

Chapter 16 Predation risk and decision making in poeciliid prey

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16.1 Introduction

VARIATION IN PREDATOR abundance is one of the strongest selective pressures operating in natural ecosystems and influences a wide range of physiological, morphological, and behavioral traits in prey species. Several influential reviews on this topic (Lima & Dill 1990; Endler 1995; S. Lima 1998) have demonstrated that predation risk exerts a considerable influence on life-history patterns (see Pireset al., **chapter 3**), genital morphology (Langerhans, **chapter 21**), male courtship and female mate choice (Rios-Cardenas & Morris, **chapter 17**), dominance and aggressive interactions (Magurran, **chapter 19**), foraging behavior and habitat use (Grether & Kolluru, **chapter 6**), and, of course, the expression of antipredator strategies such as schooling and predator inspection (Krause et al., **chapter 13**; this chapter). The risk sensitivity hypothesis posits that prey optimize the trade-off between predation risk and other important behavioral activities in order to maximize fitness (Sih 1980; Lima & Dill 1990; S. Lima 1998). At one extreme, the cost of not responding to an increase in predation risk might result in the loss of life. On the other hand, overreacting to changes in risk will cause a reduction in other activities (e.g., foraging, courtship), which can also severely affect an individual's fitness.

Optimizing the balance between predation risk and behavioral activities requires two key processes. First, prey must acquire accurate and reliable information about predation risk (Kats & Dill 1998). Second, they must act on this information and implement corresponding adjustments

to their behavior. Both of these processes—information gathering and decision making—require a considerable level of cognitive processing. The aim of this chapter is not to review the literature on behavioral responses of prey to changes in predation risk, as this subject has already been covered in some detail for a number of taxa (see reviews by Lima & Dill 1990; S. Lima 1998). Rather, we extend the discussion of behavioral decisions under predation risk by considering the risk-related cues that drive these decisions and also the cognitive requirements that underpin the decision-making process. Specifically, we will argue that decision making under the risk of predation is fundamental to a prey animal's survival and fitness and, consequently, that predation risk may be partly responsible for driving the evolution of cognition.

Research on the evolution of cognition has tended to focus on the importance of social interactions (the social-intelligence hypothesis: Humphrey 1976; Byrne & Whiten 1988) or complex foraging tasks (Clutton-Brock & Harvey 1980) among animals that form hierarchical social groups (e.g., primates) rather than the role of predation risk per se (Zuberbuhler & Byrne 2006). However, responding to predators has a strong social component, particularly since grouping is one of the most common responses to increased predation risk (Krause & Ruxton 2002). Prey that form groups not only benefit through safety in numbers (e.g., risk dilution) but may also increase their chances of survival as a result of their social interactions with other group members (Krause & Ruxton 2002; Krause et al., **chapter 13**). For example, the use of predator-specific alarm calls (e.g., Marler 1957), cooperation among individuals during

predator inspection (e.g., Milinski 1987), and the ability to learn by observing/listening to the responses of others (social learning: Heyes & Galef 1996; Brown & Laland 2003; Webster & Laland, **chapter 14**) require a considerable level of cognition. Although other tasks (e.g., foraging, competitive interactions) are likely to have facilitated the evolution of social complexity, we expect strong selection on any social behaviors (and their underlying cognitive processes) that increase a prey individual's chance of surviving an encounter with a predator.

Predator-prey interactions are often likened to an evolutionary arms race; as the predator gets the upper hand over its prey, the prey responds in some manner to attempt to stay one step ahead. Much of the literature regarding the predator-prey arms race has tended to revolve around morphological or behavioral traits, such as attack speed and escape velocities of predators and prey, respectively (Dawkins & Krebs 1979; Abrams 2000). However, such traits are underpinned by physiological or cognitive mechanisms that have received far less attention in this context. Considering the arms race from a cognitive perspective, we expect the increased cognitive capacity of prey living in high-risk environments to be counteracted by heightened levels of cognition underlying predator attack strategies. Thus, we hypothesize that predator and prey are trying to “outsmart” one another (Brown & Braithwaite 2005). If this argument is correct, we expect to observe a relationship between cognitive ability and variation in predation risk.

Fishes, and poeciliids in particular, are an ideal group for evaluating the experimental support for these ideas. First, fishes display surprisingly complex cognitive abilities (e.g., cooperation, tool use, spatial memory) that are traditionally assigned to high-intelligence organisms, such as primates (Bshary et al. 2002; Brown et al. 2006b; Bisazza, **chapter 15**). Second, members of the same species often occupy a large variety of habitats, making it possible to establish correlative links between ecological variables (e.g., predation risk) and cognitive ability. Here, we draw on evidence from several species of poeciliid to evaluate the evidence that predation risk is an important factor driving the evolution of cognitive ability in prey (Zuberbuhler & Byrne 2006). We first examine how the interaction between brain morphology and the detection of sensory cues allows poeciliid prey to gain information about their risk of predation (section 16.2). We then evaluate how the decision-making process—for example, deciding when and how to respond to a predator-related cue—is influenced by both predation risk and an individual's personality (section 16.3). Finally, we assess the relationship between predation risk and cognitive ability, focusing on how living with risk affects brain development and the evolution of cerebral lateralization (section 16.4).

