



Paternal-Tadpole Interactions During Tadpole Deposition in the Three-striped Poison Frog, *Ameerega trivittata*

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Abstract – Anurans (frogs and toads) have the widest diversity of parental care strategies among tetrapods, yet relatively little is known about parental-offspring behavioral interactions for most species. In most species in the clade Dendrobatoidea, a parent transports tadpoles on their dorsum from a terrestrial hatching site to a water source for continued development. Tadpoles typically swim off their parent's back upon reaching a water source. However, we hypothesized that males may actively attempt to remove tadpoles following initial observations of male three-striped poison frogs, *Ameerega trivittata*, attempting to forcibly remove tadpoles by “wiping” them from their dorsa upon reaching a water source. We describe and quantify male wiping behavior and its success in removing tadpoles. Additionally, we describe and quantify tadpole behavior upon being removed from a male's dorsum. Twenty males were videotaped transporting and removing tadpoles at Brownsberg Nature Park, Suriname. Male wiping behavior was unsuccessful 92% of the time (n = 415 attempts). In successful cases, tadpoles swam in circles next to the male. Males then responded by jumping to a new location in the pool or moving out of the pool. Male wiping behavior appears to be both energetically and temporally costly in contrast to other members of the Dendrobatoidea, where tadpoles swim off the male's dorsum when reaching an aquatic deposition site. These findings add to our understanding of life history variation in this diverse clade of frogs and suggest a bet-hedging behavior that may further influence this species' evolutionary response to climate change.

Keywords – Amphibians, Dendrobatoidea, *Ameerega trivittata*, Poison frog, Tadpole transport, Male transport behavior, Parental behavior, Bet-hedging

Parental investment in the care of offspring can be costly to parents, who seek to minimize their energy expenditure while enhancing their fitness (Trivers, 1972, 1974). Anurans (frogs and toads) display the highest diversity of reproductive modes of tetrapod vertebrates (39 modes, enumerated in Haddad & Prado, 2005) and provide an exceptional opportunity to document and test parental investment hypotheses. Numerous studies document the decisions, costs, and behaviors involved in parental care (Buxton & Sperry, 2017; Schulte et al., 2020; Stynoski et al., 2018; Summers & Earn, 1999; Summers & Tumulty, 2014; Wells, 2007). How such strategies evolve and persist within lineages, especially those mediated by the behavior of both parent and offspring, requires considering trade-offs between investment in offspring and self.

Parental care occurs in 10–15% of anuran species (Schulte et al., 2020; Wells, 2007) and is found in 56 of 76 families (Schulte et al., 2020). Parental care may involve a complex array of energetically costly

behaviors (Crump, 1996; Dugas et al., 2016a; Summers, 2019; Wells, 2007), including the selection of egg and tadpole deposition sites (Beck et al., 2017; Buxton & Sperry, 2017; Crump, 1991), egg attendance (Blommers-Schlösser, 1975; Poo & Bickford, 2013; Simon, 1983; Vockenhuber et al., 2009), guarding of tadpoles (Fernández & Fernández, 1921; Vaira, 1997), tadpole provisioning (Brust, 1993; Crump, 1996; Dugas et al., 2016b; Perry & Roitberg, 2006; Weygoldt, 1980), egg transport (Wells, 1981), froglet transport (Diesel et al., 1995), and tadpole transport (Beck et al., 2017; Inger, 1966; Inger et al., 1986; Pašukonis et al., 2019; Ringler et al., 2013; Schulte & Mayer, 2017; Smith, 1887; Wells, 2007; Weygoldt, 1980; Wyman, 1859).

Tadpole transport involves tadpoles moving onto the parent's dorsum after hatching in a terrestrial location and their transport to an aquatic site (e.g., ephemeral pools, ponds, streams, tree holes, palm fronds, or phytotelmata) for continued development and metamorphosis. Species exhibiting this behavior are found in the families Aromobatidae (Lescure, 1976; Souza et al., 2017), Dendrobatidae (Caldwell & de Araujo, 1998; Weygoldt, 1987), Dicroglossidae (Goyes Vallejos et al., 2018), and Ranidae (Inger et al., 1986). Depending on species, transport is maternal (Summers, 1992; Wells, 1980a, 1980b; Weygoldt, 1980; Young, 1979), paternal (Ringler et al., 2013; Summers, 1992; Wells, 1978), or flexibly negotiated (Ringler et al., 2015; Tegnér, 2014; Tumulty et al., 2014).

