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To beg or to freeze: multimodal sensory integration directs behavior in a tadpole

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Abstract Effective coordination of behaviors such as foraging and avoiding predators requires an assessment of cues provided by other organisms. Integrating cues from multiple sensory modalities may enhance the assessment. We studied cue integration by tadpoles of *Oophaga pumilio*, which live in small arboreal water pools. In this species, mothers periodically visit their tadpoles and feed them with unfertilized eggs. When mothers visit, tadpoles beg conspicuously by vibrating until fed. However, animals other than mother frogs including potential predators may visit water pools. Thus, when a visitor appears, tadpoles must use visitor cues to decide whether to beg or to remain inactive to avoid predation. To elucidate the cues that prompt these behaviors, we videotaped behavior of *O. pumilio* tadpoles in response to isolated and multimodal cues. Tadpoles swam more when exposed to visual or visual and chemical cues of adult *O. pumilio* but only exhibited begging when exposed to visual, chemical, and tactile cues together. Visual, chemical, and tactile cues from either male or female adult *O. pumilio* stimulated swimming and begging, but the same cues from similarly sized heterospecific frogs did not. Lastly, tadpoles exposed to a potential predator did not beg and swam less than tadpoles with no stimulus. Together, these findings suggest that *O. pumilio* tadpoles use multimodal cues to modulate swimming behavior accordingly in the presence of egg provisioners, predators, and other visitors and that tadpole begging is induced by multimodal cues of conspecific frogs such that tactile and perhaps chemical cues supplement visual cues.

Keywords Amphibian · La Selva Biological Station · Maternal care · Mother–offspring communication · *Oophaga pumilio* · Phytotelm

Introduction

How an animal uses the information provided by cues from other organisms to select among behaviors that are critical to its survival is an important question in behavioral ecology (Stauffer and Semlitsch 1993; Mathis and Vincent 2000; Warkentin 2005). For example, an animal must evaluate cues before deciding between foraging and antipredator behaviors. Nestling white-browed scrubwrens (*Sericornis frontalis*) assess acoustic cues before displaying these two behaviors; they beg more vigorously during playbacks of parental food calls but become silent during playbacks of predator footsteps (Magrath et al. 2007). To maximize detection and clarity of cues, an animal should use the sensory modality or modalities (chemical, acoustic, visual, and/or tactile) that most successfully transfer information within their specific habitat conditions (Scheffer et al. 1996; Kolliker et al. 2006).

Multimodal cues combine information from two or more sensory modalities and can often provide more accurate information than cues in a single modality because they improve detection and localization, reduce ambiguity, and

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amplify the information content (Narins et al. 2005; Partan and Marler 2005). For example, during an otherwise identical visual display, female red-winged blackbirds (*Agelaius phoeniceus*) use male acoustic vocalizations to distinguish between the contexts of aggression and courtship (Beletsky 1983). Multimodal systems are most likely to evolve when information is transferred a short distance across habitat substrates that facilitate multimodal transmission (Partan and Marler 2005). For example, male wolf spiders (*Schizocosa* sp.) court females using visual display and vibration cues but switch to using only visual cues when the substrate does not transmit vibrations to females (Scheffer et al. 1996). Multimodal integration is a topic of much recent theoretical and empirical study due in part to advances in experimental audiovisual technology (Stauffer and Semlitsch 1993; Uetz and Roberts 2002; Narins et al. 2005; Partan and Marler 2005; Smith and Evans 2008; Bro-Jorgensen 2010; DeLuna et al. 2010).

Multimodal systems are categorized as either redundant or nonredundant (Partan and Marler 2005). In redundant systems, cues produce the same response whether presented alone or together, such as in honeybees (*Apis mellifera*), in which both the waggle (visual/tactile) and wingbeat (acoustic) components of the waggle dance independently serve to recruit other bees (Michelsen et al. 1992). In nonredundant systems, cues produce different responses when presented alone versus when presented together. Nonredundant systems can either be simultaneous, such as in the dart poison frog *Epipedobates femoralis*, in which males display full aggression only when acoustic and visual cues are spatially and temporally synchronous (Narins et al. 2005), or sequential, in which the first modality attracts attention and the second provides more subtle information (Wilczynski et al. 1989; Stauffer and Semlitsch 1993; Parris et al. 2006).

