

Ontogenetic changes in chemical alarm cue recognition and fast-start performance in guppies (*Poecilia reticulata*)

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Funding information

National Natural Science Foundation of China, Grant/Award Number: NSFC 31770442; China Scholarship Council, Grant/Award Number: 201508505022; Youth Top-notch Talent Cultivation Program of Chongqing Normal University, Grant/Award Number: 14CSBJ08

Editor: J. Wright

Abstract

Risk recognition and fast-start performance are critical to fish survival when faced with predators. Many fish species have been shown to recognize risks associated with chemical cues released by injured conspecifics. However, little is known about the ontogeny of “risk” recognition via damage-released chemical alarm cues and fast-start performance in prey fishes. The objectives of this study were to determine whether risk recognition and fast-start performance in guppies (*Poecilia reticulata*) exhibit ontogenetic variation, and whether there is a trade-off between risk recognition and fast-start performance. To achieve these objectives, individual guppies from replicate groups were assayed on one of the 1st, 7th, 14th, 21st, or 28th day after their birth. We found that both the risk recognition and fast-start performance in guppies exhibited ontogenetic variation, as on days 1 and 7, fish did not exhibit risk recognition when exposed to alarm cues from conspecifics, but by day 14, such recognition was evident. Noticeable increases in maximum linear velocity (V_{max}), maximum linear acceleration (A_{max}), and escape distance (S_{120ms}) were concurrent with progressive ontogenetic stage, and no significant correlations were found between risk recognition and fast-start performance at any ontogenetic stage. Our findings reveal ontogenetic variation in damage-released chemical cue recognition and fast-start performance in guppies.

KEYWORDS

antipredator responses, damage-released chemical cues, developmental trade-offs, information use, ontogenetic shifts

1 | INTRODUCTION

In aquatic environments, chemosensory cues are pervasive (Hara, 1992; Wisenden, 2000) and are a dominant form of communication between animals (Elvidge & Brown, 2015; Ferrari, Wisenden, & Chivers, 2010). Epidermal damage-released chemical alarm cues (hereafter referred to as chemical alarm cues or alarm cues) are typically released during a predation event and, therefore, serve as a reliable indicator of immediate predation risk (Wisenden & Millard, 2001). Experimentally, alarm cues are often used to manipulate the perception of ambient

risk levels in focal animals (Chivers & Smith, 1998; Ferrari et al., 2010) without exposing them to predation. An increasing number of aquatic organisms, ranging from cnidarians to fish and amphibians, have been shown to display risk recognition to chemical alarm cues from injured conspecifics (Spivey et al., 2015; Wisenden, 2000).

Responses to conspecific alarm cues in some fishes shift with ontogeny from antipredator to exploratory or foraging behaviors (Harvey & Brown, 2004; Mitchell & McCormick, 2013) as size differences between alarm cue sender and alarm cue receiver accumulate and render them susceptible to different sources of predation (Elvidge & Brown,

TABLE 1 The body sizes of guppies at different ontogenetic stages

	Ontogenetic stage (day post-birth)				
	1	7	14	21	28
Testing fish					
Body mass (mg)	5.11 ± 0.13	8.91 ± 0.18	15.8 ± 0.75	26.2 ± 1.48	49.3 ± 2.11
Total length (mm)	6.83 ± 0.06	8.18 ± 0.10	9.59 ± 0.13	10.9 ± 0.20	13.7 ± 0.22
Donor fish					
Body mass (mg)	5.19 ± 0.12	8.77 ± 0.18	15.1 ± 0.60	26.1 ± 1.37	48.8 ± 1.76
Total length (mm)	6.77 ± 0.08	8.16 ± 0.09	9.45 ± 0.11	10.9 ± 0.19	13.6 ± 0.21

The data are presented as means ± SE ($n = 20$ for each group).

2015; Elvidge, Ramnarine, Godin, & Brown, 2010). Interestingly, Atherton and McCormick (2015) demonstrated that cinnamon clownfish (*Amphiprion melanopus*) are able to detect and react to conspecific chemical alarm cues at the embryonic stage, suggesting that risk recognition via chemical alarm cues in oviparous fish may be innate. It is unclear, however, whether or not this innate recognition is present from birth in live-bearing fishes, or whether it develops with ontogeny.