Transport of tadpoles involves a variety of temporal, energetic, territorial, and predation risks and trade-offs, resulting in a potential reduction in fitness for the transporting adult. Transport to a deposition site may take four to nine days in some species (Downie et al., 2001; Luddecke, 1999; Quiguango-Ubillús & Coloma, 2008; Wells, 1980b), though for most Dendrobatoidea species tadpoles are deposited within a day (Jowers & Downie, 2005; Ringler et al., 2013). In *Ameerega trivittata*, males traveled over 750 m transporting tadpoles from their territory to a tadpole deposition site and then returned to their territory (Pašukonis et al., 2019). During transport periods, males may incur fitness costs through lost mating opportunities and loss of territory (Pašukonis et al., 2019; Townsend, 1986). In addition, transport may expose both parents and tadpoles to higher predation risks (Donnelly, 1991; Saporito et al., 2010).

Tadpole transport is obligatory (Ringler et al., 2013; Schulte et al., 2020) in almost all of the approximately 341 species of dendrobatoid frogs (Frost, 2024). Tadpoles move onto the parent's dorsum from their terrestrial hatching site during transport initiation. In *Hyloxalus toachi*, *Allobates femoralis*, and *Dendrobates tinctorius*, males position themselves on top of the newly hatched tadpoles and rotate over them, initiating tadpole movement to the male's dorsum (Goyes Vallejos et al., 2018; Pašukonis et al., 2017; Quiguango-Ubillús & Coloma, 2008; Rojas & Pašukonis, 2019). Similar behavior for picking up tadpoles occurs with male *Dendrobates auratus* sitting in a distinctive posture with flattened hind legs on the hatching tadpoles that wriggle over his hind legs and onto his dorsum (Wells, 1978). Upon reaching the aquatic deposition site, a number of studies indicate that the tadpoles swim off the parent's dorsum (Eaton, 1941; Fandiño, et al., 1997; Downie et al., 2001; Pašukonis et al., 2017; Poleman, et al., 2010; Rocha, et al., 2018; Wells, 1980a, 1980b, 2007).

Tadpoles are deposited at a single or among several water sources (Erich et al., 2015; Wells, 1980c). The bet-hedging hypothesis supposes that spreading offspring into different locations improves offspring survival in unpredictable biotic and abiotic environments (Erich et al., 2015; Spieler & Linsenmair, 1997). Aquatic predators influenced choice in *Mannophryne trinitatis* whose males retained their tadpoles for 3 to 4 days while searching for predator-free pools. If unsuccessful in finding a predator-free pool, they deposited their tadpoles in wet leaf litter (Downie et al., 2001).

Despite the initial descriptions of tadpole transport almost a century and a half ago (Smith, 1887), to the best of our knowledge, no subsequent studies have described and quantified the behavior of males or females forcibly removing tadpoles from their dorsum when reaching a water source. However, during a previous study of *Ameerega trivittata* (d'Orgeix et al., 2015), two of the authors (Cd'O & RJ) observed males attempting to dislodge tadpoles from their dorsa using their hind limbs in a wiping movement mentioned by Ringler et al. (2013).

Based on these preliminary observations of male frog and tadpole interactions in *A. trivittata*, we hypothesized that male frogs may actively promote the introduction of tadpoles into the aquatic habitat through hind-limb "wiping" behaviors, but we do not know the ubiquity or success of such behaviors in

tadpole removal. In this research, we explored the hypothesis that males actively engage in wiping by documenting the relative frequency of male hind-limb wiping at ponds and estimating wiping success in removing tadpoles from the male dorsum. Our objective was to provide preliminary observations and data that can serve as the impetus for future research examining this and similar behaviors in the context of parental care and the role of tadpole transport behaviors in mediating offspring survival in changing environments.

Methods

Ethics Statement

The Foundation for Nature Preservation (STINASU) of Suriname gave us access to Brownsberg Nature Park (BNP) to film frog behavior. Permits for filming frog behavior were provided by the Suriname Nature Conservation Department (permit # 254). Frogs were not disturbed, caught, or handled. Videotaping was conducted from distances of 2–5 m.