16.2 Information gathering: prey assessment of predation risk

Poeciliids, like other prey fishes, have a large number of sensory modalities available to them to assess changes in their risk of predation (Coleman, **chapter 7**). Specializations in each of these sensory systems are revealed by variations in brain morphology that tend to correlate with the behavior and ecology of the species (Kotrschal et al. 1998; Gonzalez-Voyer et al. 2009). For example, the optic tectum and telencephalon (part of the forebrain) are well represented in the brains of shallow-water fishes that rely heavily on visual cues (e.g., for foraging and navigation). In contrast, fishes living in deep waters (>1000 m) tend to rely more on mechanoreception and olfaction, and the size of the optic tectum and telencephalon is much reduced (Kotrschal et al. 1998). Environmental characteristics, therefore, exert considerable influence on brain morphology and the way in which prey can detect and manage their level of risk.

The sensory cues that are available to prey fishes to assess their level of predation risk depend on the physical properties of the water (e.g., depth, turbidity) as well as habitat structure (e.g., open water versus complex environments). In addition, environmental variation, such as habitat heterogeneity and changing light levels that are related to diurnal patterns of predator activity, may serve as important cues regarding changes in risk. We discuss each of these in turn and highlight the manner in which poeciliid studies have contributed to our understanding of how prey animals assess their risk of predation.

16.2.1 Chemical cues

Chemical cues provide an important source of information to prey regarding local predation risk (Kats & Dill 1998). These cues may originate from a predator in the form of predator odors (sometimes referred to as “kairomones”) that are passively released through normal metabolic processes or odors associated with the recent feeding habits of a predator (e.g., urine, feces) (Wisenden & Chivers 2006). Other chemical cues that can provide important information to both predators and prey are damage-released chemical alarm cues (hereafter referred to as “alarm cues”) and disturbance cues. The detection of such cues may cause prey to increase their level of vigilance, adopt risk-sensitive behavioral strategies, or directly engage in predator avoidance tactics, depending on the severity of the threat posed (Chivers & Smith 1998).

Alarm cues are chemicals that occur in the epidermis of the skin and are released when a fish is captured or injured by a predator (Pfeiffer 1977; Smith 1977, 1982, 1992; Pfeiffer 1982; Chivers & Smith 1998). Alarm cues occur

in many fish species, including poeciliids (Chivers & Smith 1998; reviewed in Brown & Chivers 2006), and the detection of these cues elicits a generalized behavioral response in fishes known as the “fright response” or “fright reaction” (hereafter referred to as “fright response”), which is characterized by avoidance of the cue source, an increase in shoal cohesion, a reduction in activity, movement toward the substrate, and erratic swimming such as dashing and skittering (Chivers & Smith 1998).

A response to alarm cues has been reported in only a few species of poeciliid: mosquitofish (Reed 1969; Garcia et al. 1992), swordtails (Mirza et al. 2001), and guppies (Nordell 1998; Brown & Godin 1999b; Brown et al. 2009). For example, Brown and Godin (1999b) used a combination of laboratory and field-based studies to show that guppies (*Poecilia reticulata*) respond to alarm cues from injured conspecifics but not to cues from swordtails (which were previously thought to lack alarm cues, but see below). Interestingly, the nature of the fright response was dependent on the population origin of the alarm cue donor; guppies from a high-predation risk population showed a stronger response (movement toward the substrate) to alarm cues from a high-predation donor than to those from a low-predation donor (Brown & Godin 1999b). The finding that both juveniles and adults avoided alarm cues in these experiments suggests that this response may be largely genetically based or formed at an early developmental stage (Brown & Godin 1999b).

Alarm cues that originate from heterospecifics can also serve as indicators of increased predation risk (Chivers & Smith 1998; Smith 1999), and cross-species responses are particularly beneficial for prey that form mixed-species shoals. Mirza et al. (2001) exposed swordtails (*Xiphophorus hellerii*) to either conspecific skin extract, guppy skin extract, or distilled water. The swordtails displayed a fright response toward both skin extracts (containing alarm cues) but showed a stronger reduction in activity levels in the presence of conspecific extract than heterospecific extract.

Alarm cues not only function as indicators of increased predation risk but also provide an opportunity to acquire a learned response to novel stimuli. Many studies have demonstrated that prey fishes can acquire a fright response by associating novel visual, auditory, and/or chemical cues with alarm cues that originate from either conspecifics or heterospecifics (reviewed in Brown 2003; Kelley & Magurran 2003, 2006; Brown & Chivers 2006). Following a single association of the stimulus and alarm cue, prey can learn a response to novel predators (Magurran 1989; Mathis & Smith 1993; Chivers & Smith 1994), risky habitats (Chivers & Smith 1995), or even nonbiological stimuli such as flashing lights (Hall & Suboski 1995; Yunker et al.

1999) and artificial noises (Wisenden et al. 2008), although learning occurs more rapidly in response to biologically relevant cues (Csanyi 1986). Other mechanisms of learning have been shown to occur in poeciliids (e.g., social learning, Brown & Laland 2003; see also Webster & Laland, chapter 14), but poeciliids are noticeably absent from the literature on associative learning using alarm cues.

Disturbance cues are more generalized chemical cues that originate from fish that are distressed but not injured. Disturbance cues are thought to consist of ammonia that is excreted from the gills during periods of increase metabolic activity (Wisenden et al. 1995). The detection of disturbance cues influences the behavior and survival of a variety of fishes (e.g., Iowa darters, *Etheostoma exile*, Wisenden et al. 1995; Jordao & Volpato 2000; Bryer et al. 2001; Mirza & Chivers 2002; Jordao 2004) but has not yet been demonstrated in poeciliids.