While strong responses to chemical alarm cues are likely to accrue survival benefits for prey (Ferrari et al., 2010), adopting antipredator behaviors incurs some costs stemming from concurrent decreases in other fitness-related activities (Jones & Godin, 2010; Lima & Dill, 1990; Skelly, 1992; Spivey et al., 2015). Ecological trade-offs between immediate risk avoidance and maintaining a developmental trajectory to maximize future fitness is particularly important for larval and early life-history stages in animals (Brown, Rive, Ferrari, & Chivers, 2006; Garcia, Thurman, Rowe, & Selego, 2012; Roulin, 2001; Stamps, 2007). In view of high energy requirements and high mortality rates in fishes in these early developmental stages (Mangel & Munch, 2005; Pedersen, 1997), we speculated that larval fish would ignore predation risk to maximize food intake, resulting in deficient responses to chemical alarm cues. Hence, the first objective of this study was to determine whether or not the response to alarm cues varies with ontogeny in guppies (*Poecilia reticulata*), and identify the age at which this response develops.

Prey survival is largely dependent on efficient escape performance following risk recognition (Godin, 1997; Smith, 1997). Fast-start swimming, which is a brief, sudden, and anaerobically powered burst of movement away from a threatening stimulus, is crucial for survival in predator-prey interactions (Domenici & Blake, 1997; Killen, Reid, Marras, & Domenici, 2015; Xia, Ma, Guo, Huang, & Fu, 2015). This fast-start evasion response is an antipredator mechanism that is likely a major factor contributing to the evolution of variation in morphology and behavior among fishes (Walker, Ghalambor, Griset, McKenney, & Reznick, 2005; Webb, 1984), as more efficient fast-starts increase the probability of successfully evading a predation strike (Walker et al., 2005).

Evading predators requires the ability to detect them through environmental stimuli. Post-detection, these stimuli are integrated as sensory information and processed by the central nervous system. Secondary physiological responses may then occur, and together the central and peripheral changes in physiology determine the behavioral

response to a stimulus (Scott & Sloman, 2004). According to the evolutionary trade-off hypothesis, fitness benefits as the result of a change in one trait may be opposed by losses as a result of a concomitant change in another trait (Roff & Fairbairn, 2007). It is unknown whether trade-offs occur between perception (risk recognition) and performance (fast-start escape). The ongoing differentiation and growth of tissues and the development of sensory-motor integration during early ontogeny may constrain performance in both perception and response (Herrel & Gibb, 2005). Furthermore, fishes in different life-history stages likely face different kinds of predation pressure (Elvidge et al., 2010; Holmes & McCormick, 2010), suggesting that there may be ontogenetic changes in fast-start performance. We predicted that guppies would exhibit ontogenetic variation in fast-start performance in their early life-history stages and that fish with weaker responses to risky cues may display greater fast-start escape performance. Thus, the second objective of this study was to identify ontogenetic variation in fast-start performance in guppies and to determine whether there is a trade-off between the intensity of risk recognition and fast-start performance.

2 | MATERIALS AND METHODS

2.1 | Experimental fish

We used guppies, a common model species in investigating various behavioral and evolutionary questions relating to predation (Magurran, 2005; Templeton & Shriner, 2004). The established laboratory populations were held in 36-L recirculating tanks supplied with dechlorinated and activated carbon-filtered water on a 15-hr: 9-hr light-dark cycle. Water temperature was maintained at $25 \pm 1^\circ\text{C}$, with dissolved oxygen content kept above 7 mg/L and pH ranging from 6.8 to 7.3. Fish were fed twice daily to satiation with commercial bloodworms (*Tubifex tubifex*).

Individual gravid females were separated and held in several round-loop tanks (≈ 6 L, $N = 16$) when they showed obvious parturition symptoms (i.e., conspicuous black abdominal spot). Of these, only females ($N = 8$) of similar size (2.59 ± 0.047 g, 4.48 ± 0.10 cm standard length) and fecundity (68.8 ± 1.92 offspring per brood) were selected and their offspring were used in this study. The cohort of newborn guppies was divided into five experimental groups (with each group being tested at a different ontogenetic stage) and

further subdivided into three replicate groups. These guppies were then maintained at conditions identical to those described above, except that they were fed to satiation with live brine shrimp (*Artemia salina*). Risk recognition and fast-start performance were assessed at one of five intervals (the 1st, 7th, 14th, 21st, and 28th days) post-birth, with each fish being tested only once at a given ontogenetic stage. Test fish ($N = 20$ per replicate group) were allowed 12-hr recovery periods separating the measurements of risk recognition and fast-start performance. The body size of the test fish (Table 1) was measured after the assessments following sedation with tricaine methanesulfonate (MS-222).

