

Multiple selection pressures influence Trinidadian guppy (*Poecilia reticulata*) antipredator behavior

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Animals alter their behavior to avoid a variety of different types of predators. Trinidadian guppies (*Poecilia reticulata*) have been an important system for examining the evolution of antipredator behavior because geographically isolated populations experience different amounts of aquatic predation. Although the influence of aquatic predators has been well documented, selective pressures from other types of predators are less well understood. We examined the response of wild-caught individuals from upstream and downstream populations to an aquatic predator and a simulated aerial predator. As previously documented, fish from the downstream population responded more strongly to the aquatic predator than did fish from the upstream population, inspecting for longer periods of time. Guppies also exhibited a strong behavioral response to the potential aerial predator. Although both populations displayed a similar magnitude of response, they differed in the specific behaviors used. Upstream fish tended to freeze on the tank bottom, whereas downstream fish tended to hide under shelter. Field observations suggest that these strategies are related to habitat features specific to each site. The behaviors used against aerial predators differed substantially from the behaviors used against aquatic predators, suggesting that different types of predators exert conflicting selection pressures. This research demonstrates the importance of considering multiple selection pressures acting on an organism when trying to understand the evolutionary history of behavioral and morphological traits. *Key words*: aerial predators, aquatic predators, fish, guppy. [*Behav Ecol* 15:673–678 (2004)]

Predation is an important selection pressure that can affect prey individuals, populations, and communities. Accordingly, prey species have evolved means for avoiding encounters with predators or surviving attacks. Morphological adaptations such as spines (see Spitz, 1992), aposematic signals (see Brower and Calvert 1984), or cryptic coloration (see Grant 1999) are commonly used as defenses. Behavioral modifications can also be effective defenses against predators.

Nearly all organisms are preyed upon by many different species of predators. However, most studies investigating antipredator behavior have only examined the responses of prey to one type of predator (Sih et al., 1998). In a multipredator environment, prey species can use general antipredator behaviors, such as temporal shifts in activity levels (Krupa and Sih, 1998), increased vigilance (Lima, 1992), or non-specific alarm calls (Marler, 1955). If the predators vary in hunting tactics or locations, prey should develop specific behavioral responses for each type of predator (see Cheney and Seyfarth, 1990).

There are often costs to antipredator behaviors (Lima, 1998). These costs may be even greater when predator-specific behaviors are used in a multipredator environment (Sih et al., 1998). For instance, using a specialized behavior to avoid one type of predator may make the prey animal more vulnerable to another type of predator. Therefore, specific behaviors should be favored only when predation pressures are strong. Different populations of a species may experience varying intensities or types of predation, leading to differences in their antipredator behavior. Thus, examining the behavior of

different populations can provide important insights into their predation history.

The guppy (*Poecilia reticulata*) has been widely used to examine behavioral and evolutionary questions relating to predation because this species exhibits great polymorphism among geographically isolated populations. In the Northern Range Mountains of Trinidad, West Indies, guppies are found in most streams, and can be grouped into distinct population types by their stream location. Guppies found in small tributaries vary in morphology, life history, and behavior from those found closer to the river mouth (Breden et al., 1987; Endler, 1980; Haskins et al., 1961; Liley and Seghers, 1975). For example, upstream fish tend to be larger and more brightly colored than downstream fish (Endler, 1978; Houde and Endler, 1990; Rodd and Reznick, 1997) and forage individually, whereas downstream fish often form large schools (Magurran and Seghers, 1994).

Because large fish are incapable of colonizing areas above waterfalls, upstream guppies experience few predatory fish (Hart's rivulus, *Rivulus hartii*, and freshwater prawns, *Macrobrachium* spp.), whereas downstream guppies frequently encounter numerous predators (e.g., *Hoplias*, *Crenichichla*, *Chichlasoma*, and *Airus*; Liley and Seghers, 1975).

The substantial selective pressure that aquatic predators have exerted on the evolution of *P. reticulata* is well documented (Endler, 1987; Fraser and Gilliam, 1987; Reznick and Endler, 1982; Reznick et al., 1990; Rodd and Reznick, 1997; Seghers, 1974b), leading many researchers to conclude that variation seen in guppy morphology and behavior result directly from the degree of aquatic predation each population has experienced.