Research suggests that larval amphibians, like many other aquatic taxa, primarily acquire information from chemical cues and only rarely or secondarily from other types of cues such as visual, tactile, and vibrational (Waldman 1985; Petranka et al. 1987; Stauffer and Semlitsch 1993; Kiesecker et al. 1996; Mathis and Vincent 2000; Hickman et al. 2004; Waldman and Bishop 2004; Rot-Nikcevic et al. 2005; Warkentin 2005; Parris et al. 2006). The relative importance of chemical over visual cues for aquatic organisms such as tadpoles may be a consequence of environmental conditions such as poor visibility in sediment-filled pond waters (Stauffer and Semlitsch 1993; Mathis and Vincent 2000; Parris et al. 2006). Tadpole vision is known to be functional to some degree (Rot-Nikcevic et al. 2005; Parris et al. 2006; Gouchie et al. 2008), but it may be myopic with poor acuity (Manteuffel et al. 1977; Mathis et al. 1988). Terrestrial adult frogs sometimes use visual, vibrational, chemical, or tactile cues as well but are better known for conspicuous acoustic communication (Summers et al. 1999; Heying 2001; Ryan 2001; Waldman and Bishop 2004; Narins et al. 2005; Caldwell et al. 2010).

For tadpoles, chemical cues can stimulate various changes in morphology (McCollum and Leimberger 1997; Relyea 2001), life history (Skelly and Werner 1990), and behavioral decisions (Petranka et al. 1987; Lima and Dill 1990; Horat and Semlitsch 1994; Skelly 1995; Eklov 2000; Mathis and Vincent 2000; Bridges 2002). When tadpoles detect chemical cues of predators, they often rapidly respond by minimizing activity or by not moving (freezing), which are behavioral responses that can greatly reduce the chance of being detected and eaten by a predator (Wassersug and Sperry 1977; Lawler 1989; Azevedo-Ramos et al. 1992; Stauffer and Semlitsch 1993; Skelly 1994). However, antipredatory freezing can reduce the time spent performing other important behaviors such as feeding (Skelly and Werner 1990; Bridges 2002), air breathing (Baird 1983; Feder 1983), and competing with conspecifics (Werner and Anholt 1996). Reducing the time spent performing these other behaviors can have long-term detrimental effects on the growth and metamorphosis of tadpoles (Skelly and Werner 1990; Skelly 1994; Bridges 2002). Because of the possible negative fitness consequences of exhibiting antipredator behaviors if no predator is present, it is highly adaptive for tadpoles to correctly identify predator cues.

Many species of tadpoles, especially in the tropics where most anuran species are found, do not live in large water bodies such as ponds or swamps but instead complete their development in small pools of water such as those in treeholes or in the axils of a bromeliad plant (i.e. phytotelmata, Crump 1996; Wells 2007). In a few species with phytotelm-dwelling tadpoles, parent frogs regularly provision their offspring with unfertilized eggs (*Osteopilus brunneus*, Lannoo et al. 1987; *Dendrobates granuliferus*, van Wijngaarden and Bolaños 1992; *Osteocephalus oophagus*, Jungfer and Weygoldt 1999; *Mantella laevigata*, Heying 2001; *Phrynohyas resinifictrix*, Schiesari et al. 2003; *Leptodactylus fallax*, Gibson and Buley 2004). In some of these provisioning species, bidirectional mother–offspring communication during feeding bouts has been described (*Oophaga pumilio*, Weygoldt 1980; *Anotheca spinosa*, Jungfer 1996; *Dendrobates vanzolinii*, Caldwell and deOliveira 1999; *Colostethus beebei*, Bourne et al. 2001; *Chirixalus eiffingeri*, Kam and Yang 2002). In these species, once the tadpoles have received a cue that a mother frog has arrived, they display a conspicuous behavior that can be likened to the begging behavior of the young of some mammalian and avian species. For example, in *C. eiffingeri*, a nocturnal rhacophorid frog in which mothers rear their group-dwelling tadpoles in bamboo stumps, mother frogs communicate with offspring via chemical and tactile cues and tadpoles respond by swimming vigorously towards the mother's body (Kam and Yang 2002). In *O. pumilio*, the strawberry poison frog, females return intermittently to tadpoles living in the axils of bromeliads and lay unfertilized eggs following a pronounced tadpole vibration behavior. Rather than swimming normally with undulating tail movements, vibrating *O. pumilio* tadpoles stiffen their tails and move their entire body vigorously in one place, typically against the adult's body (Weygoldt 1980). However, the cues that *O. pumilio* tadpoles use to detect the presence of their mothers prior to exhibiting vibration behavior are not known.