16.2.2 Visual cues

Visual cues from predators, such as exposure to live fish predators or to fish or bird predator models, have been used to assess antipredator behaviors in a number of poeciliids (e.g., Magurran et al. 1992; Magurran & Seghers 1994b; Smith & Belk 2001). Commonly observed responses to these cues include a reduction in activity levels, increased shoaling and hiding, movement toward the substrate, and predator inspection. For example, *Brachyrhaphis episcopi* from high- and low-predation populations were exposed to a series of scenes hidden behind a trapdoor. Each shoal was exposed to each scene (blank control, live cichlid, or novel object) for 15 minutes, and their shoaling and inspection behavior assessed. Fish from high-predation areas formed tighter shoals and exhibited higher rates of inspection when exposed to a live cichlid than did those from low-predation populations (fig. 16.1a and b). No population differences were observed in responses to the blank scene (control) or the novel object (fig. 16.1a and b).

In addition to generalized schooling behavior, predator inspection is perhaps the best-studied response to visual predator cues, and studies with guppies have provided some key illustrations of the predator-deterrent function of this apparently paradoxical behavior. Predator inspection occurs when a small group of fish leave the shoal and slowly approach the predator, often swimming along the length of its body, before returning to the shoal (Pitcher et al. 1986). In the guppy, predator inspection is variable across populations, with fish from high-risk populations inspecting in larger group sizes (Magurran & Seghers 1994b). Most studies of predator inspection behavior have focused on the role of visual cues, but prey fishes will also inspect chemical

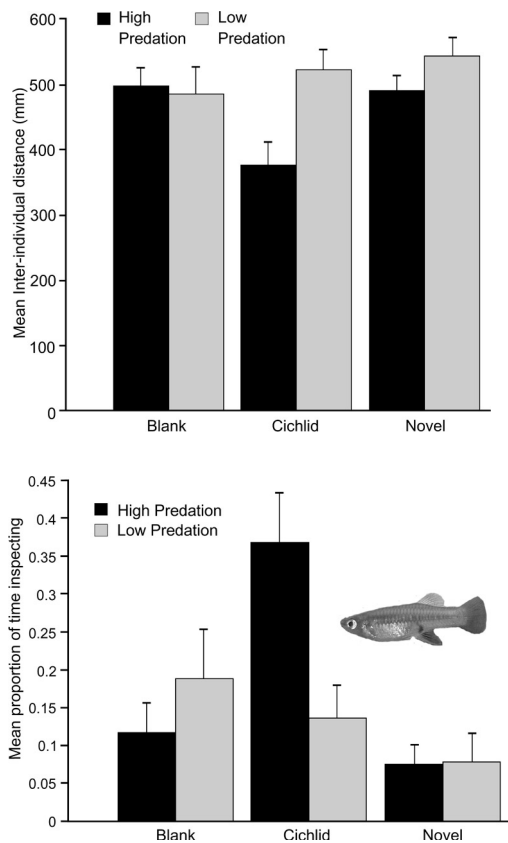


Figure 16.1 Mean (\pm SE) (a) interindividual distance and (b) proportion of time inspecting the compartment for shoals of *Brachyrhaphis episcopi* exposed to a blank scene (control), a live cichlid predator, and a novel object. There was no overall treatment effect on mean interindividual distance (repeated measures ANOVA: $F_{2,72} = 1.928$, $P < 0.05$), but post hoc analysis revealed that high-predation fish formed tighter shoals in response to the live cichlid than low-predation fish did (Fisher's PLSD, $P = 0.007$). There was a significant overall treatment effect on time spent inspecting the compartment; shoals spent a greater proportion of time inspecting the compartment containing the cichlid than either the blank scene or the novel object ($F_{2,72} = 5.495$, $P = 0.006$). C. Brown, unpublished data.

cues by moving toward the source (Brown & Godin 1999a; Brown & Godin 1999b; Brown & Cowan 2000; Brown et al. 2000).

Several studies have demonstrated that fish tend to show a bias in the eye that faces a predator during inspection (i.e., lateralization of inspection behavior; see also section 16.4.3 and Bisazza, chapter 15). For example, mosquitofish (*Gambusia holbrooki*) tended to explore a novel environment using their left eye but closely approached a predator using their right eye (De Santi et al. 2001). Interestingly, this eye bias during predator inspection depends on the predation pressure of the population; *B. episcopi* from high-predation populations preferred to use their right eye when viewing a predator, whereas those from low-predation populations favored use of their left eye (C. Brown et al. 2004). These patterns may be attributable

to differences in the stimuli that are perceived as threatening (C. Brown et al. 2004); thus, prey from high-risk populations may view a predator as a potential threat, while fish from low-risk populations may perceive the same stimulus as a harmless object. Alternatively, the population differences in left-right eye bias could be dependent on the frequency of left-right lateralized individuals in the population (i.e., frequency-dependent selection; see section 16.4.3).

Important information about potential predation threats can also be obtained by individuals that observe the behavior of others. For example, because predator inspection is thought to provide the inspectors with important information regarding the attack motivation of the predator (Pitcher et al. 1986; Murphy & Pitcher 1997), any changes in the behavior of the inspectors arising as a result of this information may be adopted by observing (noninspecting) fish (Pitcher et al. 1986; Magurran & Higham 1988). Observing the behavior of conspecifics (i.e., social learning, Brown & Laland 2001; Webster & Laland, chapter 14) may be an important way to acquire information regarding the threat posed by novel predators. Fish can also learn about potential threats by observing the behavior of heterospecifics (Krause 1993b; Mathis et al. 1996), but this has yet to be demonstrated in poeciliids (see Webster & Laland, chapter 14).

