposition. Average phytotelm size was 112 ± 42 ml ($N = 16$, range 29–172 ml).

During seven observations in the artificial pool surveys, *D. variabilis* tadpoles disappeared from test pools (up to Gosner stage 35). This did not appear to be the result of predation, as no potential predators were present in the pools. Furthermore, we observed larger tadpoles (up to Gosner stage 35) suddenly appearing in previously empty pools ($N = 4$), and have caught males in the process of transporting late stage tadpoles on their backs ($N = 2$).

Tadpole behavior

Tadpoles of both species foraged on detritus, algae, small aquatic insects (e.g., mosquito larvae). In *D. imitator*, tadpoles additionally consumed trophic eggs. The time to consumption appeared to depend on size of the tadpole, with the smallest (8–11 mm total length, TL) not consuming the eggs at all ($N = 2$), the medium-sized tadpoles (11–19 mm TL) consuming the eggs in a day or two ($N = 15$), to the largest (19–30 mm body TL) consuming the eggs within hours ($N = 10$). To consume a trophic egg, the tadpole chewed a hole in the vitelline membrane to access the nutritive egg. The tadpoles of *D. imitator* appeared to recognize the presence of adults, especially during egg feeding. All *D. imitator* tadpoles observed in natural pools were solitary ($N = 112$). However, in artificial pools, 92% ($N = 49$) of tadpoles were solitary, 6% with a conspecific ($N = 3$) and 2% with a congeneric (with *D. variabilis* $N = 1$). Of the *D. variabilis* tadpoles observed in natural pools, 13% (2 of 16) were found with conspecific tadpoles. We observed a similar percentage in artificial pools of 13% (7 of 56) and two instances with a congeneric tadpole (*D. fantasticus* and *D. imitator*). In artificial pools, 71% (5 of 7) of these multiple depositions resulted in conspecific cannibalism during the period of observation. Dragonfly (Anisoptera, $N = 13$, $N = 2$) and damselfly (Zygoptera, $N = 2$, $N = 0$) larvae were also found in the artificial and *Aechmea* bromeliads (values respectively), however predatory mosquito larvae (*Toxorhynchites* sp., Culicidae) and Dytiscid beetles (Dytiscidae) were never observed in surveyed pools. The pools that contained predators were larger and were types of phytotelm used more frequently by *D. variabilis.*

Interspecific interactions

Aggressive interactions between these species were observed twice. In both cases, a male *D. imitator* was observed defending its territory from an intruding *D. variabilis* male, calling at short intervals while approaching the intruder until it left his territory.

Statistical comparisons between both species

For a generalized overview of comparisons between the two species see Table 2. *Dendrobates imitator* tadpoles occupied significantly smaller phytotelmata than *D. variabilis* ($t = 10.23$, df $= 40$, $p < 0.001$, Figure 2). The species showed no statistical differences in adult body sizes or mean male size ($t = 0.28$, df $= 224$, $p = 0.783$). *Dendrobates imitator* females were slightly larger than those of *D. variabilis* (mean of 18.2 vs. 18.0 mm, $t = -1.05$, df $= 60$, $p = 0.297$). Clutch sizes of *D. imitator* were significantly smaller than *D. variabilis* ($t = 26.50$, df $= 65$, $p < 0.001$). The frequency with which conspecific tadpoles were placed together in natural pools differed significantly between the two species ($t = 15.17$, df $= 1$, $p < 0.001$), with *D. variabilis* placing tadpoles with conspecifics more frequent than *D. imitator*. The frequency of phytotelmata types used by each species was significantly different ($t = 79.65$, df $= 5$, $p < 0.001$).

Table 2. Overview of observed differences between *D. imitator* and *D. variabilis.*

Observation	*D. imitator*	*D. variabilis*
Habitat use		
Forest type	Early secondary to old growth forests	Secondary to old growth forests
Vertical distribution	Semi-arboreal (0–2 m)	Semi-arboreal, scansorial (0–7 m)
Territoriality	Present	Absent
Home range sizes	Very small (10 m^2)	Small to large (20–100 m^2)
Maintenance of territories	Vocal bouts, wrestling	None observed
Tadpole deposition sites	Phytotelmata of terrestrial plants	Primarily phytotelmata of epiphytes
Egg placement	Away from water	Above surface of water in phytotelm
Clutch sizes	1.6 ± 0.5 eggs	3.6 ± 0.6 eggs
Phytotelmata size for tadpole deposition	24 ± 11 ml	112 ± 42 ml
Social behavior		
Mating system	Socially monogamous	Promiscuous
Parent care	Biparental	Male parental or none
Pair bonding	Present	Absent

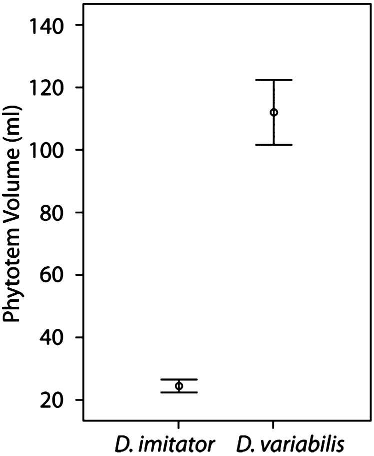

Figure 2. Error bar plot showing differences in sizes of natural phytotelmata used by each species for tadpole deposition (error bars represent 1 Standard Error).