Other types of predators also prey on guppies and may have considerable impact on guppy populations and behavior. In Trinidad, for example, several potential aerial predators feed on guppies, yet the degree of aerial predation experienced by guppies is unknown. The fishing bat (*Noctilio leporinus*) eats many small fish (Bloedel, 1955; Brooke 1994), including guppies (Worth, 1967). In addition, a number of avian predators,

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including green kingfishers (*Chloroceryle americana*), American pygmy kingfishers (*C. aenea*), belted kingfishers (*Ceryle alcyon*), great kiskadees (*Pitangus sulphuratus*), and several species of fish-eating herons (Aves: Ardeidae), are abundant in the Northern Range (Liley and Seghers, 1975; French, 1991), and feed on small fish such as guppies (Remsen, 1991; Miranda and Collazo, 1997; Ramsawak G and Rooks C, personal communication). The effect of these aerial predators on guppy evolution is virtually unstudied.

In the present study, we investigate the behavioral response to an aquatic and potential aerial predator of guppies originating from two different populations. Our aim was to determine the suite of behavioral responses that guppies use to avoid aerial predators and to understand the relationship between these behaviors and those used against aquatic predators. In combination, these data allow us to better understand the function of behavioral plasticity for coping with a multi-predator environment.

METHODS

Collection and maintenance

We used adult guppies collected from the Yarra River and a tributary of the Marianne River (Marianne Tributary) in the Northern Range Mountains of Trinidad, from 18–28 May 1998. The Yarra River is a large slow-moving stream that empties into the Caribbean Sea and contains many large piscivorous predators. The Marianne Tributary is a small mountain stream with fast-moving water and many riffles; it contains few aquatic predators. Guppies from these streams were housed in one of four population-specific 28-l holding tanks, in a laboratory at Denison University in Granville, Ohio, USA. The fish were maintained at approximately 23°C on a 12-h light/12-h dark schedule, and fed commercial flake food and frozen brine shrimp (*Artemia salina*).

Aerial predator trials

General apparatus

An experimental tank was constructed from a rectangular 19-l aquarium. We divided it into two equal wells with clear plastic, and used aquarium sealant to prevent water flow between the wells. We covered three outer walls with opaque paper to prevent outside visual stimuli. The fourth side provided no visual stimulus except for a fixed-position video camera. The aquarium had an opaque partition so that fish could not see between the two wells of the tank. The top of the tank was used to provide the simulated aerial predator stimulus and was unobstructed. No substrate was added to the tank; however, each well contained an area of “cover” that consisted of a 6.5 × 6.5-cm opaque tile mounted on three 3-cm glass legs that was placed in a corner. We filled both wells of the test tank to 18 cm with fresh water at the beginning of each day of trials. To minimize the effects of social interactions on the guppies’ behavior, we isolated each individual in a separate 4-l tank for 24 h before the testing period.

For the aerial predator, we used a realistic, life-size, three-dimensional model of a flying green kingfisher that was painted to accurately resemble the coloration of this species. The model was attached to a wire so that it could be moved freely, passing approximately 10 cm above the center of each well.

Experimental procedure

We conducted all trials between 3 November and 17 November 1998, during daylight hours in which guppies are normally active (from 1000–1600 h). To reduce the effects of individual variation, the same guppies were used for both the

aerial and aquatic predator trials. A paired experimental design was used so that one fish from the Yarra River ($N = 21$) and one fish from the Marianne Tributary ($N = 21$) experienced exactly the same stimulus. We randomly placed a fish from each population into one of the two wells to avoid any biases in stimulus presentation. Both males and females were used, although mixed-sex trials were avoided. Before the start of a trial, we allowed the guppies to acclimate to the new tank for 10 min. This time period appeared to be adequate for the fish to resume normal behavior (swimming) in all cases. After the acclimation period, we videotaped a 3-min pretrial period before presenting any stimulus.

After the pretrial, we used a wooden dowel to move the model bird along the wire at a constant velocity (approximately 20 cm/s). The model was above each well for about 1 s, and was concealed from the fish’s view before and after the stimulus. We recorded the behaviors of both guppies for 3 min after the simulated aerial predator encounter.

One observer measured the behavioral response of the fish in each well concurrently from video-tape by using Apple Newtons with Ethoscribe software (Tima Scientific). To account for any differences in the two observers, each coded data on a single well for all trials.

