Ethology

RESEARCH PAPER

A Test of Local Enhancement in Amphibians

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Abstract

Local enhancement is an underexplored social learning mechanism that is often observed in organisms that live in groups. This mechanism occurs when individuals are attracted to areas where conspecifics have previously been, but which are not present when the animal actually moves into the area. We tested for local enhancement in wood frog tadpoles (*Lithobates sylvatica*) and spotted salamander larvae (*Ambystoma maculatum*) in three experiments that exposed individuals to one side of a test chamber which was empty and another that contained a group of three conspecifics. Side preference of the focal individual was recorded once the conspecifics were removed. Tadpoles showed a clear preference for moving to areas where a group of tadpoles had previously been located. Conversely, this preference was not observed in salamander larvae. In addition, salamander larvae took significantly more time to initially choose a side. These results indicate that tadpoles exhibit local enhancement, whereas aquatic salamander larvae do not. This difference in social learning could be largely due to differences in aquatic ecology between tadpoles and salamander larvae.

Introduction

Social learning is a process whereby organisms are exposed to the behavior of others and subsequently modify their behavior in a similar way (Heyes 1994). Although there are many forms of social learning, this process often involves complex behaviors that can enhance fitness. For example, by watching conspecifics, blue tits (*Cyanistes caeruleus*) across the British Isles quickly learned to open milk bottles to drink the nutrient-rich cream that accumulated on top of the milk (Buxton 1948; Fisher & Hinde 1949; Fragaszy & Perry 2008). Although actions themselves, such as those required to drink milk from a glass bottle (i.e., social facilitation or copying), are the most easily identifiable forms of learned social information, organisms employing other forms of social learning may gain knowledge about other aspects of their environment. One such form, known as stimulus enhancement, occurs when individuals are drawn to specific objects that they have witnessed other individuals interact with (Zentall et al. 1996). In this way, organisms may develop new familial traditions (Fritz et al. 2000), learn about new food items (Visalberghi & Addessi 2001; Davis & Burghardt 2011), or acquire the ability to use novel tools (Zuberbühler et al. 1996).

One subset of social learning that has received little attention is local enhancement (Thorpe 1963). This process occurs when an individual is engaged in a behavior in a specific area, and an observing animal subsequently increases the frequency with which they occupy this space even after the demonstrator is gone (Thorpe 1963). Despite the apparent limited setting in which local enhancement occurs and the limited number of studies that have tested for this mechanism (see below), this process has the potential to dramatically affect an organism's fitness by providing critical information on suitable nesting sites, acceptable foraging patches, or areas that contain potential predators. For example, Slagsvold & Wiebe (2011) hypothesized that local enhancement may be an important mechanism for learning to forage in birds, and Cadieu et al. (1995) demonstrated that Atlantic canaries (*Serinus canaries*) tend to forage in the same locations as their fathers. Great tits (*Parus major*) also show increased search effort in areas in which other birds have recently been foraging (Krebs et al. 1972). The common eastern bumblebee (*Bombus impatiens*) also displays local enhancement in flower preference based on the color of flowers that conspecifics have been seen on (Worden & Papaj 2005). Although these studies involve species that are highly social for a large part of their life cycle, recent studies on social learning are challenging the idea that social learning evolves only in this context. The common octopus (*Octopus vulgaris*) is normally a solitary and territorial animal, but has been shown to utilize stimulus enhancement to attack objects after watching conspecifics perform similar behaviors (Fiorito & Scotto 1992). A recent study by Wilkinson et al. (2010) showed that the red-footed tortoise (*Geochelone carbonaria*), which is solitary throughout its life and receives no parental care, can quickly complete a challenge for access to a preferred food item after watching conspecifics perform the task, but completely fails to complete the challenge if this social information is not available. These studies suggest that although learning is important in group settings, it is not restricted to only those species that are highly social. Moreover, Wilkinson et al. (2010) hypothesized that an animal's ability to learn from social cues may not be a consequence of their level of social interaction (the adaptive specialization hypothesis), but rather a general consequence of their capacity to learn any new information, regardless of the type of cue. As a general result, any species that lives in close vicinity with conspecifics for at least part of their life cycle (regardless of whether they are actually social) may utilize social learning during that period as long as they possess some capacity for learning.