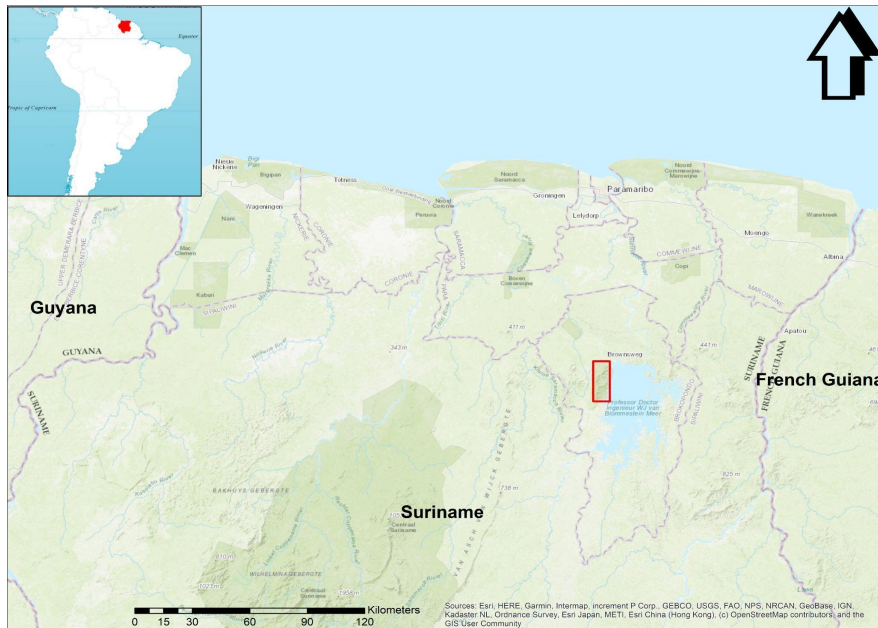
Study Species

Ameerega trivittata (the three-striped poison frog) is one of the largest and most widely distributed species of Dendrobatidae (Grant et al., 2006; Silverstone, 1976). This diurnal species inhabits the forest floor of neotropical environments (Luiz et al., 2015). Unlike males, females are not territorial. Females move freely while being courted by territorial males (Roithmair, 1994a). An average clutch size of 40 eggs is laid terrestrially in leaf litter within a male's territory. Once the eggs are laid, unlike other species with paternal care involving cleaning or watering of eggs, male frogs sit with one side of their bodies touching the eggs (Roithmair, 1994b). Tadpoles hatch 15–22 days after oviposition. Males then transport the entire clutch of 22 to 41 tadpoles (Roithmair, 1994b). Males deposit the tadpoles into small pools of water and streams (Pašukonis et al., 2019; Roithmair, 1994b). In Suriname, Polder (1976) reported population density being greater beside forest roads than in undisturbed forests.

Study Site

Brownsberg Nature Park, in north-central Suriname (4°56'N, 55°10'W), with an above sea level elevation of approximately 500 m, is operated under the authority of the Foundation for Nature Preservation in Suriname (STINASU) (Lim et al., 2005) (Figure 1). A network of dirt roads and paths varying from 2–5 m in width cut across the park and form seasonal pools on forest edges. Between May 4 and June 18, 2014, we recorded videos of male transport and tadpole deposition behavior at this site.

We videotaped *A. trivittata* behavior in seasonal pools varying in size from 1.5–15 m in length to 0.5–6 m in width with depths of 8 cm–1 m. Males used both small and large pools for tadpole deposition (Figure 2).

Figure 1*Maps Delineating Study Site Location*

Note. An overview of Brownsberg Nature Park is indicated by the red rectangle on the map. The insert shows Suriname's location in South America.

Figure 2*Pools for Tadpole Deposition by Male Ameerega trivittata*

Note. Seasonal pools on the main road headed towards Brownsberg Nature Park lodge. Several contributors to this study are seen waiting for *Ameerega trivittata* males transporting tadpoles.

Filming Methodology

We used Nikon D3300 and D5200 cameras with video speeds of 30 frames per second fitted with 100–300 mm telephoto zoom lenses. We filmed frogs from 2–5 m away. The filming took place between 0530 and 2030 h.

To locate and minimize disturbance to males transporting tadpoles, we used two strategies. A “stationary” strategy entailed an observer sitting by a potential tadpole deposition site (pool) and waiting for a male transporting tadpoles to appear. “Active searching” involved walking slowly along roads with pools and using 8 x 40 or 10 x 40 binoculars to search ahead for males transporting tadpoles. Once a male was located, we followed the individual at approximately 4–15 m until he entered a pool. The observer moved very slowly until they were positioned close enough (2–5 m) to videotape their behavior. We videotaped the male until he either moved out of videotaping range or left the pool. Two researchers (Cd'O & VK) videotaped males in different pools during the same time period. However, because individual males were not visually distinguishable, it is possible that the same male could be recorded on a different time or day; thus, video recordings may not be independent.