Aquatic predator trials

General apparatus

We constructed an experimental tank similar to that used in the aerial predator trials. Unlike the tank described above, this aquarium had a clear partition so that fish could see between the two wells of the tank, and only one of the wells contained a tile for cover.

Experimental procedure

We conducted the aquatic predator trials between 8 December 1998 and 7 February 1999 during daylight hours in which guppies are normally active (from 1000–1600 h). Live small-mouth bass (*Micropterus dolomieu*) were used as the aquatic predator because they resemble native cichlid guppy predators (especially *Crenicichla*). We used two different bass collected from Ebaugh Pond, Denison University (Licking County, Ohio, USA), to help prevent habituation. The bass were not fed (brine shrimp) for 1 day before each set of trials to encourage their interest in the guppies. We randomly selected one guppy from the Yarra River population ($N = 14$) or the Marianne Tributary population ($N = 15$) for each trial so that fish from each population were equally exposed to both of the aquatic predators. We used approximately the same number of males and females for both populations.

Each guppy was allowed to acclimate to the test tank for 10 min before the trial began. This proved to be enough time for the guppy to resume normal behavior (swimming) in all but one case; this individual was excluded from the data analysis. After the acclimation period, we recorded a 3-min pretrial before providing any stimulus. These data allowed us to compare normal behaviors between the two populations and establish a baseline to compare with the predator response. After the pretrial period, we slowly introduced a smallmouth bass into the second well and began the poststimulus period. The bass remained visible to the guppy for the full 3-min trial. All guppy behaviors were video recorded during both the pre- and postfish periods.

Trial analysis

Behaviors were classified as “swim” (normal swimming), “freeze” (remaining completely motionless, usually on the bottom), “hide” (moving under cover and remaining motionless),

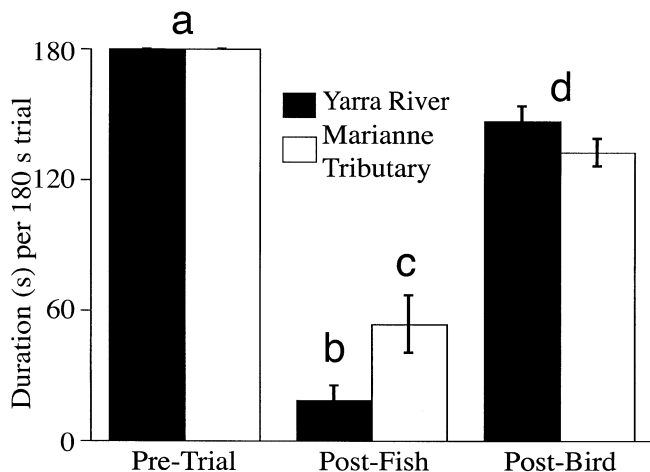


Figure 1
The mean duration (\pm SE) guppies from the Yarra River (high predation) and Marianne Tributary (low predation) spent swimming during the 3-min period before and after the predator was introduced. The amount of swimming was identical during the pretrial period for both sets of trials so only one set of pretrial data are shown. For the aquatic predator trials, $N = 13$ (Yarra) and $N = 15$ (Marianne). For the aerial predator trials, $N = 21$ for both populations. Each letter indicates a statistically different class ($p < .01$).

“drop” (a fast vertical movement to the bottom of the tank), “dash” (brief periods of uncharacteristically rapid swimming), “inspect” (closely approaching and directly facing the predator), “drift” (not actively swimming, but moving slightly), or “other” (anything not otherwise included). Ethoscribe was used to compute the duration and frequency of each behavior. When behaviors occurred frequently (used by more than half of the individuals), we compared the duration of time individuals spent using a behavior; when a behavior was infrequently used, the number of individuals using a given behavior was compared instead.

We also measured the vertical location in the tank for each guppy during the pre- and postpredator periods. Locations were classified as “high” (above 10 cm), “mid” (5–10 cm), and “low” (below 5 cm). A fourth category, “cover,” was used to denote that the guppy was underneath the tile, regardless of its behavior. We calculated the overall duration of time spent in each location and compared the proportion of time each population spent in each location before and after the predatory stimulus. To account for any initial population differences in location use, we subtracted the pre- from the poststimulus location duration and used these differences to compare population responses to the predators.

