

The effects of different predator species on antipredator behavior in the Trinidadian guppy, *Poecilia reticulata*

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Abstract Different types of predators often elicit different antipredator responses in a common type of prey. Alternatively, some prey species may adopt a general response, which provides limited protection from many different types of predator. The Trinidadian guppy, *Poecilia reticulata*, is faced with a wide range of different predators throughout its range and is known to display varying levels of antipredator behavior depending on the predator assemblage. Pike cichlids, *Crenicichla frenata*, are regarded as the primary aquatic guppy predator in streams in the northern mountain range in Trinidad. As such, they are seen to be responsible for many of the differences in morphology, life history traits, and behavior between guppy populations from areas with few predators and those from areas with many pike cichlids. In this study we investigated how guppies responded when faced with different predator species using three common aquatic predators. We exposed shoals of ten guppies to one out of four treatments: no predator (control), pike cichlid, acara cichlid (*Aequidens pulcher*), and wolf fish (*Hoplias malabaricus*); and we made behavioral observations on both focal individuals and the shoal as a whole. Guppies showed significantly greater levels of predator inspection and shoaling behavior, foraged less, spent more time in the surface water, and stayed in significantly larger shoals when faced with pike cichlids than in other treatments. We discuss these results in the context of multiple predator effects.

Keywords Antipredator behaviour · Guppies · *Crenicichla* · *Aequidens* · *Hoplias* · Multiple predators

Introduction

Many studies investigating behavioral responses in predator–prey interactions have focused on single predators and assumed an additive effect of numerous predators on prey populations (Soluk 1993). However, most prey are subject to predation from multiple predators, which hunt their prey in different ways, and many studies investigating the effects of multiple predator species have yielded results, which suggest that predators rarely attain an additive effect (e.g., Martin et al. 1989; Soluk 1993).

Performing antipredator behaviors is costly as it reduces the time available for other activities such as foraging (Dugatkin and Godin 1992). To maximize their fitness, therefore, prey should be able to modify their antipredator behavior depending on the risk they face, which will differ as a function of the number and type of predators present (Lima and Dill 1990; Vance-Chalcraft et al. 2004). When faced with multiple different types of predator it may be most beneficial to a prey species to adopt a more general antipredator behavior, which is effective against a wide range of predators, for example, grouping (Crowder et al. 1997; Krause and Ruxton 2002). However, when faced with a single predator species, a prey may adopt a specific antipredator behavior, which is highly effective at reducing the hunting success of that particular predator (Lima 1992). As a result, prey species may evolve a range of different antipredator behaviors (both specific and general) in environments where they are likely to encounter multiple predator species (Kishida and Nishimura 2005). In addition,

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many antipredator behaviors are relatively plastic and prey can alter the strength and/or duration of their response to a predator depending on the level of risk it poses (Lima and Bednekoff 1999).

Predator-specific antipredator behaviors were observed in many animals from different taxa (e.g., estuarine fish, *Leiostomus xanthurus* (Crowder et al. 1997); mayflies, *Baetis bicaudatus* (McIntosh and Peckarsky 1999); anuran larvae, *Rana catesbeiana* and *Rana clamitans* (Eklov and Werner 2000); freshwater snails, *Physella gyrina* (Turner et al. 1999); mountain log-skinks, *Pseudemoia entrecasteauxii* (Stapley 2004); and rock squirrels, *Spermophilus variegates* (Owings et al. 2001). In many of these studies, a common prey type was faced with two predator species from different taxa, for example, snake and bird predators (Stapley 2004), fish and invertebrate predators (McIntosh and Peckarsky 1999; Turner et al. 1999; Eklov and Werner 2000; Fairchild and Holomuzki 2005; and others), and fish and bird predators (Crowder et al. 1997; Templeton and Shriener 2004). However, many prey species are also faced with multiple different predators from the same taxon, which may also exert different predation risks and thus elicit different antipredator responses. For example, rock squirrels throw substrate and tail-signal at significantly higher rates in the presence of gopher snakes, *Pituophis melanoleucus*, than in the presence of rattle snakes, *Crotalus atrox* (Owings et al. 2001). Similarly, the intensity of mobbing behavior in black-capped chickadees, *Poecile atricapilla*, differed in response to different raptor species as a function of differences in predator size (Templeton et al. 2005).