16.2.3 Spatial and temporal variation in risk

Predation risk is rarely constant, and prey fishes are usually subjected to risk that can vary on either a spatial or a temporal scale. Spatial changes in predation risk are usually associated with habitat heterogeneity and depend on the preferred habitat of the predator(s). In guppies, for example, the deeper parts of streams are often occupied by dangerous predators such as the pike cichlid (*Crenicichla frenata*), whereas riffles at the river's edge may be occupied by less dangerous predators such as Hart's rivulus (*Rivulus hartii*), which predominantly preys on juvenile guppies (Liley & Seghers 1975). Guppies respond to this spatial variation in risk and have been observed occupying the outer edges of stream margins, which may allow them to avoid both species of predator (Fraser et al. 2004).

Temporal variations in predation risk can be predictable if, for example, risk varies diurnally or in accordance with lunar or seasonal changes in predator activity or abundance (Lima & Bednekoff 1999). Alternatively, periods of increased predation risk can be highly irregular and depend on predator-prey encounters and/or detection of their associated cues. In the guppy, diurnal changes in predation risk may arise as a result of the activity patterns of different predators. For example, guppies that occur with the nocturnal wolf fish (*Hoplias malabaricus*) are inhibited

from feeding at night and suffer reduced growth and daytime courtship compared with their upstream counterparts that do not occur with this predator (Fraser et al. 2004). Theories examining the temporal nature of predation risk suggest that the level of predation pressure and its temporal distribution have several implications for the evolution of, and the amount of “effort” invested in, antipredator responses (the risk allocation hypothesis, Lima & Bednekoff 1999; Sih et al. 2000). For example, relatively low densities of predators that are highly unpredictable in space or time might correspond to a relatively high risk environment in comparison to those situations where predator density is high but highly predictable. Experiments examining these phenomena have yet to be conducted in poeciliids, but a study using cichlids found a temporal-predictability effect for low-predation levels but not for high-predation levels (Ferrari et al. 2008).

16.3 Decision making under risk of predation

16.3.1 When to respond?

Once a prey individual has detected cues that are associated with increased predation risk (section 16.2), it must decide how to respond to these cues. Since many predator-related cues are continuously present in the environment, the initiation of antipredator behaviors may be contingent on the detection of threshold levels of a particular cue. For example, glowlight tetras (*Hemigrammus erythrozonus*) exposed to low concentrations of a putative alarm cue do not show an overt antipredator response but do increase their vigilance toward other sensory cues involved in risk assessment (G. Brown et al. 2004). Due to the time and energy constraints associated with living in high-risk environments, we expect there to be population differences in the threshold levels of predator-related cues that initiate an overt antipredator response. Specifically, we expect that higher levels of risk-related cues will be required to stimulate antipredator behavior in fish from high-predation populations than in those from low-predation ones (but see Brown et al. 2009) because there are likely to be higher levels of background predator-related cues in high-predation environments. However, threshold responses may also depend on variability in the level of risk-related cues; in line with the risk allocation hypothesis (see above), prey are expected to exhibit stronger responses when cues are unpredictable and weaker responses to cues that are constantly present in the environment (Ferrari et al. 2008). Given that poeciliid populations are often exposed to varying levels of predation risk, this hypothesis could be tested relatively easily.

An extension of the ideas presented above is the prediction that prey from high- and low-risk populations should show differential stress responses to risk-related cues. We predict that prey living in high-risk environments will be better adapted for coping with stress; thus, higher levels of stress-inducing stimuli will be required to induce a stress response in fish from high-risk populations than in fish from low-risk ones. Indeed, it appears that fish from high-predation pressure environments are better able to cope with stress induced by constant harassment by predators. This is evidenced by their reduced opercula beat rates when exposed to mild stresses, suggesting that both the physiology and the psychological response of the fish have altered in some fashion via natural selection or ontogenetic plasticity (Brown et al. 2005a). Ontogenetic plasticity, however, has received very little attention in this context and would be a rewarding avenue for future research.

Laboratory-reared fish from high- and low-predation areas also differ in their response to a mild stressor in a fashion reminiscent of their wild-caught parents, suggesting that the stress response has a heritable component (fig. 16.2). Interestingly, lab-reared fish that showed a small change in opercula beat rate over the 15-minute experimental period had higher levels of blushing (sequestration of blood) in the nasal cavity. However, this relationship was significant only in fish reared from high-predation parents and not from low-predation parents (fig. 16.3). This suggests that the fish sequester blood in this region rather than increasing their opercula beat rate when under stress. It is likely that reduced opercula movement lowers the probability of detection by predators when the fish choose a cryptic antipredator response rather than schooling (Brown et al. 2005a).

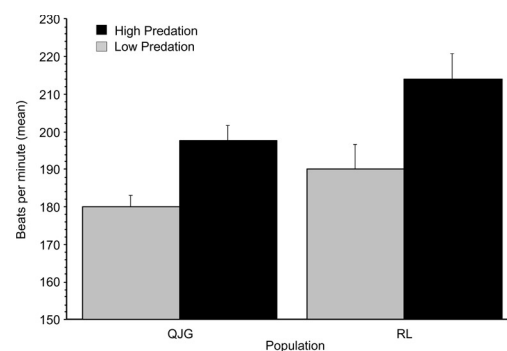


Figure 16.2 Mean (\pm SE) opercula beat rate for two populations (QJG = Quebrada Juan Grande, RL = Río Limbo) of lab-reared *Brachyrhaphis episcopi* from high- and low-predation areas. (Predation effect ANOVA: $F_{1,30} = 11.814$, $P = 0.002$.) C. Brown, unpublished data.