Amphibians are one group of organisms in which the potential for social learning has historically been viewed as limited. Most amphibians are solitary during the adult portion of their lives, potentially limiting the evolution of social learning mechanisms (according to the adaptive specialization hypothesis). Nevertheless, many amphibian species spend their larval stages in relatively dense populations. Except for several species of toads (Beiswenger 1975; Watt et al. 1997; DeVito 2003), these populations generally do not form aggregations and are not coordinated for the purposes of foraging or defense. Furthermore, larval population densities rapidly decrease over time due to predation and the onset of metamorphosis, indicating that the window for which social learning is applicable for amphibian larvae may be limited.

Despite these limitations, recent research has found that during the short time that amphibian larvae live in groups, at least two species can acquire information through social learning mechanisms (Ferrari et al. 2007; Crane et al. 2012). In a study by Ferrari et al. (2007), naïve wood frog (*Lithobates sylvaticus*) tadpoles were paired with a predator-experienced tutor and exposed to chemical stimuli from that predator. In subsequent trials, the naïve tadpoles were tested alone and they exhibited antipredator behavior to the same stimulus, indicating social facilitation had occurred in this species. In a similar study, Crane et al. (2012) demonstrated the social facilitation of antipredator behavior in another amphibian, the ringed salamander (*Ambystoma annulatum*). Given the recent advancements in our understanding of social learning in nonsocial species, we set out to determine whether amphibian larvae exhibit a second form of social learning. In particular, we tested whether naïve wood frog tadpoles and spotted salamander (*Ambystoma maculatum*) larvae exhibit local enhancement.

Methods

Animal Collection and Maintenance

Two clutches of wood frog eggs and two clutches of spotted salamander eggs were collected in Mar. 2014 from separate fishless ponds near Hanover, Indiana. The egg masses were kept individually in small containers fully submerged in a mixture of pond water and DI water and supplied with an aerator. After hatching, tadpoles from both clutches were placed in a single large tub and were fed a mixture of Spirulina and Chlorella algae (Saurian Enterprises, St. Louis, MO, USA). Salamander larvae from both clutches were placed in a single tub after hatching. Larvae were fed with water from a small pool that contained numerous microinvertebrate prey items including copepods (class: Maxillopoda) and cladocerans (class: Branchiopoda), but did not contain other salamander larvae.

Experiment 1: Local Enhancement in Tadpoles

The first experiment tested whether tadpoles were attracted to areas where conspecifics had previously been located (i.e., local enhancement). Trials were conducted in 0.8-L containers [7 × 14.5 × 10 cm]. This test chamber was divided into three equally sized zones by drawing two vertical lines 4.5 cm from both ends of the container. Before each trial, the bottom of the experimental chamber was filled with 1 cm of clean sand and 0.5 l of conditioned (room temperature) DI water. A (3 cm diameter) glass test tube was then filled with 0.5 cm of sand and 30 ml of water. Three tadpoles were then randomly chosen and placed in the test tube; a solid glass test tube was used to ensure that chemical stimuli were not a factor in the experiment. The test tube was randomly placed in one end of the experimental chamber so that the sand in the tube was level with the sand in the experimental chamber. A cylindrical glass tube (3 cm diameter) was then placed in the center to provide an acclimation space for the test animal. After acclimating the group of tadpoles for 30 s, an individual tadpole was placed in the center tube. As soon as the individual tadpole was introduced, a 5-min observation period was initiated. Following this observation period, the test tube containing the three tadpoles was removed and placed in a location not visible to the experimental tadpole. A 10-s acclimation period was then initiated, after which the cylinder restricting the individual tadpole was removed. Another 5-min observation period was immediately initiated during which we recorded the latency to choose a side, the side that was chosen first, and the amount of time the tadpole spent in each zone [conspecifics, center (neutral), empty]. Following each trial, all tadpoles were placed in a separate holding container and were never reused. The sand and water were emptied from all containers. The containers were then rinsed with warm tap water followed by DI water. This protocol was then repeated (N = 26).