Because maternal feeding behavior in *O. pumilio* only occurs during daylight hours (Graves 1999; Haase and Pröhl 2002), visual cues may play a larger role in perception by tadpoles than in nocturnal species that exhibit mother–tadpole communication (Kam and Yang 2002). The goal of the present study was to determine the sensory mode or modes that *O. pumilio* tadpoles use to perceive mother frogs before expressing begging behavior. We also investigated whether *O. pumilio* tadpoles can distinguish between male and female adult conspecifics and between adult conspecifics and other species of sympatric adult frogs. Lastly, we examined tadpole response to the presence of potential predators. We hypothesized that *O. pumilio* tadpoles use multimodal cues to decide whether to beg in the presence of a potential egg-feeding frog or to freeze in the presence of a potential predator.

Methods

Study site and species

This study was conducted at the La Selva Biological Station in Costa Rica between October 2009 and February 2011. La Selva is comprised of primary and secondary lowland tropical wet forests and receives approximately 4 m of rain annually, with more precipitation falling from May to December (McDade and Hartshorn 1994).

O. (*Dendrobates*) *pumilio*, or the strawberry poison frog, is a leaf litter-dwelling dendrobatid frog that is found in Atlantic lowland forests ranging from Nicaragua to Panama. It is a diurnal, aposematic species that sequesters toxic alkaloids in the skin after eating ants and mites (Saporito et al. 2007a). Adult *O. pumilio* at La Selva are red with blue hind limbs, and this conspicuous coloration serves as an aposematic signal to predators (Saporito et al. 2007b). After courtship, this species displays complex parental behavior (Weygoldt 1980; Brust 1993). Eggs are fertilized in leaf litter on the forest floor, and egg clutches are guarded and hydrated by fathers for 7–12 days (Weygoldt 1980; Brust 1993; Haase and Pröhl 2002). Once tadpoles hatch (stage 25; Gosner 1960), mothers return to their clutch and transport each tadpole singly to its own water-filled axil in a water-holding plant such as a bromeliad (Brust 1993; Weygoldt 1980). Then, mothers return to each tadpole at 1–8-day intervals for approximately 6 weeks to provision them by laying unfertilized eggs into the water (Brust 1993). Maternal provisioning is obligatory for tadpole survival, as tadpoles only eat eggs (Brust 1993). Mother frogs do not recognize their offspring but rely on specific location cues to ensure that provisioning is provided for their own offspring (Stynoski 2009). In *O. pumilio*, adults are diurnal and the majority of maternal provisioning takes place between 0700 and 1100 hours (Graves 1999; Haase and Pröhl 2002). When mothers visit tadpole-occupied axils, tadpoles exhibit a conspicuous vibration behavior against the mother's body, which likely facilitates egg laying by mother frogs (Weygoldt 1980; Stynoski 2009). Eggs are not deposited in sites that do not contain a live tadpole (Stynoski 2009). Tadpoles will beg from unrelated mothers visiting their bromeliad axil when housed in aquaria but unrelated mothers do not provide eggs (Weygoldt 1980). Predation is a major source of tadpole mortality in bromeliads (67%; Maple 2002).