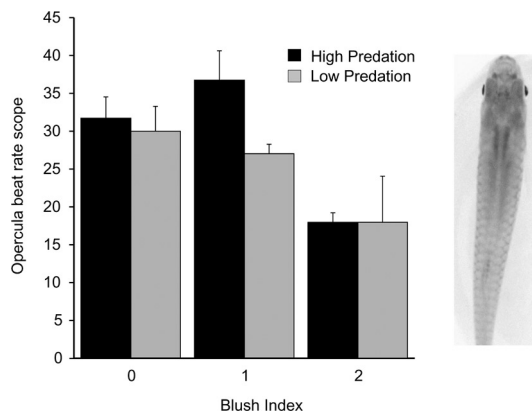


Figure 16.3 Change in opercula beat rate (scope: max. – min. opercula beat rate) over a 15-minute stress trial for lab-reared fish from high- and low-predation areas against nasal blush index. Lab-reared fish had a higher rate of blushing in the nasal cavity ($F_{2,31} = 5.258, P = 0.011$), but this relationship was significant only in fish reared from high-predation parents ($F_{2,12} = 8.528, P = 0.005$) and not from low-predation parents ($F_{2,16} = 1.184, P = 0.331$). C. Brown, unpublished data.

16.3.2 How to respond? Predator-specific defenses and threat sensitivity

Although it seems intuitive that prey should tailor their responses toward particular types of threat, this can be costly if a prey's response to one predator increases its risk to another (Sih et al. 1998). Again, from the cognitive perspective, we anticipate that greater cognitive skills are required to recognize and respond differentially to different types of predator threat, as multiple risk factors represent a greater level of complexity. It may not be the diversity of predators per se that results in selection on prey for increased cognitive ability but, rather, the variation in attack strategies that the multipredator environment presents. In mammals, for example, the different attack modes displayed by avian and ground predators (which require incompatible prey escape responses) are thought to have facilitated the evolution of complex predator-specific alarm calls in vervet monkeys and ground squirrels (Macedonia & Evans 1993).

In fishes, avian predators (e.g., herons, kingfishers, cormorants) present a different type of threat than piscivorous predators do because birds approach from above and perpendicular to the fishes' plane of movement, while fish predators tend to attack either from the same level or below (Katzir & Camhi 1993). Avoiding attacks from these two classes of predators involves strategies that are diametrically opposed. In Panamanian streams, for example, *B. episcopi* is frequently found in the shallows, thereby avoiding predation by large in-stream piscivores (C. Brown, personal observation). This behavior, however, makes them highly vulnerable to avian predators such as the tiger heron (*Tigrisoma lineatum*). Presumably their very presence in shal-

low areas suggests that the in-stream predators represent a greater threat than that posed by avian predators. Thus, the different attack modes utilized by piscivorous and avian predators present an ideal opportunity to examine the relationship between predator attack strategies and prey cognitive complexity in fishes.

Templeton and Shriner (2004) compared the response of guppies from a high- and a low-risk population toward a live piscivorous predator (resembling the pike cichlid) and an aerial predation threat (a three-dimensional model of a green kingfisher). The populations differed in their behavioral responses depending on the type of threat; the aerial-predator stimulus caused high-predation fish to seek cover, whereas low-predation fish tended to freeze. In contrast, the aquatic predator caused high-predation fish to spend more time performing inspection behavior than low-predation fish (Templeton & Shriner 2004). Maintaining vigilance toward aerial threats while also being alert to piscivorous predators is likely to present a significant challenge. Lateralization of the brain hemispheres may be an important mechanism by which prey in high-risk environments can remain vigilant to different types of threat (see section 16.4.3). Given the potential complexity resulting from multiple threat sources, it may be that fish develop a generalized antipredator response that minimizes the overall threat (a kind of predator-community response) rather than specific responses to each predatory species. However, this latter approach may well place them in danger of secondary attacks from other predators.

Prey that have encountered predators or risk-related cues must also decide on the strength of their antipredator response. This is often termed "risk sensitivity" and refers to the observation that prey individuals display different levels of antipredator behavior according to the strength or severity of the threat posed (Helfman 1989). For example, guppies are more likely to avoid hungry predators than satiated ones (Licht 1989). Smith and Belk (2001) examined the theory of threat sensitivity in detail by presenting western mosquitofish with predators (live green sunfish, *Lepomis cyanellus*) that varied in size (large or small), diet (fed mosquitofish or chironomid larvae), and hunger level (hungry or satiated). Shoals maintained a greater distance from mosquitofish-fed predators than chironomid-fed predators and were more likely to occupy the upper half of the aquarium in the presence of hungry predators than satiated ones (Smith & Belk 2001). Inspection behavior was also affected by diet, with mosquitofish maintaining a greater distance from hungry predators than satiated ones. Mosquitofish and other poeciliids are therefore capable of quite complex behavioral decisions depending on the information contained in different types of sensory cue.

16.3.3 Individual variation in responses to risk

Behavioral ecologists have long been interested in explaining population-level differences in the behavior of fishes with reference to the environment that they occupy. More recently, however, it has become apparent that prey often display individual-specific responses to predation. Sex- and age-specific responses to predation risk are perhaps among the best studied of these. For example, female poeciliids must maximize their reproductive fitness via longevity, and they display better-developed antipredator responses than males (Magurran & Seghers 1994c; Magurran & Garcia 2000). In contrast, males are often blasé about the presence of predators and will continue to court females irrespective of the level of threat. Furthermore, young and old (small and big fish) may respond differently to a given predator based on the relative threat that it poses (Werner & Hall 1988; Persson et al. 1996; Magnhagen & Borcharding 2008).