2.2 | Risk recognition

Whole guppy carcasses were used as alarm cue donors to generate a tissue homogenate using a mortar and pestle, as the size of the donors precluded the removal of the epidermis (after Brown, Macnaughton, Elvidge, Ramnarine, & Godin, 2009; Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013). Each test fish was exposed to a homogenate consisting of the carcass of one guppy of the same ontogenetic stage diluted into a 100- μ l aliquot.

The tests were conducted in Petri dishes (diameter ≈ 15 body lengths: 10 cm for day 1; 12 cm for day 7; 14.5 cm for day 14; 15.5 cm for day 21; 20 cm for day 28; Table 1). The depth of water in the Petri dishes was ≈ 0.5 body lengths (3.6 mm for day 1; 4.0 mm for day 7; 4.8 mm for day 14; 5.3 mm for day 21; 6.4 mm for day 28), with temperature ($25 \pm 0.5^\circ\text{C}$) and dissolved oxygen levels (>7 mg/L) stable throughout the experimental period. The functional concentrations of chemical alarm cues in the test Petri dishes were similar among the different ontogenetic stages (~ 0.02 mg/ml).

The undersides of the Petri dishes were outfitted with a gray sheet of paper with a hatched design (Figure 1) so that the position and movement of the fish could be measured. One end of the Petri dish was supplied with a small sponge to serve as the "stimulus area," and we designated the "risky area" (Figure 1) based on pilot experiments. The boundary between areas was determined based on the experimental fish having demonstrated a clear avoidance response (if they exhibited risk recognition) when they approached it.

Individual fish were placed into the Petri dishes and were allowed to acclimate to the novel environment for 15 min, after which 100 μ l of either tank water (control) or guppy alarm cue was carefully injected via pipette into the sponge in the stimulus area. The behavior of the experimental fish was then video recorded for 5 min and subsequently analyzed to measure the amount of time spent using the risky area. The Petri dishes were thoroughly rinsed and wiped clean between trials to rid any trace of residual chemical cues.

2.3 | Fast-start performance

Fast-start swimming performance was measured with a custom fast-start instrument (for details see Yan, He, Cao, & Fu, 2012). The instrument consists of a high-speed camera (500 frames/s, BASLER A504K, Germany) connected to a computer, a testing tank ($40 \times 40 \times 15$ cm) engraved with 1×1 cm square grid lines on the bottom, an LED matrix light source, and an electrical pulse generator producing direct current. The fish were given 15 min to acclimate to the test arena. The water depth in the tank was 0.8 cm, with temperature and the dissolved oxygen levels identical to those used in the first assay. The water in the testing tank was replaced between trials.

The fast-start responses were elicited by an electrical impulse (0.75 V/cm; 50 ms duration) when the fish was in an intermediate position within the filming zone. The high-speed camera was used to record the entire escape process (time span: 2 s). The recording was initiated as soon as the LED (synchronized with the electrical stimulus) was illuminated. The resulting images were initially processed using nEOiMAGING and ACDSsee 12 software and were subsequently digitized using TpsUtil and TpsDig software (<http://life.bio.sunysb.edu/morph/>) to examine the displacement of the center of the fish's head. The latency to respond (t_{latency} , ms) and kinematic variables (maximum linear velocity [V_{max} , m/s], maximum linear acceleration [A_{max} , m/s^2], and escape distance [$S_{120 \text{ ms}}$, mm] achieved by each fish within 120 ms post-stimulus) were extracted from the digital video (Domenici & Blake, 1997; Xia et al., 2015). In addition, the individual relative V_{max} (rV_{max}), relative A_{max} (rA_{max}), and relative $S_{120 \text{ ms}}$ ($rS_{120 \text{ ms}}$) values were calculated by dividing the V_{max} , A_{max} , and $S_{120 \text{ ms}}$ values by individual body lengths.