Other frog species used in this study to elicit responses by tadpoles of *O. pumilio* included *Rhaebo* (*Bufo*) *haematiticus*, *Craugastor* (*Eleutherodactylus*) *bransfordii* and *Craugastor fitzingeri*. These species are common brown litter frogs that are sometimes found in bromeliads at La Selva. Only frogs of similar size to *O. pumilio* and located on bromeliads were collected ($N=4$ of each species).

Cupiennius getazi and *Cupiennius coccineus* in the spider family Ctenidae are nocturnal wandering spiders commonly found in bromeliads of Central American forests (Barth and Seyfarth 1979; Barth and Cordes 1998). They spend the majority of time facing prosoma down in a high humidity retreat such as the area above the water in a bromeliad axil, but turn to face outward from their retreat at dusk and hunt insects in this sit-and-wait position for a few hours thereafter (Barth and Seyfarth 1979). Wandering spiders use some visual cues but rely most heavily on mechanosensory cues to detect their prey when it moves (Schmid 1998). The eyes of *Cupiennius* sp. function well in dim moonlight (Barth et al. 1993). Maple (2002) suggested that wandering spiders are the primary predator of *O. pumilio* tadpoles, and these spiders are frequently seen at the field site. Furthermore, Maple (2002) demonstrated that *O. pumilio* tadpoles are most frequently found in axils of bromeliads that are of the size and species in which spiders are seen least frequently, suggesting that spiders eat the tadpoles or that mothers place tadpoles in these axils in the interest of avoiding predation by spiders. Spiders in general are known predators of other species of tadpoles (Caldwell and de Araújo 1998; Vonesh and Warkentin 2006; Jara 2008).

Experimental design

We collected animals from the Huertos Plots at La Selva, which are abandoned plantations that provide a seminatural infrastructure of trees in rows adjacent to primary forest. Locating tadpoles in natural bromeliads is disruptive to the microcommunity of the plant, is inefficient, and sometimes results in injured tadpoles. Thus, during previous studies, an extensive field setup of artificial phytotelmata was constructed that allows mother frogs to deposit and care for offspring in their natural habitat while being easily observed (Stynoski 2009). Artificial bromeliad axils made from 15-ml polypropylene beakers (“cups”; $N=800$) were tied to trees in pairs. Holes drilled in the sides of cups maintain rainwater volume at approximately 8 ml, and cups are wiped out every 2–3 months to prevent buildup of algae and debris. Mother frogs regularly deposit and rear their tadpoles in these cups as they would in natural bromeliads (Stynoski 2009). Tadpoles in cups develop to metamorphosis unless they die or are eaten by predators.

We caught frogs and spiders by hand, with an aquarium net, or with a plastic zipper bag from bromeliads within the Huertos Plots and temporarily placed them in plastic bags with leaf litter for transport to the laboratory. We collected tadpoles with a 3-ml wide-mouthed pipette and placed them individually in glass vials with rainwater. Once in the laboratory, tadpoles acclimated to laboratory conditions for at least 2 h in rainwater in a testing apparatus which consisted of a lidded clear plastic cup (1 oz) that was seated within a larger lidded clear plastic container also filled with water to the same level. Then, we placed these cups with the tadpole in the position where the trial was to take place, let the tadpole acclimate for an additional 5 min, and then performed experimental manipulations as outlined below. Immediately following manipulations, tadpoles were videotaped for 10 min with a video camera (JVC) or an infrared video camera (ActiveVision) in the case of trials that took place in a dark box. We decided upon a trial duration of 10 min for all behavioral trials following observations of a similar average duration of mother visits to cups in the field (JLS, unpublished data). Animals were used in only one trial across all experiments. We returned animals to their site of capture after behavior trials. We scored tadpole behavior using the program JWatcher 1.0 to determine the percentage of time that tadpoles were resting (not moving), swimming (moving with flexible tail movements), or vibrating (stiffening the tail and moving rapidly in one place). Tadpole vibration behavior can vary greatly in tadpoles of relatively early and late stages (JLS, unpublished data), so we only used tadpoles from stages 30 to 40 (Gosner 1960).