Discussion

The phytotelmata used for tadpole deposition by *D. imitator* are significantly smaller (in volume) than those used by *D. variabilis* (Figure 2). In our natural plots, *D. imitator* primarily used leaf axils of *Heliconia* spp., *Xanthosoma* spp. and *Dieffenbachia* spp. for both egg and tadpole deposition, although eggs were typically deposited away from the pool. If present, *Heliconia* spp. appeared to be preferred over other phytotelmata. This is likely a result of reduced predation risk associated with *Heliconia*, as both the male and female could be found sleeping within the leaf axils. The leaf axils used in *Heliconia* were comprised of the basal sheathing leaf, which provided a long passage with a small opening at the top (barely large enough for a single frog to enter), and at the bottom, a pool (where the leaf fuses with the stem). In contrast, *D. variabilis* uses primarily leaf axils of bromeliads, in particular *Guzmania* and *Aechmea* species, for both egg and tadpole deposition. *Dendrobates variabilis* displayed little preference for either type; however, bromeliads occur in higher densities, and as a result, they are used more frequently. The availability of pool types occurs over a vertical gradient. Species of *Heliconia*, *Dieffenbachia*, *Xanthosoma* and Marantaceae are terrestrial plants and the bromeliads utilized are epiphytes, reaching into the upper layers of the canopy. The distribution of each species appears to reflect the distribution of its oviposition sites.

The parental care strategy of *D. variabilis* was limited to male tadpole transport and deposition (male parental care) and there is no evidence that this species displays biparental care. The attendance of embryos and tadpoles by males varied considerably, and some males returned to transport tadpoles whereas other did not. The adults appeared to be transient and rarely remained in the same area for extended periods. In contrast, *D. imitator* pairs were frequently observed feeding trophic eggs to tadpoles. *Dendrobates imitator* adults occupied considerably smaller home ranges than *D. variabilis* (on average 5 times smaller, unpublished data). *Dendrobates imitator* also demonstrated a high level of site fidelity and actively defended territories, remaining in the same area for extended periods. Little territoriality or site fidelity was observed in *D. variabilis.*

These differences in reproductive modes were also associated with differences in social behaviors. Males and females of *D. variabilis* were observed to be promiscuous and showed little mate fidelity. Paired individuals would remain together only during oviposition and were rarely observed interacting with prior mates. This contrasts with *D. imitator*, where paired males and females were observed interacting daily and were never observed courting additional mates.

The mating strategies of males and females in dendrobatid frogs appear to depend on both ecological factors and the nature of parental care. In some species of *Dendrobates* with uniparental male care (e.g., *D. auratus* and *D. leucomelas*) males are highly site-specific, and females can apparently profit reproductively from 'mate-guarding', or aggressively attacking other females that attempt to mate with the male (Summers, 1992). However, in other species, males are less site-specific and it appears that females are unable to monopolize male parental care through aggressive mate-guarding (Summers & Amos, 1997). This is the case for *D. variabilis* and some populations of *D. ventrimaculatus* (Summers & Amos, 1997; but see Poelman & Dicke, 2007). In these species, there appears to be a scramble competition for the use of phytotelmata. Multiple clutches are laid on the periphery of newly available pools, and multiple tadpoles are frequently deposited in a single pool (Summers & Amos, 1997). This leads to high levels of tadpole competition, and also cannibalism between both related and unrelated tadpoles (Summers & Amos, 1997; Summers & Symula, 2001).

The tadpole deposition behavior of *D. variabilis* appeared to be quite flexible, with some observations of multiple individuals attempting to breed in a single pool (which has also been observed in *D. ventrimaculatus*). This type of scramble competition provides the opportunity for various forms of reproductive parasitism (Summers & Amos, 1997). In previous research on *D. ventrimaculatus*, Summers and Amos (1997) obtained observational and molecular genetic evidence (using microsatellites) that reproductive parasitism does occur. Our observations on *D. variabilis* suggest that the opportunities for reproductive parasitism may be even more complex in this species. We observed, on multiple occasions, *D. variabilis* moving tadpoles from test pools to alternate pools, after the tadpoles had been deposited in a pool. This behavior allows the male to move any tadpole that he has already deposited to a new pool, where it would have the opportunity to cannibalize embryos below the water line in the pool, or younger, smaller tadpoles that had already been placed in the pool. The lack of site fidelity, the opportunistic nature of the larval deposition strategies and the observations of individuals of both sexes mating with multiple mates in *D. variabilis* supports the contention that this species has a promiscuous mating system.