These sources of individual variation in responses to risk are often overlooked because many studies take a single snapshot in time and individuals are only observed once and often in a group context. Making multiple observations of the same individual, however, may reveal individual responses that are stable or consistent over a variety of contexts and that are suggestive of personality traits. Personality traits typically transcend demographic variability and are relatively stable over time. Use of the word “personality” to describe consistent individual differences in behavior has been avoided in the fish literature largely due to fear of anthropomorphism. In its place we are often confronted with alternative terminology such as “coping style” (Clement et al. 2005), “temperament” (Shaklee 1963), or “behavioral profile” (Magellan & Magurran 2007a). Despite a general reluctance to accept that fish have personalities, there is a growing body of literature that suggests that not only are they pervasive (Wilson 1998; Bell 2005; Dingemanse et al. 2007), but personality traits have fitness consequences (Smith & Blumstein 2008) and may therefore be subject to natural selection (Gottlieb 2002; Brown et al. 2007a; see also section 16.3.3.3).

16.3.3.1 The shy-bold continuum. In fishes, two personality traits in particular—boldness and aggression—have been the subject of a number of studies. From a poeciliid perspective much of the attention has focused on the former. The shy-bold continuum refers to the likelihood that an individual is prone to risk taking (Wilson et al. 1993). It is immediately evident, therefore, that there is likely to be a link between predation pressure and the evolution and development of personality traits. Budaev (1997) investigated the social tendencies and exploratory behavior of 29 gup-

pies and found that, in the broader context, individual guppies could be placed on two personality dimensions that he defined as the “approach” and “fear avoidance” continua. The contexts in which the fish were tested included exploration of a novel environment, predator inspection, and schooling. Each of these contexts represents a situation where the subject has to make a decision between opposing tendencies (i.e., a trade-off scenario).

Brown et al. (2005b) utilized replicate high- and low-predation streams in Panama to determine how predation pressure influences an individual’s position on the shy-bold continuum. Other studies with this species have concentrated on exploration of a novel environment (open-field paradigm) and the time taken to emerge from cover (C. Brown et al. 2004; Brown et al. 2005b). Later studies revealed correlations between the tendency to explore a novel environment and the tendency to leave a shoal to investigate a novel object (Brown et al. 2007a). Once again, all contexts rely on the fish making relatively dichotomous decisions in a mildly stressful situation. In addition to variation that could be explained by demographic variables (size and sex), fish from high-predation areas tended to be bolder than those from low-predation areas. It seems likely that the constant threat of predators in the environment favors individuals that are more likely to accept a higher degree of risk for a given payoff. In a high-predation context, shy fish would spend a significant proportion of their lives hiding from predators and would likely have reduced growth rates and lower fecundity as a result of missed foraging opportunities. In contrast, bold fish would emerge from cover sooner to gain access to resources. Indeed, there is expected to be a strong link between growth rates, fecundity, and personality, as fast-growing individuals must behave in a risky manner to acquire resources and meet their high metabolic demands (Stamps 2007; Biro & Stamps 2008).

16.3.3.2 The development of personality. Personality traits in humans are known to be influenced both by genetics (i.e., they are heritable) and by individual experience (McGue & Bouchard 1998). Indeed, Budaev (1997) suggests that the term “temperament” is best reserved for the heritable components of personality, which are then shaped by experience to form personality. The fact that personality traits are heritable paves the way for identifying the genes responsible. Quantitative trait loci analysis in zebrafish (*Danio rerio*, Cyprinidae) suggests that regions on chromosome 9 and 16 are significantly associated with boldness, showing signs of dominance and additive effects, respectively (Wright et al. 2006). A similar approach could be adopted in poeciliids when the guppy genome is sequenced. Brown et al. (2007a) investigated the relative contributions of the genetic and experiential components of personality traits by collecting

poeciliids (*B. episcopi*) from high- and low-predation populations, breeding them, and rearing their offspring in the lab under two conditions. Half of the lab-reared offspring were left undisturbed (simulating a low-predation experience) while the other half were chased with a net every day for two weeks (simulating a high-predation experience). Prior to initiating the treatment, fish from each population showed boldness scores that were consistent with their wild-caught parents. However, simulated predator exposure increased boldness scores irrespective of the source population, demonstrating the manner in which predation experience during ontogeny shapes personality traits.

16.3.3.3 Personality and fitness. Such population (and individual) variation in response to predation pressure suggests that there are likely to be fitness consequences associated with displaying various personality traits in a given context (Stamps 2007; Biro & Stamps 2008; Smith & Blumstein 2008). The tendency to explore, for example, is likely to open up new resources to bold individuals and thus potentially expose them to novel predators and pathogens (Wilson et al. 1993; Fraser et al. 2001). Recent work with poeciliids shows that the expression of bold behavior has direct influences on fitness measures. In *B. episcopi* there is a strong correlation between a fish's position on the shy-bold continuum and its relative body mass (Brown et al. 2007a). Bold fish tend to be heavier than shy fish, and the rate at which they put on mass per unit length is also greater. Boldness may also enhance male reproductive success via female mate choice. During a simulated predator encounter, female guppies preferred to mate with males that approached a model predator over males that did not (Godin & Dugatkin 1996). This preference was expressed irrespective of male coloration (which is an important cue in mate choice and is correlated with boldness) and body length (Godin & Dugatkin 1996).