Experiment 1: sensory perception of a conspecific adult frog

Seven treatment groups (chemical, visual, visual + chemical, tactile + chemical, visual + tactile + chemical, dark control, and control; $N=12$) were arranged as follows. In the chemical cue group, we put 20 drops of water possibly containing adult chemical cues into the tadpole's cup. We prepared this water by pooling the water from six vials within each of which an adult frog had soaked for 4 h in 15 ml of rainwater prior to the trial (as in Kam and Yang 2002 where water similarly conditioned with adult chemical cues elicited a strong tadpole response). In the visual cue group, we placed an adult *O. pumilio* in the larger container holding the tadpole's cup such that tadpoles could see the adult frog but not touch it or receive chemical cues (but could potentially receive vibrational cues). In the visual + chemical group, tadpoles were simultaneously exposed to 20 drops of adult conditioned water and an adult in the larger container surrounding the tadpole's cup. In the tactile + chemical cue group, we placed an adult *O. pumilio* in the tadpole's cup, but the trial took place in a dark box. In the visual + tactile + chemical group, an adult *O. pumilio* was placed in the tadpole's cup in ambient lighting. No cues were presented to dark control and control groups, but we videotaped the tadpoles in cups in a dark box or in ambient lighting, respectively. During trials in a dark box, we allowed tadpoles to acclimate to the laboratory for 2 h in ambient lighting and then to the trial position for 5 min inside of the box before videotaping them with an infrared camera. Because tactile cues of adult frogs cannot be presented without also introducing potential chemical cues, we could not examine the effects of visual + tactile or tactile cues alone using live adult frogs. In preliminary tests with models of frogs, tadpoles did not elicit a begging response, presumably because models did not move and/or because they were inadequate replicas of adult *O. pumilio*; thus, we did not use models in the current study.

Experiment 2: distinguishing between provisioning and nonprovisioning adult frogs

To test for an ability of tadpoles to distinguish between adult frogs of the same or different species, as in the visual + tactile + chemical trials described above, we placed either conspecific or heterospecific frogs in the small cup with the tadpole ($N=12$). Similarly, we tested for the ability of tadpoles to distinguish between sexes of adult *O. pumilio*, which unlike heterospecific frogs are visually similar in terms of shape and movement, by placing either a male or a female adult in the cup with the tadpole ($N=12$).

Experiment 3: behavior modulation with the perception of a potential predator

We compared the behavior of tadpoles with a spider placed in their cup at the beginning of the trial to that of tadpoles with no stimulus ($N=10$). Spiders were held in the lab without food for 7 days prior to the trial to ensure that all spiders were hungry. We noted whether the spider struck at the water's surface with its mouthparts and whether the spider entered the water. In addition, we allowed the video camera to run for a total of 20 min after the 5-min pretrial acclimation period in order to view tadpole behavior both in a first and second 10-min time bout.

Statistical analysis

All analyses were completed in R 2.10.1 (2009). We subjected the data to an arcsine transformation as is appropriate for proportion data (Crawley 2005), performed tests for homogeneity of variances, and then conducted linear models of the transformed data for each experiment separately. We used the proportion of time that tadpoles were either swimming or vibrating as response variables when testing the effects of sensory mode, sex of adult frog, and whether an adult frog was a conspecific or heterospecific. To examine the effects of predator presence, we only compared the proportion of time tadpoles were swimming because tadpoles did not vibrate in any of these trials.