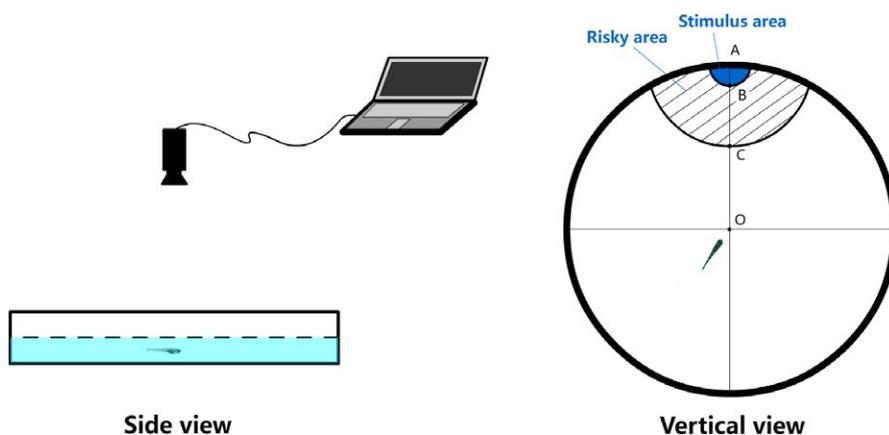


FIGURE 1 Experimental setup used to assess risk recognition in guppies. $AC = 1/2 AO$; $AB = 1/4 AC$. [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Statistical analyses

All measures were first examined for normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test) between treatments. As the physical parameters of the experimental setup used for assessment of risk recognition were variable (i.e., larger Petri dishes for older fish), ontogenetic stage was not used as a factor. Instead, the differences in fish in response to water or alarm cues at each ontogenetic stage were examined with paired-samples *t* tests.

The effects of ontogenetic stage on fast-start performance (t_{latency} , V_{max} , A_{max} , $S_{120\text{ ms}}$, or rV_{max} , rA_{max} , $rS_{120\text{ ms}}$) were tested with one-way analysis of variance (ANOVA) or Kruskal–Wallis tests followed by either Tukey's HSD (ANOVA) or Nemenyi post hoc tests with chi-square corrections for tied ranks in the "PMCMR" library (Pohlert, 2014). For each ontogenetic stage, the intra-individual relationships between the times spent using the risky area in the risk assessment trials and the fast-start measures (V_{max} , rA_{max} , $S_{120\text{ ms}}$, rV_{max} , rA_{max} , and $rS_{120\text{ ms}}$) were examined using Pearson's correlation in SPSS.

2.5 | Ethical note

All experimental procedures were performed in accordance with the Guidelines on the Humane Treatment of Laboratory Animals established by the Ministry of Science and Technology of the People's Republic of China, and in line with ASAB guidelines for the treatment of animals in behavioral research (<http://asab.nottingham.ac.uk/ethics/guidelines.php>).

3 | RESULTS

3.1 | Risk recognition

We detected ontogenetic differences in time spent using the "risky area," with significant decreases demonstrated by the homogenate group relative to the control group on the 14th ($t_{39} = 2.44$, $p = .025$), 21st ($t_{39} = 2.77$, $p = .012$), and 28th ($t_{39} = 2.68$, $p = .015$) days post-birth, whereas guppies in the first week post-birth (1st and 7th days) demonstrated no significant differences between the homogenate and control groups ($p > .05$; Figure 2).

3.2 | Fast-start performance

Fast-start performance metrics generally demonstrated positive relationships with ontogenetic stage (Figure 3), with the exception of latency to respond to the electrical stimulus (t_{latency} ; Kruskal–Wallis $\chi^2_4 = 2.82$, $p = .59$). We observed significant overall differences between stages in V_{max} (ANOVA $F_{4,95} = 4.79$, $p = .0015$; Figure 3a), with significant pairwise difference between days 1 and 28 (Tukey's HSD, $p = .0021$), and days 7 and 28 ($p = .0042$), with non-significant differences between days 14 and 28 ($p = .088$), and 21 and 28 ($p = .32$). A_{max} differed significantly overall across stages, generally increasing with age (Kruskal–Wallis $\chi^2_4 = 10.5$, $p = .033$; Figure 3b) although there were no significant pairwise differences between stages

(all $p > .05$). $S_{120\text{ ms}}$ also varied positively with ontogenetic stage (Kruskal–Wallis $\chi^2_4 = 21.2$, $p < .0001$; Figure 3c), with significant pairwise differences between days 1 and 28 ($p = .0009$), while days 7 and 28 ($p = .069$) and days 1 and 21 ($p = .084$) were nearly significant. The relative performance measures, however, generally decreased with ontogeny, with this trend being statistically significant for both rV_{max} (ANOVA $F_{4,95} = 8.54$, $p < .0001$; Figure 3d) and $rS_{120\text{ ms}}$ (Kruskal–Wallis $\chi^2_4 = 19.2$, $p = .001$; Figure 3f), but not rA_{max} (Kruskal–Wallis $\chi^2_4 = 0.623$, $p = .96$; Figure 3e).