After preliminary viewing of the videos, we classified two major categories of behaviors during tadpole deposition for quantification, male parental behavior and tadpole behavior. Male behaviors were “wiping,” noted by Ringler et al. (2013) in *A. femoralis*, and “jumping.” In *A. trivittata*, wiping involves lifting a hind limb upwards to the dorsum and moving the limb and toes across the dorsum in a posterior-to-anterior movement over or against the tadpole(s). “Jumping” occurred when a tadpole, deposited into the water, touched the male, who immediately moved to a new location. A “bout” was defined as the number of wipes occurring at a single location before a male moved to another location. Videos depicted both wiping and whether a tadpole was removed by the wipe unambiguously. This enabled subsequent quantification of these behaviors. All videos were analyzed separately by three researchers (AM and TW) at 1 x and ¼ x speed to assess and quantify behaviors. Any discrepancies in behaviors and totals were rechecked by Cd'O.

Statistical Analysis

We analyzed male wiping success from video data using generalized linear mixed effects models in R version 4.2.3 (R Core Team, 2023) using the *lme4* package (Bates et al., 2015). A “successful” wiping attempt was defined as removing a tadpole with a single wiping movement, while in an “unsuccessful” attempt, the tadpole remained attached to the male's dorsum. Attempts were scored per tadpole as a binomial response (1 = successful, 0 = unsuccessful), and we used a logistic link function in an intercept-only model to generate predictions of mean success probability with 95% confidence limits. Our goal was to estimate wiping success probability with estimates of uncertainty appropriate to the data-generating process involving a series of wiping attempts from multiple individuals and multiple time points. We included video recording as a random intercept, acknowledging that parameters may describe variation that includes multiple behavioral recordings from individual males. We assessed the statistical significance of the parameter estimate for mean wiping success probability based on the overlap of confidence intervals with 0.5, the expected probability under the null hypothesis that successes and failures are equally probable commonly used in binomial models. Importantly, failure to reject the null hypothesis does not preclude the estimation of mean and variance in wiping success; instead, it tests whether the probability of wiping success is high or low relative to a coin flip.

Phylogenetic Literature Review

To determine if the behaviors we observed were previously described for *A. trivittata* or other species of poison frogs, we conducted a literature review of the Dendrobatoidea genera for citations of tadpole deposition and transport behavior using Google Scholar through 4/10/2025. Search terms each genus of Dendrobatoidea were “Genus” AND (“tadpole deposition” OR “tadpole transport”). Current

genera of Dendrobatoidea were determined by Frost (2024). Duplicate papers within a genus were removed. We then screened each paper for any specific behavioral descriptions involving a parent attempting to remove transported tadpoles, such as “wiping” (Ringler et al. 2013), or descriptions of how tadpoles dispersed from a parent’s dorsum, such as “swimming.” Papers meeting these criteria were cited. Ambiguous behavior descriptions such as “deposited” were not considered specific enough to determine how the tadpoles left the parent’s dorsum and were not cited.

Results

Phylogenetic Literature Review

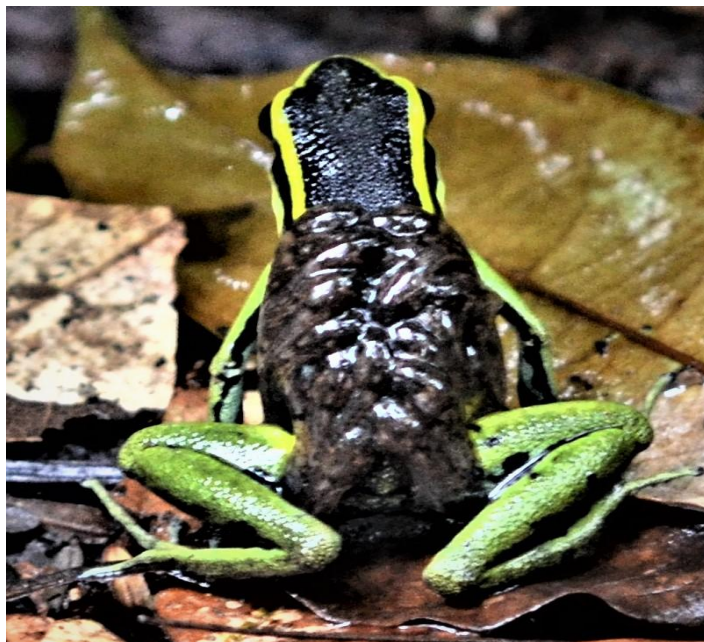
There is a single mention of a parent attempting to remove transported tadpoles in the 20 Dendrobatoidea genera examined (Table 1).