Our observations of *D. imitator* suggest that this species has biparental care and a monogamous mating system. Observations on *D. vanzolinii* (Caldwell, 1997; Caldwell & de Oliveira, 1999), the only other species known to exhibit symmetric biparental care, are similar to our observations on *D. imitator*. Both species used small phytotelmata for tadpole deposition (mean of 17.5 ml in *D. vanzolinii* vs. 24.1 ml in *D. imitator*). Egg deposition was generally away from the water in the phytotelmata, whereas trophic eggs were placed below the surface of the water in pools containing tadpoles (Caldwell & de Oliveira, 1999). Males of both species transported single tadpoles to pools and deposited them in the absences of females. The frequency of feeding varied between species, with *D. vanzolinii* feeding on average every 4.8 days and *D. imitator* feeding on average every 7.3 days. However, feeding behavior was almost identical, with males of both species guiding females to a tadpole site and undergoing courtship behavior to induce egg deposition. *Dendrobates imitator* was observed to care for as many as four tadpoles at once whereas *D. vanzolinii* was observed to care for as many as two. The two species displayed similar levels of territoriality and paired females were always found within the territories of males. Territories appeared to be more than twice as large in *D. vanzolinii*. However territory size is likely to depend on abundance of phytotelmata, and phytotelmata were less abundant in sites used by *D. vanzolinii* (unpublished data). All territories of both species surround phytotelmata.

Factors which lead to the evolution of biparental care in poison frogs are likely associated with the tradeoff between nutrition and risk of predation and competition mediated by phytotelmata size. Experimental evidence demonstrating an effect of pool size on larval growth rates is consistent with this tradeoff hypothesis (Summers & McKeon, 2004). This tradeoff may have been critical in the transition from terrestrial pool breeding to phytotelm-breeding (Summers & McKeon, 2004), and may also have been a critical factor in the transition to biparental care (Summers & Earn, 1999). In particular, the use of very small pools may be limited by the availability of nutrients, but may also have reduced the risk of predation and competition. In species with male-only care, tadpoles are not fed after they are deposited, which constrains them from using small pools with little available food. Although males may increase the availability of food to tadpoles by depositing smaller tadpoles or enticing females to lay eggs near the surface of an occupied pool (Summers & Amos, 1997), this is an irregular and inefficient feeding mechanism. Provisioning of trophic eggs is more efficient, but it requires female participation in parental care. Hence, one hypothesis for the evolution of biparental care in poison frogs is that it allows the use of very small phytotelmata (Caldwell & de Oliveira, 1999; Summers & Earn, 1999). The use of such small pools could have become necessary for the ancestors of *D. imitator* and *D. vanzolinii* for several different reasons (Caldwell & de Oliveira, 1999; Summers & Earn, 1999). For example, environmental changes could have shifted the abundance of small relative to large phytotelmata, causing selection to favor the use of small phytotelmata.

Our behavioral observations are consistent with the occurrence of social monogamy with pair-bonding in *D. imitator* (where pair-bonding is defined simply as a social and reproductive relationship between a male and a female that share parental care duties; Johnson & Burley, 1998). It is important to point out that although we did not observe the maintenance of pair bonds between successive field seasons, this doesn't mean bonds are only maintained for short periods. It's likely that most these bonds are maintained, at least, the duration of the peak breeding season (4–6 months) and possibly for multiple seasons. Pair bonds may relax, or break, during the dry season, especially in regions that experience longer periods of aridity (i.e., Huallaga Canyon populations). In these areas, during the driest months breeding stops, males rarely call or interact with females, and the adults remain hidden within the moist leaf litter and axils of plants (unpublished data). Further, given the limited number of 'optimal' breeding sites, males frequently face aggression from competitors and eventually lose their territories, which may also result in the loss of their mates.

Social monogamy is a relatively rare social system in ectotherms, although it is common in birds (Black, 1996). In many cases the prevalence of social monogamy is associated with the occurrence of biparental care (Whiteman & Cote, 2004), which in some cases has been suggested to be causal (see hypothesis 1 below). A number of different hypotheses have been proposed to explain the evolution of monogamy (either social monogamy, genetic monogamy, or both). Below we summarize the most well-established hypotheses:

1) Biparental care (Wittenberger & Tilson, 1980; Gronell, 1984): selection for biparental care may favor monogamy if the value of exclusive co-

operation between a male and a female (in terms of reproductive success) outweighs the potential benefits of polygamy for either sex.