Guppies, *Poecilia reticulata*, are small cyprinodontid fish common throughout a multitude of different aquatic habitats in Trinidad's northern mountain range and are subject to a wide range of different aquatic predators (Seghers 1973). Of these predators there are three commonly co-occurring fish species, the pike cichlid, *Crenicichla frenata*; the blue acara cichlid, *Aequidens pulcher*; and the wolf fish, *Hoplias malabaricus*, which may exert different levels of risk to guppies (Seghers 1973; Reznick and Endler 1982; Kelley and Magurran 2003). Pike and acara cichlids are medium-sized, active, diurnal predators while wolf fish can attain a much larger size (up to 50 cm) and often hunt at night (Seghers 1973). While acaras are omnivorous, pike cichlids are highly carnivorous as are wolf fish, which often hunt using a sit-and-wait, ambush strategy, unlike the more active pursuit strategies of the two cichlid species (Seghers 1973; Botham 2004 personal observation). Pike cichlids (*Crenicichla* spp; see Coleman and Kutty 2001) are regarded as the most dangerous of these predators to guppies, while it is often suggested that acara cichlids may only be a very slight guppy predator because of their more omnivorous diet (e.g., Seghers 1973;

Reznick and Endler 1982). Kelley and Magurran (2003) found that guppies were more wary of pike cichlid and acara models than a snake model. They also found that wild guppies from a high predation river approached pike cichlid models at a closer distance than the other predator models, but did not show any difference in schooling behavior or inspection rate between the different predator treatments. Pike cichlids have therefore often been used as the model predator for high predation treatments in studies investigating behavioral and morphological differences between guppy populations from different river systems where they were proven responsible for high guppy mortality (e.g., Mattingly and Butler 1994). However, acaras were also used in many predation experiments (e.g., Godin and Davis 1995; Krause and Godin 1995) and feed on guppies both in the field and laboratory (Botham et al. 2005; Botham and Krause 2005a). Wolf fish are major piscivores (Bistoni et al. 1995; de Almeida et al. 1997), but due to their predominantly nocturnal lifestyles and great size, have often been overlooked as major guppy predators. However, their effect on populations of Hart's rivulus, *Rivulus hartii*, another small fish sympatric with guppies, was well documented (e.g., Fraser et al. 1999; Gilliam and Fraser 2001) and because juveniles sometimes hunt in daylight (M. S. Botham et al., personal observation) and feed both diurnally and nocturnally in the laboratory (Botham and Krause 2005b), they should be considered in studies relating guppy evolution to predator faunas. For example, nocturnal predation by wolf fish causes guppies to reduce their courtship during the day to compensate for lost feeding opportunities during the night (Fraser et al. 2004). In a field study investigating the effects of shoaling behavior on prey choice, shoals of guppies were attacked frequently by all three of these predator species (Botham et al. 2005).

In this study we conducted a laboratory experiment to investigate whether different predators elicit different antipredatory behavior in guppy shoals. Specifically, we tested how different predators affected the behavior of guppies: (1) whether they spent a greater time in the surface waters (as suggested from field observations on guppies from high predation localities; e.g., Seghers 1973); (2) whether they spent less time foraging and swimming and more time inspecting and remaining stationary; and (3) whether guppies kept at different distances and showed different levels of shoaling behavior depending on predator species. We exposed shoals of ten female guppies caught from the Arima River in Trinidad to one of the four treatments where an acara, a pike cichlid, a wolf fish, or no predator (control) was present. Observations were made on the behavior of a focal individual guppy and on characteristics of the shoal as a whole. We expected that guppies would show greater levels of inspection in pike cichlid treatments than acara and wolf fish treatments, and that