All statistics were two-tailed tests. Parametric tests were used when the data met the appropriate assumptions; nonparametric equivalents were otherwise substituted (Zar, 1984). To compare swimming behavior in the pre- and postpredator periods, we used the Wilcoxon signed-rank test (WSR). Population comparisons of behaviors frequently used in the postpredator periods were done with one-way ANOVA or Mann-Whitney U (MWU) tests; infrequently used behaviors were compared by using Fisher’s Exact test (FE). One-way ANOVAs were used for each set of location data. Because we performed several different tests using the same data, some caution should be used in interpreting the results. In this article, we treat all p values less than 0.01 to be statistically significant but also report the results of all marginally significant tests for each reader to consider.

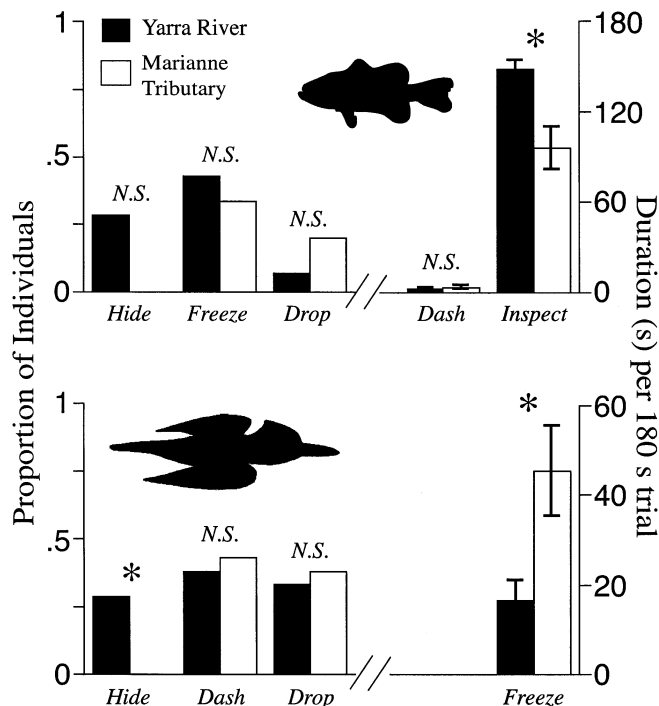


Figure 2
The proportion of individuals or mean duration (\pm SE) of nonswimming, antipredator behaviors used by guppies from the Yarra River and Marianne Tributary, after the introduction of the smallmouth bass or kingfisher model presentation. For the aquatic predator trials, $N = 13$ (Yarra) and $N = 15$ (Marianne). For the aerial predator trials, $N = 21$ for both populations. *N.S.* indicates p values greater than .01; p values less than .01 are indicated by an asterisk.

RESULTS

Aerial predator trials

Behavior

After the aerial predator stimulus, guppies from both populations significantly decreased the amount of swimming (WSR, Yarra: $N = 21$, $Z = -4.11$, $p < .01$; Marianne: $N = 21$, $Z = -3.92$, $p < .01$) (Figure 1). The two populations did not differ in the duration of swimming (ANOVA, $N = 42$, $F = 1.34$, $p = .25$), after the predator introduction.

Although the aerial predator stimulus affected fish from the Yarra River (downstream) and Marianne Tributary (upstream) to the same degree, the populations differed in the specific antipredator behaviors that they used (Figure 2). Guppies from the Yarra River frequently hid when the model bird was presented, whereas fish from the Marianne Tributary never used this behavior (FE, $N = 42$, $p < .01$). Instead, Marianne guppies froze on the bottom of the aquarium significantly longer than Yarra guppies (MWU, $N = 42$, $U = 129$, $p < .01$).

Fish from both populations sometimes dropped or dashed after the stimulus, but there were no population differences in the frequency of these events (FE, $p = 1.0$ for both populations). The behaviors of drift, inspect, and other were not used by fish from either population.

Location

Both populations tended to spend more time in the lower vertical zones of the tank after the aerial predator stimulus. Yarra fish spent less time in the highest zone and more time under cover after the aerial stimulus was presented, although these changes were not statistically significant (ANOVA, $N = 42$, high: $p = .10$; cover: $p = .01$). Marianne fish decreased the

amount of time spent in the middle zone and increased the amount of time spent in the low zone after the aerial stimulus was presented (ANOVA, $N = 42$ for each). The two populations differed in their change of location in response to the aerial predator; Marianne fish decreased their use of the middle zone and increased their use of the low zone more than Yarra fish did after the predator stimulus (ANOVA, $N = 42$ for each).