3.3 | Intra-individual variation

The time spent using the risky area was not significantly correlated with t_{latency} , V_{max} , A_{max} , $S_{120\text{ ms}}$ or rV_{max} , rA_{max} , and $rS_{120\text{ ms}}$ at any ontogenetic stage (all $p > .05$).

4 | DISCUSSION

Our results suggest that both the risk recognition and fast-start performance in guppies exhibit ontogenetic variation, developing concurrently with increasing body size. To our knowledge, this study is the first demonstration of ontogenetic development of innate responses to the damage-released chemical cues of conspecifics in the early life-history stages of live-bearing fish. Of note, in the first week after birth, fish did not exhibit risk recognition when exposed to chemical cues from conspecifics at the same size class. Our findings could therefore provide insight for improving fish conservation and artificial stocking strategies involving the release of larval fishes.

The mechanism underlying our observed ontogenetic variation in risk recognition of guppies may be complex and multifaceted. From a developmental biology perspective, chemical alarm substances in fishes typically are released only after mechanical damage to the skin (Smith, 1992). In this study, the donors contributing to the homogenate were of the same age as the test subjects. Thus, whether the alarm cue was present in the skin of the larval fish in the first week after its birth is a question worthy of consideration and presents future research opportunities. Alternatively, the olfactory system is not fully developed in the early life cycle (Bettini, Lazzari, & Franceschini, 2012), so newborn guppies may be incapable of detecting alarm cues or may have different response thresholds requiring higher concentrations of alarm cues to elicit a response. From an ecological perspective, the timing of the transition in response between life-history stages should vary with the specific cost–benefit trade-offs associated with each stage (Ferrari et al., 2010; Hammill, Rogers, & Beckerman, 2008; Jones & Godin, 2010; Spivey et al., 2015). Prey animals often negotiate trade-offs between the costs of antipredator responses and the benefits of other fitness-related life activities (Brown et al., 2006; Roulin, 2001; Skelly, 1992; Stamps, 2007). For example, Brown and Smith (1996) showed that there is a significant trade-off between hunger level or foraging motivation and predator-avoidance behavior in fathead minnows (*Pimephales promelas*). Similarly, reticulate sculpins (*Cottus perplexus*) deprived of food for 2 days failed to respond to conspecific

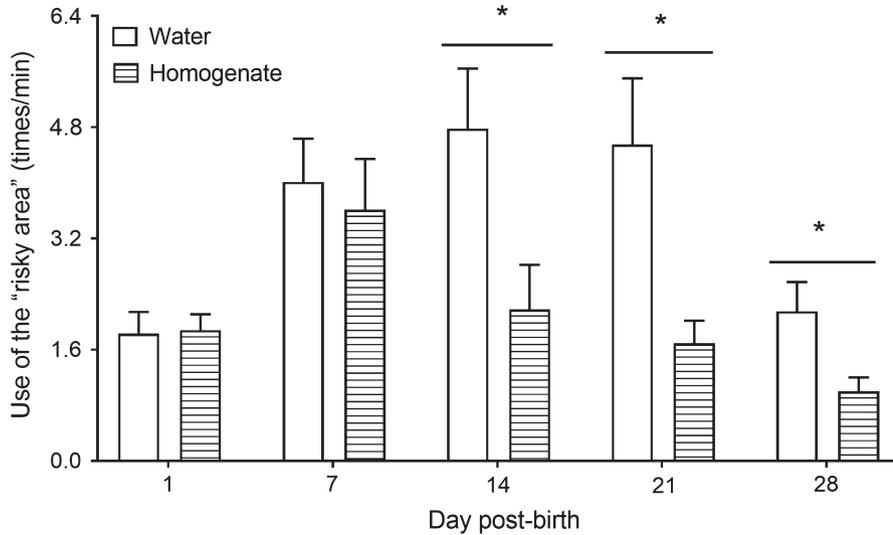


FIGURE 2 The ontogeny of risk recognition in guppy in terms of using the risky area. The data are presented as the mean \pm SE ($n = 20$). An asterisk (*) indicates a significant difference between the homogenate group and the control group ($p < .05$)