Male-Tadpole Behavioral Interactions

Twenty *Ameerega trivittata* male-tadpole interactions were recorded on video. Recordings were made with males at varying depths in the water ($\bar{x}$ = 1.2 cm in depth, range 0.5–2.5 cm, sd = 0.47, n = 42). Males transported 1–23 tadpoles ($\bar{x}$ = 12, sd = 6.34, n = 19) (Figure 3).

Figure 3

Male Ameerega trivittata Transporting Tadpoles on his Dorsum

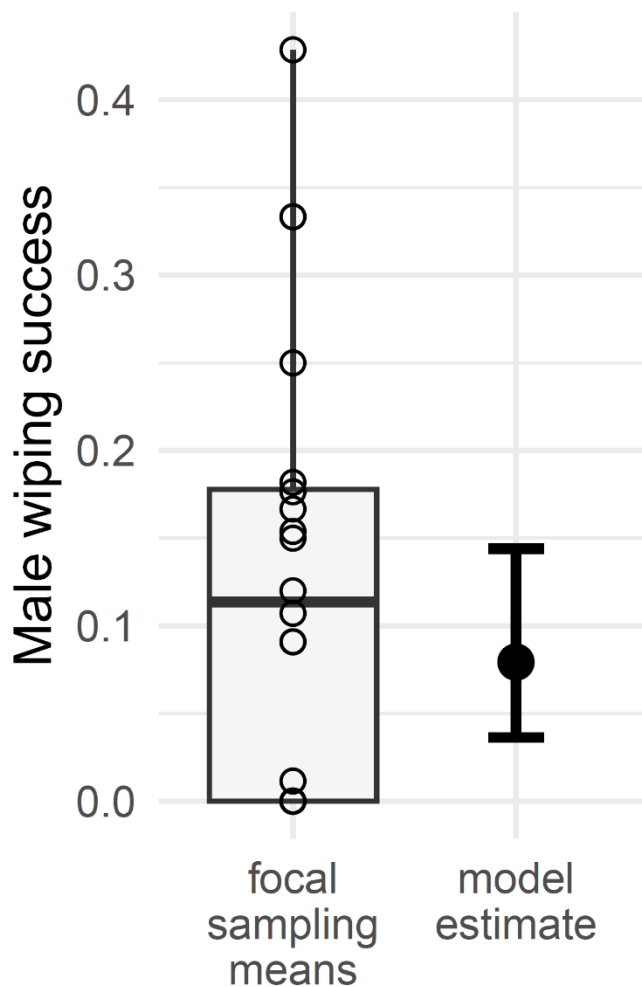


All males attempted to remove tadpoles from their dorsa by wiping. Males jumped to a different location in the pool or moved into the forest after a bout, whether the male was successful or not in removing the tadpole(s). The movement of males after a bout did not appear to reflect a reaction to the researcher as males moved away, towards, or even under the portable chair where a researcher sat. Males exhibited similar wiping behavior, alternating between the left and right hind legs. Three hundred and eighty-five of the 415 wipes recorded (92.8%) did not result in successful removal of a tadpole from the male’s dorsum (Video S1). Wiping success (Video S2) varied widely across focal animal samples and never exceeded 42.9% in any individual recording (Figure 4). The modeled success probability was 0.079 (confidence

limits: 0.036 – 0.144; Figure 4). In other words, wiping was predicted to be unsuccessful on average 92.1% of the time, significantly less than chance. However, in 14 out of 20 focal animal samples, males were successful in removing tadpoles at least once. Successful males wiped an average of 4.4 times to remove their first tadpole ($\bar{x} = 4.4$, $sd = 3.6$, range = 1-12, $n = 14$), and a total of 62.9 wipes, on average ($\bar{x} = 62.9$, $sd = 65.6$, range = 7-242, $n = 14$). Males that were unsuccessful in removing tadpoles averaged 103 total wipes ($\bar{x} = 103$, $sd = 204.6$, range = 1-520, $n = 6$) without success. None of the 14 successful males were able to remove all tadpoles while they were under observation.

Figure 4

Successful Removal of Tadpoles from Male Wipes



Note. Male *Ameerega trivittata* wiping success shown using observations for each of 20 focal animal video recordings (left side: data points and boxplot containing minimum, maximum, median, and the first and third quartiles) and using predictions from a binomial mixed effects model (right side: intercept parameter estimate $\pm$ 95% confidence intervals).

Observations ended when a male moved out of the pool and into the surrounding vegetation or moved out of the video range. Observations of individual males ranged from approximately 1 min to over 3 hr. The male observed for over 3 hr spent the entire time, in multiple bouts totaling 110 wipes attempting to dislodge the single tadpole he was carrying, until leaving the pool at approximately 1900 h. and returning to the forest.