Experiment 2: Local Enhancement in Salamander Larvae

The second experiment tested whether salamander larvae were attracted to areas where conspecifics have previously been located (i.e., local enhancement). The same protocol was used as in Experiment 1, except the test subject, and individuals being observed were salamander larvae.

Experiment 3: Tadpoles’ Responses to an Empty Test Tube

A third experiment was conducted to ensure that tadpoles from Experiment 1 were attracted to the conspecifics they had observed inside the test tube and not to the general presence of a test tube. Protocol for Experiment 3 was the same as Experiment 1 except that the treatment side contained a test tube filled with only sand and water.

Statistical Analyses

For each experiment, we counted the number of individuals that chose the conspecific side first and the number of individuals that chose the empty side first and compared this to a random selection (50% on each side) with two separate chi-squared tests. For trials with tadpoles, we compared the total time spent on the treatment and empty side of the test chamber with a paired-sample Wilcoxon signed-rank test; these data did not meet assumptions of normality and could not be corrected with transformations. For trials with salamander larvae, we compared the total time spent on the treatment and empty side of the test chamber with a paired *t*-test. We compared the latency to choose a side by tadpoles and salamander larvae with a *t*-test; data for this test were log-transformed to meet assumptions of normality. In experiment 3, the total time spent on the treatment (empty test tube) and control side was compared with a paired *t*-test.

Results

More tadpoles initially chose the side of the test chamber that previously held conspecifics (n = 20) as compared to the empty side of the test chamber (n = 6) ($\chi^2 = 7.34$, df = 1, $p < 0.007$; Table 1). In addition, tadpoles spent significantly more time in the treatment zone than in the empty zone ($W = -196$, N = 26, p = 0.013, Fig. 1a).

There was no significant difference in the number of salamander larvae that initially chose the treatment side (n = 11) vs. the empty side (n = 9) of the test chamber ($\chi^2 = 0.200$, df = 1, p = 0.65, Table 1). There was also no difference in the amount of time that salamander larvae spent on the treatment side and empty side of the test chamber ($t = 0.147$, N = 20, p = 0.885 Fig. 1b).

Tadpoles were significantly faster than salamander larvae at leaving the neutral zone and selecting a side after being released from the acclimation cylinder ($t = -3.9$, df = 44, $p < 0.001$, Fig. 2).

When tadpoles were exposed to an empty test tube, they chose the treatment side five times and the empty side six times ($\chi^2 = 0.091$, df = 1, p = 0.76,

Table 1: Chi-squared results of initial side choice by tadpoles with a conspecific side and an empty side, tadpoles with an empty test tube and an empty side, and salamanders with conspecifics and an empty side. Only tadpoles with the options of a conspecific side and an empty side showed a significant preference in their initial choice

	Initial choice				
Organism	Empty	Conspecifics	χ^2	DF	p-Value
Tadpoles	6	20	7.54	1	0.007
Tadpoles w/empty test tube	5	6	0.09	1	0.763
Salamander larvae	11	9	0.20	1	0.655