Results

The sensory modality of cues from adult *O. pumilio* had a significant overall effect on the percentage of time that tadpoles spent swimming and vibrating (swim: $F_{6,\ 85}=19.54$, $p<0.0001$; vibrate: $F_{6,\ 85}=14.8$, $p<0.0001$; Fig. 1). The percentage of time tadpoles spent swimming or vibrating did not differ among light control, dark control, chemical, or tactile + chemical treatments, but tadpoles spent significantly more time swimming in the visual treatment (model coefficient; $t=6.67$, $p<0.0001$), visual + chemical treatment ($t=6.00$, $p<0.0001$), and visual + tactile + chemical treatment ($t=5.19$, $p<0.0001$) than in all other treatments, and significantly more time vibrating in the visual + tactile + chemical treatment ($t=7.39$, $p<0.0001$) than in all other treatments. In the visual + tactile + chemical treatment, tadpoles first tended to swim actively after seeing the movements of the adult frog, and then after they happened to touch the adult frog while swimming, they commenced vibration behavior. Tadpole vibration generally occurred while in contact with the body of the adult frog, but did not include nipping as suggested in previous literature (Weygoldt 1980). Adult frogs did not deposit eggs in any trials and consistently attempted to leave the cup (but were prevented from doing so by the plastic lid); they either appeared uninterested or were disturbed by tadpoles.

Tadpole swimming and vibration behavior did not differ when in the presence of either a male or female adult *O. pumilio* (swim: $F_{22,\ 1}=0.80$, $p=0.38$; vibrate: $F_{22,\ 1}=1.59$, $p=0.22$). However, tadpoles did spend significantly more time swimming and vibrating in the presence of conspecific adult frogs than in the presence of heterospecific adult frogs (swim: $F_{24,\ 1}=30.9$, $p<0.0001$; vibrate: $F_{24,\ 1}=12.87$, $p=0.001$; Fig. 2). All adult frogs in these trials behaved as those described in the paragraph above.

Tadpoles spent significantly less time swimming in the presence of a spider ($F_{40,\ 1}=14.27$, $p=0.0005$) and more time swimming in the second bout of 10 min than in the first bout ($F_{40,\ 1}=5.54$, $p=0.02$; Fig. 3). No significant effect of the interaction of stimulus and bout was detected ($F_{40,\ 1}=0.13$, $p=0.071$). In 2 of 10 trials, spiders struck with their mouthparts at the water's surface without touching the tadpole but retreated to the vial lid soon after. Tadpoles remained motionless during spider movements. Spiders did not enter the water.

Discussion

This study shows that *O. pumilio* tadpoles use multimodal cues to assess the arrival of an adult frog that could lay nutritive eggs as opposed to the arrival of a nonprovisioning animal or potential predator. We found that tadpoles swam more when presented with visual cues from adult *O. pumilio*, but did not swim more in the presence of other species of frogs. We also found that tadpoles swam less when a potential predator was above the water. After an adult *O. pumilio* entered the water, tactile and possibly chemical cues supplemented visual cues to induce tadpole begging. Reliance on such sequential nonredundant multimodal cues may act to ensure recognition of adult *O. pumilio* before a tadpole performs a conspicuous and potentially costly begging behavior at a heterospecific frog or predator. Similarly, tadpoles and embryos from species in the genus *Rana* were found to use mostly chemical cues to detect predators, although they showed more intense antipredator responses when chemical cues were further amplified by tactile cues (Stauffer and Semlitsch 1993; Smith and Fortune 2009).

The results of the present study also suggest that visual and tactile cues are of more importance to *O. pumilio*