After being removed from a male's dorsum, tadpoles swam around or next to the male in a circular pattern, frequently touching the male's body (Video S3). Upon being touched by a tadpole, males jumped to a new location with the remaining tadpoles still attached (Video S3). Seventy-three percent of the time, the new location was in the same pool, while 27% of the time, the male left the pool. We did not observe whether these males returned to the same or a different pool.

Table 1

Reported Tadpole Deposition Behavior by Dendrobatoidea

Genus	Papers reviewed	Species	Deposition Method	Reference
<i>Adelphobates</i>	34		-	
<i>Allobates</i>	211	<i>femoralis</i>	wiping	Ringler et al., 2013
			swim off in water	Pašukonis et al., 2017
		<i>paleovarzensis</i>	swim off in water	Rocha et al., 2018
		<i>spumaponens</i>	swim off in water	Kok & Ernst, 2007
<i>Ameerega</i>	97	<i>bilinguis</i>	swim off in water	Poleman et al., 2010
<i>Andinobates</i>	43		-	
<i>Anomaloglossus</i>	60		-	
<i>Aromobates</i>	36		-	
<i>Colostethus</i>	182	<i>subpunctatus</i>	swim off in water	Fandiño et al., 1997
<i>Dendrobates</i>	352	<i>auratus</i>	swim off in water	Eaton, 1941
<i>Ectopoglossus</i>	3		-	
<i>Epipedobates</i>	170		-	
<i>Excidobates</i>	13		-	
<i>Hyloxalus</i>	46		-	
<i>Leucostethus</i>	6		-	
<i>Mannophryne</i>	88	<i>trinitatis</i>	swim off in water	Downie et al., 2001
<i>Minyobates</i>	33		-	
<i>Oophaga</i>	202		-	
<i>Phyllobates</i>	136		-	
<i>Ranitomeya</i>	189		-	
<i>Rheobates</i>	11		-	
<i>Silverstoneia</i>	13		-	

Note. A dash indicates no observation of specific deposition behavior recorded for that genus based on our literature review. The phrase “swim off in water” includes descriptions based on tadpoles leaving their parents back on their own volition after entering a water source. “Wiping” indicates the parent forcibly removing the tadpoles from their backs.

Discussion

We documented the behaviors of male *Ameerega trivittata* frogs and their transported tadpoles upon reaching a water source appropriate for tadpole deposition using direct observation in the field. We found that males attempted to remove tadpoles using rear-leg wiping but were unsuccessful over 90% of the time. We did not observe a single tadpole swim off a male's back voluntarily. When a male was successful in removing a tadpole into a pool of water, tadpoles swam in circles and males jumped to a new location in the pool or moved out of the pool. Our observation that males required multiple wipes to remove

a single tadpole contrasts with reported observations of other species that apparently do not require males to forcibly remove tadpoles. We propose two non-mutually exclusive hypotheses for the adaptive significance of tadpoles potentially requiring a male to physically wipe them off into a source of water. A physical or chemical property of adherence to the male's dorsum might prevent tadpoles from being dislodged during transport to a deposition site, which might occur during a rainstorm. These documented patterns of behavior may also reflect bet-hedging where a male could control the number of tadpoles released to multiple water sources. Collectively, our results suggest an even greater diversity of parent-offspring behavior in a group of frogs already known to exhibit a range of parental care strategies.

Male Behavior

All 20 male *A. trivittata* in this study forcibly attempted to remove tadpoles from their dorsum by rear-leg wiping upon reaching water sources. Approximately 92.8% of the wipes failed to dislodge tadpoles. One male with a single tadpole failed to remove it after three hrs. and 110 wipe attempts and returned to the forest for the night. This combination of high numbers of attempts and low success probability stands in contrast to any assumption that tadpoles freely and easily leave their parent's care.

From the perspective of adult males, time spent attempting to disperse tadpoles into their free-living aquatic habitat cannot be allocated to other life functions. While we lack data to consider total time and energy allocation, our observations of poor success in removing tadpoles in open, potentially risky environments may suggest added costs to this parental care strategy. Further, such observations suggest that males may need more than a single bout, possibly even multiple days, to dislodge all their tadpoles. In contrast, males of *A. femoralis* are reported to transport tadpoles primarily during morning hours for tadpole deposition and then return to their home territories by afternoon, minimizing the loss of mating opportunities (Ringler et al., 2013). It remains unclear whether male *A. trivittata* can sense tadpole competency, but timely dispersal of tadpoles into suitable aquatic habitats might allow males to pursue additional mating opportunities.