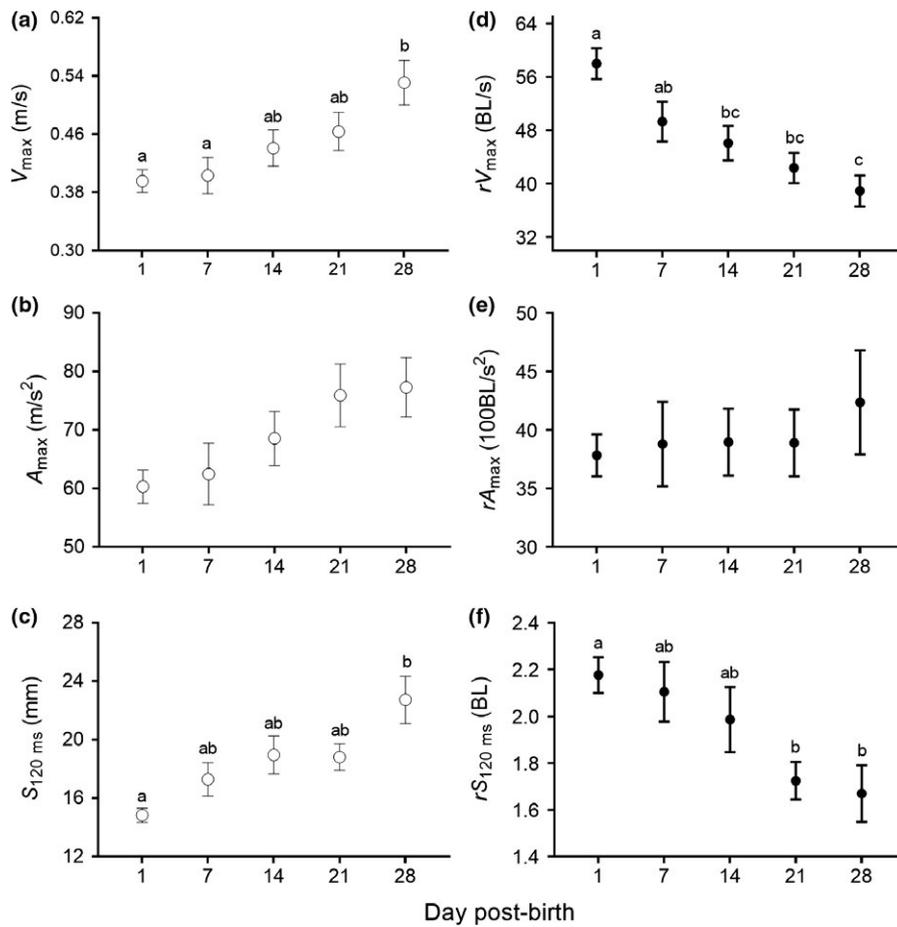


FIGURE 3 Ontogenetic changes in fast-start performance in guppies. (a) Maximum linear velocity (V_{max}); (b) maximum linear acceleration (A_{max}); (c) escape distance ($S_{120\text{ms}}$); (d) relative V_{max} ; (e) relative A_{max} ; (f) relative $S_{120\text{ms}}$. BL: body length. The data are presented as the mean \pm SE ($n = 20$). Values without a common superscript are significantly different ($p < .05$)

alarm cues; however, the same individuals fed to satiation did respond to alarm cues (Chivers, Puttitz, & Blaustein, 2000). Vigilant larvae are likely to expend more energy than non-vigilant larvae due to higher cognitive activity levels in the brain, one of the most metabolically active organs in the body (Killen et al., 2015; Roulin, 2001), driving an energetic trade-off between cognitive function and the demands of the developmental trajectory of larvae. Consequently, the absence of risk recognition in first-week larval guppies in the present study might

be the result of conflicting energy requirements with the maximization of foraging, growth, and development effectively trumping risk assessment.

The ontogeny of risk recognition varies across taxa. For example, Alemadi and Wisenden (2002) demonstrated that the transition from larva to juvenile related to independence from parental care (i.e., pre- and post-independence of juveniles) and did not affect how prey respond to alarm cues. In contrast, Harvey and Brown

(2004) showed that yellow perch (*Perca flavescens*) undergo an ontogenetic switch in which young-of-the-year responded to conspecific alarm cues with antipredator behaviors, whereas adult perch increased their foraging activities in response to the same cues. Additional studies suggest that prey are highly selective in how they use information from conspecific alarm cues, responding to and learning from only those cues that are relevant to their developmental stage and/or prey guild (Elvidge & Brown, 2015; Mitchell & McCormick, 2013).