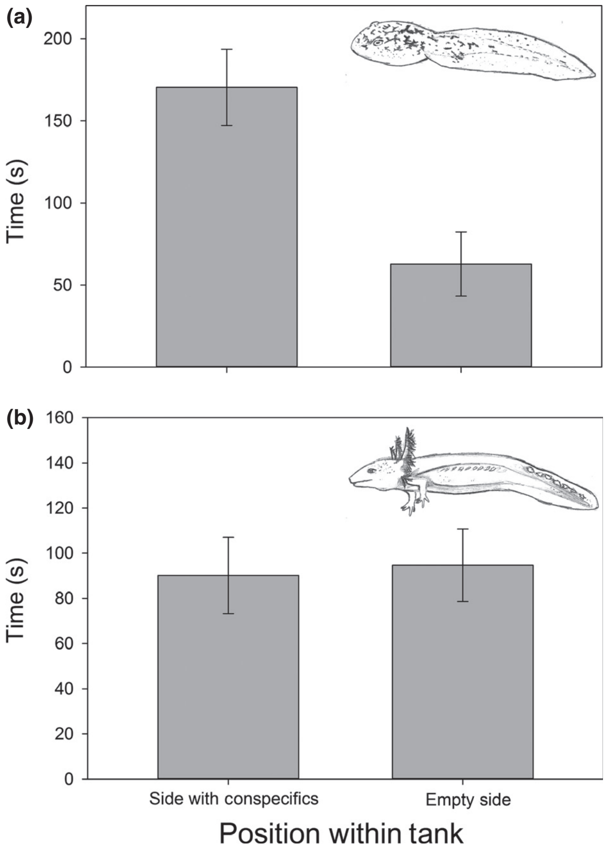

Fig. 1: x̄ (±SE) time spent by tadpoles (a) or salamander larvae (b) on a side of a test chamber that had previously contained a test tube with conspecifics or was empty. Tadpoles spent significantly more time on the side of the test chamber that had previously contained conspecifics ($W = 196$, N = 26, p = 0.013). Salamander larvae spent a similar amount of time on both sides of the test chamber ($t = 0.147$, N = 20, p = 0.885). Illustration of the tadpole and salamander larvae by Tara M. Nastoff.

Table 1). Tadpoles spent a similar amount of time on the side of the chamber with the empty test tube as compared to the empty side ($t = -0.447$, N = 11, p = 0.664, Fig. 3) indicating that tadpoles were not attracted to the test tube alone.

Discussion

We found that wood frog tadpoles rapidly chose a side (compared to salamanders), initially swam to the side in which they had observed other tadpoles, and spent a large amount of time on the side of the test chamber that had previously held conspecifics. Furthermore, experiment three indicated that tadpoles preferred to be in areas that had recently held conspecifics and were not attracted to an empty test tube. These results indicate that wood frog tadpoles are attracted to areas in which conspecifics have formerly been located, thereby exhibiting a form of social learning known as local enhancement. Although tadpoles exhibited local enhancement, salamander larvae chose a side randomly, spent an equal amount of time on both sides of the chamber, and were slow to select an initial side (compared to tadpoles). This suggests that salamander larvae were not attracted to areas in which conspecifics had previously been located and therefore do not exhibit local enhancement.

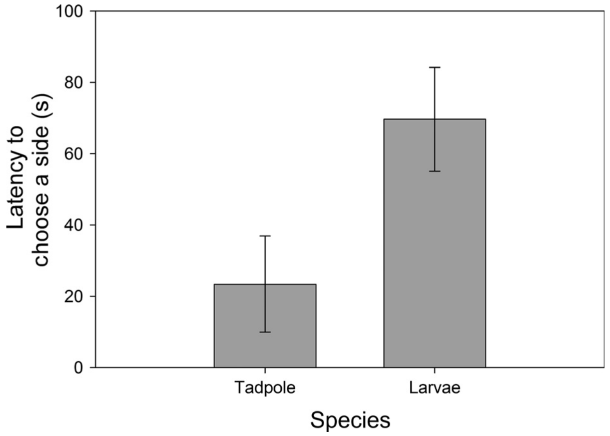

Fig. 2: x̄ (±SE) latency to choose a side (seconds) by tadpoles and salamander larvae after being exposed in an experimental chamber to one side that was empty and another side that previously contained a test tube with three conspecifics. Salamander larvae took significantly longer to move out of the neutral zone and choose a side compared to tadpoles ($t = -3.902$, df = 44, p < 0.001).