16.4 Relating predation risk to cognitive ability

16.4.1 Predators as a form of “environmental complexity”

The presence of predators in the environment may be thought of in terms of habitat complexity. Predators are just another (although very important) variable that prey must keep track of in space and time. Research on rodents has revealed that exposure to an enriched environment stimulates neuronal development and has an important influence on cognitive capacity (Park et al. 1992; Gomez-Pinilla et al. 1998). Similar observations have been made in invertebrates (Lomassese et al. 2000). Environmental

enrichment is commonly employed by zoos to reduce stereotypy and to encourage the expression of more “natural” behavior in captive animals. Such manipulations are rare in fishes and totally absent in poeciliids, despite the fact that the brains of fishes are more plastic than those of most vertebrates (Zunpanc 2006), making them an ideal model system. In general, the brains of fishes are more highly developed if they have been reared in complex environments (Marchetti & Nevitt 2003). The optic tectum and the telencephalon are most profoundly affected, both being key regions in the analysis of visual and spatial information (Salas et al. 1996; Rodriguez et al. 2006). Moreover, when exposed to enriched environments, cognitive function is also enhanced (Brown et al. 2003). No such manipulative studies have been conducted on poeciliids to date; however, some progress has been made by examining the behavior of fish captured in high- and low-predation environments (Brown & Braithwaite 2005).

16.4.2 Does predation pressure influence brain development?

Brown & Braithwaite (2005) addressed the question of whether predation pressure affects brain development using *B. episcopi*, which inhabits a number of streams each containing high- and low-predation environments. The fish were exposed to a radial maze in which they had to locate a hidden foraging patch. Contrary to expectation, fish from high-predation regions took significantly longer to learn the location of the foraging patch than fish from low-predation areas. When the video footage was analyzed more carefully, it was evident that the manner in which the fish navigated the maze varied tremendously. High-predation fish had a very strong preference to move in a counterclockwise direction, irrespective of their location relative to the rewarded arm of the maze. In comparison, the low-predation fish gradually altered their behavior and began to head directly to the rewarded arm. Despite these unanticipated results, further experimentation examining the cognitive capacity of high- and low-predation fishes is likely to be fruitful. For example, rainbowfish (*Melanotaenia duboulayi*) from high-predation areas are better at solving spatial tasks than those from low-predation areas (Brown & Warburton 1999).

Burns and Rodd (2008) examined differences in the spatial memory of guppies collected from high- and low-predation populations and compared these differences with brain size. Although there were no differences among populations in the time taken to complete the spatial-memory task or the number of errors made, high-predation fish took significantly longer than low-predation fish when deciding which maze chamber to enter. There were no differences in brain morphology between high- and low-predation

fish, but within populations, fish that made decisions most rapidly (i.e., “hasty” individuals) had smaller telencephalons (Burns & Rodd 2008). Note that male guppies were used for the spatial-memory task in this experiment, and as males are more likely to take risks than females (see section 16.3.3), population differences in memory and brain anatomy are least likely to arise in males. Future work should examine the brains of females, as females are known to show strong antipredator behavior. Although further research is required to examine the link between predation risk, cognitive performance, and underlying brain structure, it is important to note that variation in predation risk is correlated with other important ecological factors (e.g., light intensity, food availability, water temperature; Endler 1995) that are also likely to affect cognitive processes and brain morphology. Thus, a controlled, manipulative experimental approach will be necessary.

16.4.3 Does predation pressure influence cerebral lateralization?

Cerebral lateralization refers to the selective partitioning of cognitive function to the left or right hemispheres of the brain. Cerebral lateralization is often overtly expressed in fish during navigation in the form of turn preferences (see Bisazza, chapter 15, for more on lateralization). Such biases are common in the animal world and reflect the underlying interhemispherical organization of the brain in terms of both sensory processing and motor control. Over the last 10 years studies on fishes, and poeciliids in particular, have greatly contributed to our understanding of cerebral lateralization in vertebrates, and fishes are considered ideal model taxa, especially for distinguishing between lateralization at the population and individual levels. On a species, population, and individual level, fishes show remarkable variation in the strength and direction of lateralization that has yet to be revealed in any other taxa. Even within the family Poeciliidae intriguing variation exists (Bisazza et al. 1997b). In addition to turn biases, cerebral lateralization is also evidenced by eye preferences while viewing particular objects or scenes. For example, while the majority of species view predators with their right eye, some species prefer their left eye or show no preference at all. This variation is even greater when fish belonging to different families are compared (Bisazza et al. 2000a).

For some years biologists have struggled to explain why some species or populations show strongly lateralized behaviors while others do not. One likely explanation is that such variation is linked to predation pressure and the propensity to rely on group-oriented antipredator responses (Brown 2005). The escape behavior of group-living species relies heavily on synchronized responses, the success

of which is reliant on the degree of coordination between group members (chorus line effect, Potts 1984; oddity effect, Landeau & Terborgh 1986; conformity effect, Brown & Laland 2002). Theoretically, coordination would be increased if individuals within a group displayed similar lateralized phenotypes. Thus, group antipredator responses provide examples of traits under positive frequency-dependent selection because the fitness advantages associated with conforming to the behavior of other individuals *increase* with increasing frequency of the expression of that behavior within the population (Brown 2005). Thus, variation in group antipredator behavior may be one of the major selective forces favoring the skewed distribution of lateralized phenotypes observed in a wide variety of animals.