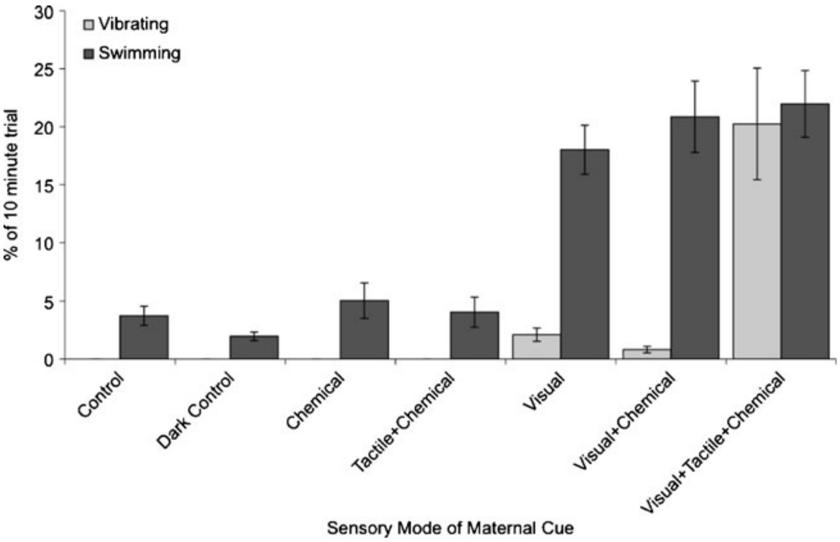


Fig. 1 Behavior of *O. pumilio* tadpoles (*N*=12) during 10 min of exposure to combinations of adult *O. pumilio* cues. Tadpoles swam significantly more when presented with visual cues alone, visual and chemical cues together, or with visual, tactile, and chemical cues together than in all other cue combinations. Tadpoles vibrated significantly more when presented with visual, tactile, and chemical cues together than in all other cue combinations. *Error bars* show SEM

tadpoles than chemical cues in differentiating among animals; this is noteworthy because tadpoles of other species have been found to use primarily chemical cues (Mathis and Vincent 2000). *O. pumilio* tadpoles begged when presented at the same time with visual, tactile, and chemical cues but did not beg when presented with both tactile and chemical cues, with both visual and chemical cues, or with chemical cues alone. Furthermore, tadpoles presented with adult *O. pumilio* cues swam more than control tadpoles when presented with both visual and chemical cues or with visual cues alone, but not when presented with chemical cues alone. It is possible that *O. pumilio* tadpoles use visual cues to assess visitors to their water pools before deciding whether to increase or decrease swimming behavior because there is potential danger in waiting for possible tactile or chemical cues from the visitor after it enters the water because the visitor might be a predator. Additionally, visual cues may be of key importance in *O. pumilio* because the adults are diurnal and their tadpoles develop in phytotelmata, which contain small volumes of clear water and often lack refuges. To our knowledge, only one other study has specifically investigated the communication between egg-fed tadpoles and their mothers and this was the study of *C. eiffingeri* by Kam and Yang (2002). These investigators found that *C. eiffingeri* tadpoles did not respond to visual cues of an adult frog in a surrounding container or to a model of an adult frog but instead used only chemical cues to detect the arrival of mother frogs (Kam and Yang 2002). It could be that *C. eiffingeri* tadpoles do not respond to visual cues because parent frogs in this species only provide nutritive eggs at night.

It is possible that provisioning mother *O. pumilio* only release a chemical, acoustic, or vibrational cue under particular spatial conditions with their own tadpoles, and tadpole responses to such cues would not be detected with our experimental design. But, it seems unlikely that additional cues are necessary for mother-to-tadpole communication in *O. pumilio*; tadpoles still begged vigorously from adult conspecific frogs even though these adults appeared to be highly motivated to escape from the testing cups and tadpoles begged equally from adults of both sexes even though only mother frogs provide eggs.

Tadpoles of *O. pumilio* begged from both male and female conspecifics, but did not beg from similarly sized individuals of other species of bromeliad-dwelling frogs. Presumably, *O. pumilio* tadpoles have the ability to distinguish between potential predators and egg provi-

Fig. 2 Behavior of *O. pumilio* tadpoles (*N*=12) during 10 min with either a conspecific adult frog or a similarly sized heterospecific frog. Tadpoles swam and vibrated significantly more in trials with adult *O. pumilio* than in those with heterospecific frogs. *Error bars* show SEM