levels of inspection would be greater in all predator treatments than in the control treatment. We also expected that guppies should: spend more time at the surface with predators present because field data suggests predators frequent the lower levels of the water column (Botham 2005) and guppies from high predation localities are often found inhabiting the surface waters (Croft et al. 2004); spend more time at a greater distance, show less activity [more stationary behavior, for example freezing (Brown and Godin 1999), and less foraging behavior (Dugatkin and Godin 1992)] and, spend more time shoaling and remain in larger shoals with predators present. In addition, we expected that these patterns in antipredator behaviors would be most pronounced in pike cichlid treatments because previous studies have suggested pike cichlids to be the most dangerous guppy predators in the Arima River (e.g., Reznick and Endler 1982).

Materials and methods

This study was carried out at Simla Research Station, Arima, Trinidad between June and July 2004 in eight experimental pools (Fig. 1). All predators were caught from the Arima River using hand seine nets. We used two adult acaras [100 mm total length (TL, tip of snout to posterior edge of caudal fin)], two adult pike cichlids (110 mm TL), and two subadult wolf fish (100 mm TL) as the test predators. These predators were housed separately in their pools with a floating refuge and were fed on five adult guppies daily. Any guppies not consumed were removed before experimental trials commenced. Adult female

guppies (25–30 mm TL) were used as prey. These were also caught, using a hand seine net, from the Arima River where they live sympatrically with all three predator species used in this study. They were housed in stock pools with the same dimensions as the experimental pools and fed on dry flaked food ad libitum. Both predators and prey were maintained under a 12-h light: 12 h dark regime at 25°C to replicate conditions in the wild.

Experimental set-up

Figure 1 shows the experimental pools used in this study. Pools were filled to a depth of 10 cm. We set up a total of eight pools, two pools for each of the four different predator treatments. In each pool we placed one individual predator in the center of the pool, except in the case of the control treatment where the central compartment was empty. The four treatments were as follows: (1) acara, (2) pike cichlid, (3) wolf fish, and (4) no predator (control). Predators were placed in a central glass cylinder with a small gap underneath to allow both visual and olfactory cues through into the main pool area, while preventing physical contact between them and the guppies. Zones were marked around the center of the pool at 10-cm intervals (see Fig. 1) using a marker pen so that we could approximately assess how close guppies swam to the predator.

Procedure

Ten female guppies were taken at random from their stock pools and placed into the experimental pool (zone 4), initially contained in an opaque removable cylinder con-

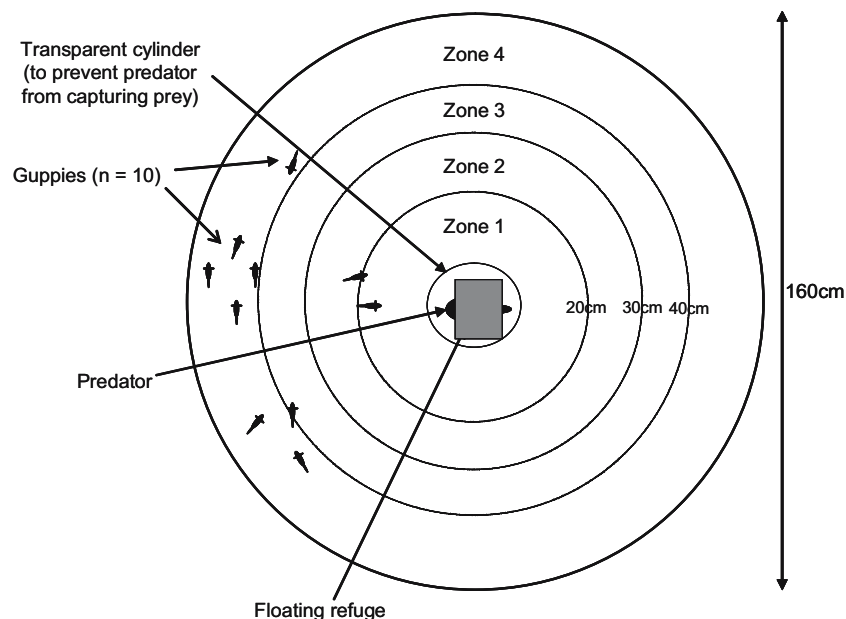


Fig. 1 Plan view of the experimental pools used to test whether guppies showed different responses to three common piscivorous fish: acaras cichlid, pike cichlid, and wolf fish