Aquatic predator trials

Behavior

Guppies from both the Yarra River (downstream) and Marianne Tributary (upstream) significantly decreased the amount of time they spent swimming after the bass was introduced (WSR, Yarra: $N = 14$, $Z = -3.29$, $p < .01$; Marianne: $N = 15$, $Z = -3.41$, $p < .01$) (Figure 1). Guppies from the Marianne Tributary swam for somewhat more time after the aquatic predator stimulus than did those from the Yarra River (ANOVA, $N = 29$, $F = 5.52$, $p = .03$).

The specific antipredator behaviors differed between the populations (Figure 2). Yarra River fish spent significantly more time inspecting the potential aquatic predator (MWU, $N = 29$, $U = 34.5$, $p < .01$) and hid slightly more often (FE, $N = 29$, $p = .03$) than did guppies from the Marianne Tributary. There were no statistically significant population differences in the freeze or dash behaviors (FE, $p > .3$ for both). Guppies did not use the behaviors of drop or other in these trials.

Location

Neither population changed the proportion of time they spent in any location after the presentation of the smallmouth bass (ANOVA, $p > .4$ for each population at all locations, except Yarra-high [decrease in post]: $p = .05$). The change in location use in response to the potential predator did not differ between the two populations (ANOVA, $p > 0.4$ for all).

DISCUSSION

We found that guppies responded strongly to a simulated aerial predator but used behaviors that were different from responses to an aquatic predator. We confirmed that variation in response to an aquatic predator between populations correlates with predation history and showed that this variation also exists when fish are exposed to novel aquatic or aerial predators. Differences in response to the two types of predator indicate that guppies live in an environment in which multiple predators are present and require different evasive behaviors that are specific to the type of predator. These results suggest that guppies may have a sophisticated level of plasticity in their antipredator behavior.

Aerial predation

In the present study, all guppies reacted strongly to the model kingfisher. After guppies detected the potential aerial threat, they rapidly switched from normal foraging behavior (swimming) to various forms of antipredator behavior. The rapid switch in behavior seen in the laboratory shows that guppies actively observe the environment above them, and that they treat at least some nonaquatic objects as predators. No explicit control stimulus was used in the present study, and it is possible that guppies were reacting to novel overhead objects instead of specifically recognizing predators. However, guppies do not react with these behaviors when they are fed in captivity or have leaves dropped near them in the field (Templeton C, personal observations), suggesting that they are capable of distinguishing among specific overhead objects and only treat certain ones as potential predators.

Population variation

The two populations differed in their specific tactics of avoiding the aerial predator. Fish from the Marianne Tributary usually froze at the bottom of the tank in response to the overhead stimulus. Instead, Yarra River guppies usually hid under cover in response to the model kingfisher. The antipredator behaviors used by guppies from each population appear to be adaptive to the specific habitat features of the two streams. The Yarra River fish were sampled in an area that is covered with aquatic vegetation (approximately 85%) at least part of the year. Hiding under this vegetation likely reduces the risk of detection and capture by aerial predators. In contrast, fish from the Marianne Tributary never hid when the model kingfisher was presented. There is little vegetation at this stream, and therefore, there should be no selective pressure to develop a defense similar to that seen in the Yarra River fish. However, much of the Marianne Tributary flows through shallow riffles, where it is difficult to detect stationary objects. In this environment, freezing on the substrate may be the most advantageous behavior against aerial predators. Thus, it appears that in addition to predator regimes, habitat features also have an important effect on the development of antipredator behaviors.

Seghers (1974a) examined the response of guppies from the Guayamare River and Paria River to nocturnal aerial predators. Fish from both populations responded by freezing, but he found that the populations differed in how long they remained stationary and the depth to which they moved after the aerial predator stimulus. Although Seghers' results differ somewhat from the data we collected, they support the view that aerial predators may have a substantial role in the evolution of guppy behavior. The variation in observed behaviors also supports the hypothesis that environmental factors specific to each stream are important in determining the most appropriate behaviors for avoiding aerial predators.

Aquatic predation

Guppies from the two populations also differed in response to the smallmouth bass. The population differences corroborate previous studies and most likely arise from the amount of aquatic predation each population has experienced throughout its evolutionary history. Guppies that experience many predators must trade off foraging and mating for antipredator behavior (Reznick and Endler, 1982; Rodd and Reznick, 1997). Because these behaviors are often costly, fish experiencing few predators should not devote as much time to antipredator behavior.