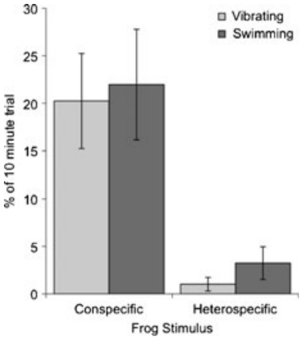
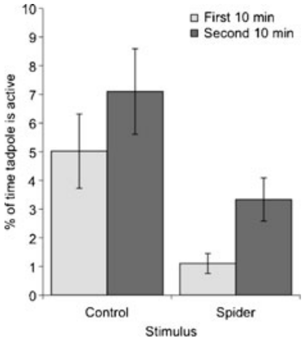


Fig. 3 Behavior of *O. pumilio* tadpoles (*N*=10) with either no stimulus or with a potentially predatory spider. Over the first 10 min of trials, tadpoles swam approximately five times less in the presence of a spider than with no stimulus. *Error bars* show SEM



sioners, or at least between nonprovisioning and potentially provisioning organisms, using cues such as body shape or movement patterns. It is important to note that *O. pumilio* tadpoles can be reared in the laboratory by unrelated conspecific frogs from very differently colored polymorphic populations (C. Richards-Zawacki, personal communication). Thus, it is unlikely that color plays a role in recognition of conspecific adults by *O. pumilio* tadpoles.

O. pumilio tadpoles presented with a spider stimulus swam approximately five times less than tadpoles presented with no stimulus. Freezing is a common response of tadpoles to the detection of a potential predator (Horat and Semlitsch 1994; Skelly 1995; Bridges 2002), even though it may reduce the time spent performing other important behaviors. For example, *Bufo americanus* tadpoles moved 41% less in the presence of predators, and this decline in movement was associated with a 28% decrease in growth rate due to reduced feeding (Skelly and Werner 1990). On the other hand, *Pseudacris triseriata* tadpoles were found to swim less in the presence of predators but did not spend less time feeding (Bridges 2002). *O. pumilio* tadpoles spend much less time swallowing maternal eggs each day than the 11% of the time that *P. triseriata* spend eating plant material (Bridges 2002; JLS, unpublished data), so it is unlikely that the time that *O. pumilio* tadpoles spend feeding is reduced as a result of freezing when a potential predator arrives. Reduction of swimming by *O. pumilio* tadpoles might only occur in the presence of predators because it might interfere with cutaneous respiration or surface breathing and because it might lower the likelihood of detecting mother frogs that arrive to provision. Freezing in response to a the presence of a predator might be more likely to occur in species such as *O. pumilio* in which tadpoles are located in relatively small pools of water in phytotelmata than in species in which tadpoles dwell in relatively large aquatic habitats. Future studies might address the degree to which movement affects tadpole survival if a predator is already sitting above the phytotelm water surface.

The freezing behavior that tadpoles exhibit in the presence of a predator may attenuate with time. Although tadpoles exposed to spiders swam significantly less than control tadpoles in the first 10 min, they did not swim less than control tadpoles in the second 10 min. Tadpoles may only see spiders as a threat worth responding to when the spider first appears above the water pool.

This study shows that *O. pumilio* tadpoles use multimodal cues to distinguish between organisms that appear above their water pool and to modulate their behavior according to visitor identity. First, they use visual cues to determine whether to freeze because a visitor is a potential predator or to swim more because a visitor is a potential egg provider. Once a nonpredatory visitor enters the water pool, *O. pumilio* tadpoles use tactile and perhaps chemical cues to determine whether or not the visitor is a conspecific adult and whether or not to exhibit begging behavior. Thus, tadpoles of *O. pumilio* supplement visual cues with tactile and perhaps chemical cues to fine-tune their behavior in the interest of eating but not being eaten.

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Ethical standards The experiments in this study comply with current Costa Rican legislation and were conducted with approval of IACUC of the University of Miami and MINAET of Costa Rica.

Conflict of interest The authors declare that they have no conflict of interest.

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