The prevalence and necessity of male wiping behaviors is unclear. In some members of the superfamily Dendrobatoidea, tadpoles reportedly swim off their parent's dorsum when submerged in a water source (Eaton, 1941; Fandiño, et al., 1997; Downie et al., 2001; Poleman, et al., 2010; Pašukonis et al., 2017; Rocha, et al., 2018; Wells, 1980; Wells, 2007). However, Ringler et al. (2013) noted that male *A. femoralis* might be able to influence the number of tadpoles deposited into the water through the time spent in the water and the number of hind-limb wiping movements. In *A. trivittata* reported here, male wiping behavior to remove tadpoles appears obligatory as we observed no tadpoles leaving its parent's dorsum under its own volition or without male intervention.

All males in this study reacted to the tactile stimuli of a dislodged tadpole touching them by jumping away, which contrasts with behavior of *R. variabilis*, *R. imitator*, and *H. nexipus*, all of which are reported to remain stationary when tadpoles make contact with them after leaving their parent's dorsum (Schulte & Mayer, 2017; Stynoski et al., 2018). Such parent-tadpole interactions following tadpole dispersal into water may have implications for the number of tadpoles entering habitat patches. A parent's fitness should be sensitive to offspring dispersal and survival. Avoidance behaviors (regardless of whether males recognize tadpoles as offspring or not) would suggest that tadpoles are distributed more widely and in a less clumped fashion than if all tadpoles were deposited at once, which could reduce tadpole-tadpole competition and spread risks of poor habitat quality (e.g., pond desiccation) or predation (Erich et al., 2015; Justicia et al., 2023).

Tadpole Behavior

Immediately after deposition into the water, all separated tadpoles swam in a circular pattern directly around or next to the male and made physical contact by bumping into his body. While it appeared that the tadpoles were attempting to swim back onto the male's dorsum and reattach themselves, we never witnessed a successful attempt. Tadpole re-attachment observations were made experimentally on

dendrobatid tadpoles, *R. variabilis*, where some of the tadpoles reattached to the dorsum of both con- and heterospecific frogs (Schulte & Mayer, 2017). One rationale for tadpole re-attachment is that this behavior may enhance the fitness of tadpoles by moving them to new locations in unfavorable conditions, such as conspecific cannibalism, predator presence, or deposition into phytotelmata with limited nutritional resources (Schulte & Mayer, 2017). However, *A. trivittata* tadpoles are not restricted to phytotelma and are omnivorous, with over 500 tadpoles occurring in a single pool (Luiz et al., 2015). Unless the tadpoles are initiating reattachment as a form of bet-hedging it remains unclear why the tadpoles appear to be attempting to reattach to the male. An untested hypothesis is that the negative fitness consequence of becoming dislodged during transport due to rain or mechanical jarring, selects for reattachment behavior.

Why do the tadpoles not swim off the male's dorsum when arriving at the deposition site, as reported for other species of Dendrobatoidea? It is hypothesized that tadpoles can get defensive, immunological, or nutritive mucous secretions by biting or sucking on the parent's skin (Stynoski et al., 2024). Preliminary support for this hypothesis is based on *Oophaga pumilio* tadpoles, an oophagous species that bites or sucks on the parent's skin when she enters the water and anecdotal observations of phytotelma-breeding species (see Table 2 in Stynoski et al., 2024).

Wyman (1859) suggested that the tadpoles adhere by the coagulation of the mucus covering the surface of the body. Myers and Daly (1980) suggest that the firmness of tadpole attachment by mucous in different species is correlated with the duration of tadpole transport and the time spent in the water to loosen the mucous. In over a century and a half since Wyman's (1859) observation, we are unaware of research addressing the properties of mucous adhesion and if the adhesive properties are related to the duration in water as suggested by Myers and Daly (1980). In species where prolonged tadpole transport has been reported, tadpoles are often deposited at multiple sites: *M. trinitatis* up to four days (Downie et al., 2005; Jowers & Downie, 2005; Wells, 1980b), *H. toachi* up to five days (Quiguango-Ubillús & Coloma, 2008), and *Colostethus inguinalis* up to nine days (Wells, 1980a). Further research is necessary to determine if the mucous adhesion properties change as a result of multiple submergence over multiple sites enabling tadpoles to disperse differentially.

While the causes of this situation of prolonged attachment remains unclear, it raises the possibility that both parent and offspring traits and behaviors – such as tadpole adhesion to the parent and the parent using physical means such as wiping – jointly contribute to reproductive success in this species at the time of dispersal into free-living aquatic habitats.