In the present study, fish from the high-risk stream spent more time inspecting the potential predator than did fish from the low-risk stream. Other studies also have found that populations differ in their ability to recognize new predators, with fish experiencing fewer predators less able to detect novel predators (Magurran and Seghers, 1990). It is possible that guppies from the Marianne Tributary did not recognize the bass as a threat; it appears that after a short inspection Marianne guppies determined that the bass was not a familiar predator and resumed normal behaviors. Because guppies in high-risk streams are exposed to many different freshwater and marine predatory fish, recognizing novel predators may increase their survival. The population differences seen in the present study support previous behavioral observations in response to sympatric predators and demonstrate that population differences in antipredator behaviors also extend to the recognition and avoidance of novel aquatic predators.

Multiple predator effects

Multiple types of predator may reduce predation risk through predator-predator interactions or may increase risk

by producing conflicting prey responses (Sih et al., 1998). Aquatic predation is a well-documented selection pressure in the evolution of guppies (Endler, 1980; Haskins et al., 1961; Liley and Seghers, 1975; Magurran and Seghers, 1990; Reznick and Endler, 1982; Rodd and Reznick, 1997; Seghers, 1974b). Our results indicate that aerial predation is also an important selection pressure. However, because aerial predation has not yet been examined thoroughly, the relationship between aerial and aquatic predation pressures is unknown.

Although some selection pressures from aerial predators reinforce those from aquatic predators, it appears that, in general, aerial and aquatic predators exert conflicting selection pressures on guppies. The primary behaviors guppies use to avoid aquatic predators are inspecting (Magurran and Seghers, 1994), schooling (Seghers, 1974b), hiding, and jumping from the surface (Seghers, 1970). The present study suggests that the most important behaviors for avoiding aerial predators are hiding, dropping in the water column, and freezing.

Although hiding under vegetation may be advantageous for avoiding both aquatic and aerial predators, the remaining suite of antipredator behaviors used against aquatic predators are not adapted for aerial predator avoidance. In fact, several of the behaviors used against aquatic predators seem to increase the likelihood of being detected or captured by an aerial predator. For instance, most aerial predators are attracted to large schools of fish (Monadjem et al., 1996; Remsen, 1991). Shoaling may have been selected against in upstream populations because the benefits gained are lower than the costs of increased aerial predation. Similarly, most aerial predators concentrate on fish closest to the surface owing to the optical difficulties associated with locating prey under water (Moroney and Pettigrew, 1987). Seghers (1974a) showed that guppies experience lower rates of aquatic predation near the surface than in deep water. Thus, vertical use of the water column may reflect the perceived risk for each type of predator.

It appears that selection pressures from two distinct types of predators have led to conflicting behavioral responses of the prey animals in this system. Because the evasive behaviors required for the two predator classes conflict, guppies should use a behaviorally plastic defense strategy that allows them to react appropriately to one type of predator, given their perceived risk of the other. Although the basic types of evasive behaviors are probably genetically determined for each population, the frequency and duration of the behavior may be more flexible, as is the case with guppy courtship behavior (Houde, 1997). Guppies may maintain enough plasticity in their antipredator behavior to assess the relative risks posed by different predators in a given situation before initiating evasive behavior.

Although the frequency of encounters with aerial predators is unknown, it seems likely that guppies are sometimes faced with both types of predators simultaneously in nature. The perceived importance of different predators and the relative costs of corresponding antipredator behaviors can be predicted for guppies facing simultaneous encounters with both predator types. Although all guppies experiencing both types of predator should remain plastic in regards to antipredator behavior, different populations should favor certain behaviors depending on their specific predation regime. For example, those populations facing more dangerous aquatic predators may favor the behaviors used to evade aquatic predators, making themselves more at risk to aerial predators, when confronted with both types of predator simultaneously. Similarly, populations experiencing lower levels of aquatic predation may tend to favor the aerial predator evasive behaviors because the aquatic predators pose relatively little risk. Thus, the potential exists for a very sophisticated degree

of plasticity in guppy antipredator behavior in these encounters, in which guppies assess the type of predator and relative degree of risk of various predator combinations, in addition to their past aquatic predator regime.

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