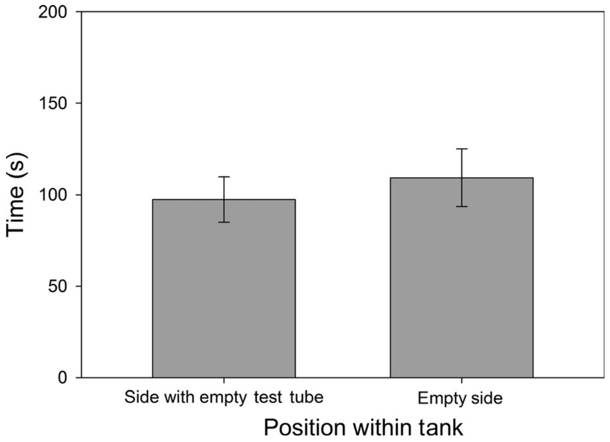

Fig. 3: x̄ (±SE) time spent by tadpoles on a side of a test chamber that had previously contained an empty test tube or no test tube (completely empty). Tadpoles spent a similar amount of time on both sides of the test chamber ($t = -0.447$, N = 11, p = 0.664).

For the evolution of any behavior, the benefits of performing the behavior must outweigh the costs

(Parker & Stuart 1976). Both wood frogs and spotted salamanders lack any form of parental care (Petranka 1998). This suggests that they must rely on innate behavior, trial and error learning, or learning from conspecifics. Galef & Laland (2005) state that for young and naïve animals, the benefits of social learning should almost always outweigh any costs, and research suggests that organisms should learn from the behaviors of others when obtaining information individually is costly. For example, European starlings (*Sturnus vulgaris*) obtain information about patch food sources via social learning because it is costly to acquire this information alone (Templeton & Giraldeau 1995). For the amphibians tested in our study, the differences in social learning are interesting because both species share very similar habitats. Wood frog eggs are deposited in shallow ephemeral woodland ponds between Mar. and Apr. (Petranka 1998). Spotted salamander eggs are deposited in similar locations at the same time, and both species regularly occur in the same breeding aggregations (Petranka 1998). Nevertheless, each of these species has a unique life history which likely leads to differences in the costs and benefits involved in social learning and therefore to the relative differences in learning strategies.

One factor that has an impact on social learning is foraging habits. Wood frog tadpoles feed primarily on algae and detritus. Although cannibalism by wood frogs does occur, it is rare due to breeding synchrony (Petranka & Thomas 1995). Spotted salamander larvae feed on aquatic invertebrates, as well as smaller amphibian larvae, including smaller conspecifics (Petranka 1998). These foraging habits have several implications, such as the dispersal of prey items. Algae and egg masses are patch resources and are generally consistent in patches. This suggests that a major benefit of local enhancement in tadpoles is the ability to quickly identify food sources by actively foraging, which decreases search time as well as time exposed to predation risk. In contrast, microinvertebrates and smaller amphibian larvae are moving prey items. As their prey is encountered randomly and consumed quickly, salamander larvae likely do not benefit from local enhancement and are more successful using an ambush strategy. Another and potentially more dangerous implication of these foraging habits is risk of predation by conspecifics. Spotted salamander larvae are quick to feed on any species of smaller larvae that they can consume. This cannibalistic behavior can even occur within a clutch, wherein early hatching larvae consume kin from the same clutch that hatch later (B. Gall pers. obs.). Because of this behavior, exhibiting local enhancement could pose a serious threat to spotted salamander larvae if one were to be attracted to a group containing larger larvae.