The delay in detachment of tadpoles in *A. trivittata* means that offspring may begin their free-living phase at different places. Tadpole deposition into different sized pools and environments thus raises questions about the effects of environmental heterogeneity and predictability on fitness (Donnelly & Crump, 1998; Justicia et al., 2023; Starrfelt & Kokko, 2012). Justicia et al. (2023) hypothesize that phytotelma breeding frogs may transport their tadpoles longer distances to find suitable deposition sites due to human-induced rapid environmental changes. Some of these changes, such as increased temperature or lack of regularity of rainfall events, could exacerbate the evaporation of small pools used by *A. trivittata* thus encouraging males to engage in bet-hedging, whereby males spread risk across multiple ponds.

Males entering pools transported 1-21 ($\bar{x} = 12$) tadpoles, fewer than the 21-44 tadpoles reported by Roithmair (1994b), suggesting that potentially some were previously deposited. In addition, our observations of twenty-three percent of the males leaving pools with tadpoles still attached supports the possibility that males disperse their tadpoles into multiple pools over time. This is potentially evidence of a bet-hedging strategy, in which offspring are dispersed over time and space, perhaps increasing fitness in unpredictable environments. The presence of aquatic predators (e.g., coleopteran and/or odonate larvae) deterred male *A. trivittata*, in Brazil, from depositing their tadpoles in artificial basins (Correa & Rodrigues, 2015). In *A. femoralis*, where bet-hedging has been hypothesized, males also spread their tadpoles over two or more pools (Erich et al., 2015).

Much remains to be tested about how delays in dispersal, potentially to multiple pools over time, affect the fitness of frogs like *A. trivittata*. Males in this study dispersed their offspring in both naturally occurring pools in forests and those formed on roads and paths. Given the diversity in reproductive modes and intraspecific plasticity among adult and larval anurans (Summers & Tumulty, 2014; Wells, 2007), we

suspect that more behavioral diversity exists in species with parental care than currently documented, even among those sharing the same basic mode of care (e.g., tadpole transport). Future research could determine if differences in adhesion properties occur between species that release their offspring all at once or distribute them over multiple sites. In addition, a closer examination of parental tadpole deposition behavior is needed to determine if wiping behavior is found in other species and if it occurs in species where bet-hedging or tadpole deposition at multiple sites occurs. Answering these questions would help elucidate how potentially temporal and energetically costly behaviors like wiping affect both parent and offspring fitness in changing environments.

Conclusions

We provide novel documentation and quantification of wiping behavior in a frog species with tadpole transport. All *A. trivittata* males observed in this study forcibly attempted to remove tadpoles from their dorsa by wiping them off using their hind limbs. In contrast to other species, where the tadpoles reportedly swim off the parents' dorsa when being deposited in a water source, the low success rate in removing tadpoles through multiple wipes appears to be energetically and temporally costly. The general lack of similar observations in other species may reflect the few close observations of deposition behaviors in the superfamily Dendrobatoidea (see Table 1), or it may be a rare behavior restricted to a few species. In addition, we describe both the reaction of males jumping away from deposited tadpoles and tadpoles seemingly attempting to re-attach to a male's dorsum. Whether the adaptive reason for tadpole removal resistance is due to the potentially fatal consequences of being dislodged during transport to a water source or a form of bet-hedging remains unknown.

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Data Availability: The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Supplementary Materials

Video S1

A male poison frog's (*Ameerega trivittata*) unsuccessfully attempting, by using his rear legs in a wiping movement, to remove a tadpole from his dorsum (100-300 mm telephoto lens with video speeds of 30 frames per second shown in half speed). Filmed in a puddle at Brownsberg Nature Park, Suriname, from a distance of approximately 2-3 m.

<https://doi.org/10.6084/m9.figshare.27599901.v1>

Video S2

A male poison frog's (*Ameerega trivittata*) successfully removing a tadpole from his back by wiping it off of his dorsum (100-300 mm telephoto lens with video speeds of 30 frames per second shown in quarter speed). Filmed in a puddle at Brownsberg Nature Park, Suriname, from a distance of approximately 2-3 m.

<https://doi.org/10.6084/m9.figshare.27478146.v1>

Video S3

Upon being dislodged from a male poison frog's (*Ameerega trivittata*) dorsum, the video (shown in half speed from the initial 30 fps using a 100-300 mm telephoto lens) illustrates the tadpole's circular swimming behavior and the male's jumping movement away from the tadpole, within seconds of removing the tadpole from his dorsum. Filmed in a puddle at Brownsberg Nature Park, Suriname.

<https://doi.org/10.6084/m9.figshare.27600051.v1>