Most studies have examined the potential benefits of lateralization by examining the behavior of individuals in isolation, and there have been few investigations of the fitness consequences of lateralization in the group context. In group-living species, it is apparent that the dual processing associated with lateralization provides a great advantage since each animal can concentrate on its group mates and predators simultaneously (C. Brown et al. 2004; Brown 2005, 2007a). It is conceivable that animals in a group that prefer to observe predators with their right eye would preferentially take up a position on that side of the group, whereas those that use the left eye would be on the opposite side. With the correct ratio of left- and right-eyed individuals in the group, coordinated antipredator responses could be optimized. It would be very interesting to examine whether there is an optimum ratio of left-/right-eyed individuals that confers enhanced coordination and vigilance to the group. Although it is known that fish do take up preferred positions within shoals based on hunger level and mortality risk (Krause 1993a; see also Krause et al., chapter 13), research suggests that shoal positions are also based on laterality (Bisazza & Dadda 2005). Schools of the poeciliid *Girardinus falcatus* comprising strongly lateralized fish are more cohesive than those comprising nonlateralized individuals, and strongly lateralized fish tend to assume optimal (central) positions in the shoal (Bisazza & Dadda 2005).

Heuts (1999) hypothesized that differential exposure to predators owing to the occupation of varying habitats (benthic vs. limnetic) might explain interspecific variation in lateralized escape responses in fish. Benthic species that rely on hiding to escape predators do not require coordinated responses at the population level, whereas those in open waters do. Likewise, Bisazza et al. (2000a) explained interspecific variation in eye use by examining species-specific shoaling habits. Brown et al. (2004, 2007b) tested this hypothesis directly by examining the lateralized responses of a single poeciliid species collected from regions of high and

low predation pressure and found substantial differences in lateralized behavior. As predicted, fish from high-predation areas are more likely to be strongly lateralized in comparison to those from low-predation environments. Lateralized behavior is not only heritable (Bisazza et al. 2000a; Brown et al. 2007b) but can be induced by simulated predation attacks during ontogeny (Brown et al. 2007b). Although this has been observed in only a single species, it provides the first solid evidence that predation pressure plays an important role in the evolution of lateralization in vertebrates.

16.5 Summary and future directions

Our review has revealed that living under the threat of predation has allowed poeciliids, like many other prey fishes, to evolve sophisticated cognitive mechanisms for information gathering and processing. Poeciliid fishes use a variety of sensory modalities to detect the presence of cues that are associated with changes in predation risk, but it is noticeable that our understanding of chemical cues for risk assessment in this group (e.g., alarm cues and predator odors) lags behind our understanding of other (i.e., visual) sensory cues. The extensive variation in predation risk observed among many populations of poeciliids presents an ideal opportunity to compare population differences in the sensitivity and responsiveness of prey to different levels of risk-related cues. It would also be interesting to further examine population differences in prey stress responses in order to reveal how predation risk can shape the physiological and psychological mechanisms that allow animals to deal with stress.

Poeciliids occupy a huge diversity of habitats and thus present an ideal opportunity to examine the impact of environmental (and other) constraints on sensory perception and brain morphology. The structure of fish brains is highly variable among species and tends to be correlated with factors such as habitat type and social complexity, though empirical studies are lacking (Kotrschal et al. 1998). The next step is to conduct manipulative studies to examine the effect of these (and other factors) on brain complexity and development. For example, fish from different populations could be reared in different environments and their corresponding morphological, physiological, and behavioral responses assessed. This would allow a rigorous investigation of the impact of predation risk on brain development while controlling for other ecological variables. For example, it would be interesting to compare cognitive plasticity (i.e., brain development and behavior) among fish originating from high- and low-predation risk environments and to examine the specific stimuli that are required to induce ontogenetic change.

It is evident from our review of the literature that poeciliids have contributed greatly to our understanding of the function and significance of cerebral lateralization in vertebrates, although there are many avenues for future research. In particular, the link between lateralization and the ability of prey to perform several tasks simultaneously (i.e., multitasking) seems to be an exciting area for future investigation. For example, exactly how does cerebral lateralization allow prey to maintain social contact with group members while remaining vigilant to predation threats, and are there constraints on the types of cognitive activity that can be performed in the separate hemispheres of the brain? What are the disadvantages of using the nonpreferred eye for a particular task (e.g., predator inspection)? Does cerebral lateralization bear some form of cost? If we return to the concept of a cognitive arms race between predators and their prey, then it is important to consider how the attack strategies of predators are shaped by cognitive processes such as cerebral lateralization. For example, do predators display lateralized attack strategies, and how successful are they at counteracting the lateralized escape responses of their prey? Such a line of thought leads to the possibility that predator and prey attacks and defense may fluctuate temporally in a frequency-dependent fashion (Hori 1993).

Viewing predator-prey relationships from a cognitive perspective allows us to make a number of predictions about the cognitive constraints on predators and prey that are imposed by the high energetic cost of maintaining expensive brain tissue. While in high-predation areas it may be worthwhile to increase expenditure on cerebral tissues owing to the potential gains to be made with respect to moving safely through the deadly predatory maze, no such investment should be made in low-predation areas. Furthermore, if prey develop generalized (predator community) responses due to environmental or cognitive constraints, one would predict that although it minimizes risk on a global scale, such a strategy increases the relative vulnerability of prey to each predatory species. Multiple predators have an important impact on community-level dynamics and may act to either enhance (through conflicting prey responses to multiple predators) or reduce (e.g., through predator-predator interactions) the level of predation risk experienced by prey (the “multipredator hypothesis,” Sih et al. 1998). Understanding how multiple predators (and their foraging modes) influence the defense strategies and cognitive investment of prey is likely to yield significant insights into the factors (and constraints) driving the evolution of cognition. We feel that these intriguing ideas—relating cognitive investment to individual behavioral strategies—represent an exciting new research direction in poeciliid predator-prey ecology.

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