2) Mutual mate-guarding (Barlow, 1986): this hypothesis emphasizes the importance to females of monopolizing male parental care, and the importance to males of monopolizing a high quality female.

3) Territorial defense (Hourigan, 1989): Monogamy may be favored if two individuals are required to effectively defend a territory in the context of feeding or other resources outside of the context of reproduction (otherwise this collapses into hypothesis 1 or 2).

4) Resource limitation (Emlen & Oring, 1977): If resources required by females are sparsely distributed this will lead to a highly dispersed distribution of females. In this situation, males may be unable to monopolize more than a single female due to constraints on the size of a territory that can be effectively patrolled and defended.

5) Low population density/low mate availability/low mobility (Ghiselin, 1969): If the probability of encountering another potential mate after leaving the current mate is sufficiently low, then monogamy may be the best option.

6) Female space use (Komers & Brotherton, 1997): When females are solitary and defend a small, exclusive home-range, males may choose to defend only a single female as a risk-reduction strategy (note that this hypothesis assumes female territory size evolved in a context other than shared parental duties).

In the case of *D. imitator*, we can assess the evolution of social monogamy as it relates to these hypotheses using the observational data presented here as well as comparisons with other closely related species. The pattern of female space use (hypothesis 6) is unlikely to explain social monogamy in *D. imitator* because there is no apparent ecological reason for females to defend a feeding territory. Defense of feeding territories does not occur in closely related species with very similar foraging behaviors, such as *D. ventrimaculatus* (Summers & Amos, 1997; Poelman & Dicke, 2007) or *D. variabilis* (this study), and we saw no evidence of it in *D. imitator*. Low population density (hypothesis 5) is not a viable explanation for monogamy in *D. imitator* because individuals occur at locally high densities (unpublished data), and so mate availability is unlikely to be a constraint on polygamy. Resource limitation (hypothesis 4) is also unlikely, as both males and females are locally abundant, and females are not highly dispersed. Territorial defense (hypothesis 3) in contexts other than reproduction is also unlikely. As discussed above, females do not appear to defend feeding territories in either *D. imitator* or closely related species such as *D. variabilis*. Furthermore, male and female *D. imitator* do not jointly patrol territorial boundaries, rather they are typically seen together in the context of reproduction. Distinguishing between hypothesis 1 and 2 is somewhat difficult, because both involve mutual territorial defense specifically associated with reproductive behavior (particularly parental care). Under hypothesis 1, both the male and female in a pair should benefit from mate-fidelity (by enhancing the efficiency and effectiveness of parental care). Hence strict mate-guarding should be unnecessary to maintain monogamy. Note that this does not preclude the possibility of sex-specific aggression (i.e., males may specialize in driving away other males, and females in driving away other females, even if both sexes profit from driving away members of either sex). Under hypothesis 2, members of one or both sexes may benefit from extra-pair matings, but are effectively prevented from engaging in polygamy by the mate-guarding behaviors of their mates. As described above, mate-guarding behaviors by females have been observed in previous research on two species of *Dendrobates* with male parental care (*D. auratus* and *D. leucomelas*: Summers, 1989, 1992). The frequency and intensity of female aggression in *D. auratus* and *D. leucomelas* contrasts with the relative lack of female aggression noted in *D. imitator* (where female aggression has only been observed in captivity) and in *D. vanzolinii* (where female aggression has not been observed). Thus, our observations to date are more consistent with the prediction of hypothesis 1 (both the male and female in a pair benefit from monogamy) than with the prediction of hypothesis 2 (one or both sexes would benefit from extra-pair matings, but mate-guarding prevents this). Note that a key prediction of hypothesis 1 is that the male and female in each pair will be genetically monogamous as well as socially monogamous. We are currently testing this prediction with the use of neutral genetic markers (microsatellites).

Overall, our results are consistent with the hypothesis that a key ecological difference between these species, involving the size of pools typically used for reproduction, is strongly associated with the evolution of biparental care in *D. imitator.* This is consistent with the results of other studies of anurans with biparental care (Caldwell & de Oliveira, 1999; Jungfer & Weygoldt, 1999; Bourne et al., 2001). In turn, biparental care is associated with long-term, affiliative male–female associations (pair-bonding), and hence with social monogamy. This is consistent with the results of recent research on some other species of dendrobatids with biparental care (Caldwell & de Oliveira, 1999; Bourne et al., 2001).

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