One possible reason tadpoles exhibit local enhancement and salamander larvae do not may be due to their methods of avoiding predation. Tadpoles occasionally move in large groups, which have been shown to benefit individuals by deterring predation. Spieler & Linsenmair (1999) studied this aggregation behavior in tadpoles from two toad species and found that in the presence of predators, if tadpoles formed large aggregations, they were able to move without being attacked. Although wood frog tadpoles generally do not form large aggregations, schooling does occur when predation risk and population density are both high (Waldman 1984). A successful antipredator mechanism combined with knowledge of food patches supports our hypothesis that wood frog tadpoles exhibit local enhancement to obtain these benefits. While tadpoles often use antipredator mechanisms, several studies of *Ambystoma* larvae have suggested that these salamander larvae more frequently use predator-avoidance mechanisms (Holomuzki 1986; Semlitsch 1987; Walls 1995; Sih et al. 2003). For example, Holomuzki (1986) found that larval tiger salamanders (*A. tigrinum*) utilize both spatial and temporal refuges when predators, including diving beetles (*Dytiscus dauricus*), were present in high densities. In contrast to tadpoles, salamander larvae likely gain little to no benefit from social learning in regard to prey acquisition, and their predator-avoidance tactic requires behavior that is opposite to behavioral changes typically facilitated by local enhancement.

These results, combined with several recent studies on nonsocial species, are challenging the notion that social learning evolves only in species that are highly gregarious (Fiorito & Scotto 1992; Wilkinson et al. 2010; Noble et al. 2014). One potential reason for this discrepancy may be related to life-history variation in sociality. For example, Noble et al. (2014) showed that young (1–2 yr old) male skinks (*Eulamprus quoyii*) rapidly learn novel tasks by watching demonstrators, whereas old (5–8 yr old) skinks performed these tasks with the same speed regardless of whether they had a demonstrator present. This difference may be due to greater frequency of territoriality in older skinks which limits the potential for social interactions between conspecifics at an older age. Amphibians in particular may be an excellent model for social learning, despite the limited social relationships. Except for breeding aggregations, adult amphibians are typically solitary (Wells 2007). However, larval amphibians often occur in large kin and non-kin groups for long periods of time after hatching (Wells 2007), and the evolution of social learning during this stage may be prominent.

To our knowledge, only two other studies have tested for social learning mechanisms in amphibians. (Ferrari et al. 2007) tested for social facilitation of predator recognition in wood frogs and found the tadpoles were capable of learning to fear a novel predator. Combined with our study, these results suggest that despite being an organism with weak social relationships, some frogs may utilize multiple social learning mechanisms. Despite the lack of local enhancement exhibited by spotted salamander larvae in this study, other forms of social learning may be beneficial (i.e., social facilitation), and therefore, these results should not be confused with a general lack of the capacity for social learning. A recent study by Crane et al. (2012) documented social facilitation of predator recognition by naïve ringed salamanders (*A. annulatum*). In this case, a larvae naïve to a predator is placed next to an experienced individual and simultaneously exposed to stimuli from that predator. The naïve individual subsequently observes the experienced salamander perform antipredator behavior, modifies their own behavior accordingly, and learns to fear a new predator (Crane & Ferrari 2013). The threat of predation is one of the most intense selective forces driving the evolution of behavior, and it is not surprising that this has facilitated at least one form of social learning in this salamander species.

The ephemeral habitats in which tadpoles and aquatic salamander larvae often coexist in are variable in terms of food availability and predation risk. While local enhancement seems like an entirely profitable behavior, it may not be an optimal strategy for all species. Although additional research is needed to determine the exact costs and benefits for each species, tadpoles have likely adapted local enhancement because the benefits of social learning outweigh the costs: They benefit from the ability to quickly identify patchy food sources as well as deter predators, their costs being competition and potential cannibalistic conspecifics (rarely). Aquatic salamander larvae may have not adapted local enhancement because for them, the costs outweigh the benefits: They do not feed on patchy food sources, and they are at high risk of predation by conspecifics. While both species share a primarily solitary adult lifestyle and the larval stages overlap both spatially and temporally, the ecology and life-history patterns in wood frogs likely favors local enhancement, whereas those of salamander larvae do not.

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