The fast-start swim response provides an excellent model system for examining the interactions between neurobiology, muscle function and locomotor biomechanics in the production of a complex survival behavior (Westneat, Hale, McHenry, & Long, 1998). Fast-start responses are usually mediated by the Mauthner cells, two bilateral giant neurons and other associated neurons in the brainstem-based escape network (Eaton, DiDomenico, & Nissanov, 1991), powered by intracellular stores of adenosine triphosphate (ATP) and creatine phosphate (Reidy, Kerr, & Nelson, 2000; Xia et al., 2015). In this study, no ontogenetic variation in escape latency (measured as the time between the stimulus onset and the first detectable movement of the fish) was found in juvenile guppies, suggesting that the timing of activation of the Mauthner neurons and associated networks to threatening stimuli was not influenced by developmental stage. In contrast, notable increases in absolute swim performance (V_{\max} , A_{\max} , and $S_{120\text{ms}}$) were detected with increasing age (ontogenetic stage), indicating that propulsive performance in fast-starts increased with growth and development (sensu Domenici & Blake, 1997), such that larger guppies with greater energy reserves have greater ability to evade potential predators. Relative levels of performance (i.e., rV_{\max} and $rS_{120\text{ms}}$), however, actually decreased with ontogenetic stage, although acceleration capacity (rA_{\max}) did not. These observations suggest that the fish demonstrated functional compensation, possibly in increased muscle shortening velocity vs. deficient muscle power, during the earliest ontogenetic stages (Herrel & Gibb, 2005; Wakeling, Kemp, & Johnston, 1999). These results are generally consistent with those reported by Hale (1999), Wakeling et al. (1999), and Dangles, Pierre, Christides, and Casas (2007).

The ideal ecological strategy for animals is a fine balance between resource acquisition (opportunities) and risk avoidance (challenges) (Lima & Dill, 1990). In the present study, the smaller amounts of time spent using the risky area in the trial arenas in the presence of conspecific chemical alarm cues may represent a "shy" or cautious strategy (Brown & Godin, 1999; Brown et al., 2013). Fishes following this strategy are likely to evolve a high capability of risk recognition but relatively low ability to escape (low challenges vs. low opportunities). Contrary to our assumption, no trade-offs appear to exist between the intensity of risk recognition and fast-start performance of laboratory-reared guppies in their early life-history stages, indicating that while both risk recognition and swim performance capabilities increase with age during the first 28 days of development, they do so at different rates and do not appear to be mutually constrained by energetic trade-offs. A recent study by Kern, Robinson, Gass, Godwin, and Langerhans (2016) revealed the

correlated evolution of personality, morphology, and performance in zebrafish (*Danio rerio*). They reported that artificial selection for boldness produced correlated evolutionary responses of larger caudal regions and higher fast-start performance, with the latter ostensibly facilitated by the former. In this regard, the non-correlation between risk recognition and fast-start performance in the present study may be due to the non-significant change in caudal regions during early life-stage development. Alternatively, the cognitive demands of using the risky area may be related to different patterns of learning and retention. Shy, risk-averse individuals may store more information in long-term memory than bolder, more risk-prone ones (Sih & Del Giudice, 2012), resulting in decreased times spent in risky areas, and thus lead to the observed lack of association between times spent in risky areas and fast-start performance. More efforts need to be devoted to understanding the dynamic relationships between antipredator behaviors and fast-start capabilities over the whole life-history spectra of fishes, particularly with regard to natural variation in forage availability and resulting interindividual differences in body condition.

ACKNOWLEDGEMENTS

We are grateful to the anonymous referees for providing helpful comments on earlier versions of this manuscript. This study was supported by the National Natural Science Foundation of China (NSFC 31770442), the State Scholarship Fund from China Scholarship Council (201508505022), and Youth Top-notch Talent Cultivation Program of Chongqing Normal University (14CSBJ08).

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How to cite this article: Xia J, Cheng M, Cai R, Fu S, Cooke SJ, Elvidge CK. Ontogenetic changes in chemical alarm cue recognition and fast-start performance in guppies (*Poecilia reticulata*). *Ethology*. 2017;123:916–923. <https://doi.org/10.1111/eth.12691>