trolled by a string pulley. After 10 min of acclimation, the cylinder was removed to release the guppies. We then made behavioral observations on a focal individual for a period of 10 min, recording their behavior, position in the water column, whether they were associated with a conspecific (time spent shoaling, defined as when the focal fish was within four body lengths of a conspecific; Pitcher and Parrish 1993), and which zone they were in every 20 s. While the cylinder used to present guppies into the experimental pool was not perforated, the water within the cylinder is likely to have contained some olfactory cues from the predator. Thus, it is possible we may have missed some of the behavioral responses exhibited during this acclimation period. However, guppies showed no obvious differences in their behavior between treatments during this period. Behaviors recorded included: swimming (locomotion), stationary (no movement), foraging, and predator inspection where it occurred. Although no food was added to experimental pools, guppies often foraged on small insects at the water surface that had fallen into the pools and/or on algae, which had started to grow on the bottom and sides of the pools. Foraging behavior was defined as guppies that were observed performing pecks at food items and predator inspection behavior was defined as guppies that approached the predator in a series of slow, jerky movements and showed lateral orientation to the predator (Kelley and Magurran 2003). In conjunction with this, a second observer recorded how many subshoals the original shoal (ten individuals) was split into every minute during the 10-min trial. From this we calculated the mean shoal size for each trial.

For each treatment we performed ten replicates using a different shoal of ten female guppies randomly selected from the stock pools. We then calculated how long guppies spent performing different behaviors and how much time they spent at different levels in the water column as proportions of the total time they were observed for. This was achieved by dividing the number of observations involving a certain behavior, position, or zone by the total number of observations for each individual guppy tested, and then converting those numbers to percentages. To analyze the time spent by guppies at different distances from the predator, we calculated the average distance from the number of observations in each zone for each focal guppy.

Data analysis

We carried out statistical tests between treatments on the time spent in the surface water, the time spent swimming, stationary, foraging, and predator inspecting, the time spent in shoaling (in association with 1+ conspecifics), the mean shoal size, and finally on the average distance (zone) from the predator. Average distance and mean shoal size data was normally distributed, therefore, a one-way ANOVA was used

to analyze these variables. However, all other variables gave nonnormally distributed data despite multiple transformations. Here we used Kruskal–Wallis tests. When Kruskal–Wallis tests resulted in significant differences across treatment groups, multiple comparisons between predator treatments were analyzed using the following formula as an extension of the Kruskal–Wallis test (Siegel and Castellan 1988):

$$|\check{R}_u - \check{R}_v| \geq zk(k-1) \sqrt{(N(N+1)/12)(1/n_u + 1/n_v)}$$

where

- k = the number of groups
- z = the critical value for the number of comparisons ($k(k-1)$ being made)
- n_u = the number of samples in the u th group
- N = the total number of samples of all groups combined
- \check{R}_u = the mean rank in the u th group (obtained from the Kruskal–Wallis test)

Critical Z values were obtained from Siegel and Castellan (1988). The results of these tests are presented using the abbreviation, MCT (multiple comparisons test). In addition, we used Mann–Whitney U tests to test for differences between the predator treatments and the control treatment when we found significant differences across treatments. Many of these multiple comparisons between pairs of treatments resulted in nonsignificant differences ($P > 0.05$). For the purpose of brevity we have only given details of those comparisons, which resulted in statistically significant differences.

Results

Predator behavior

We observed no difference in the behavior of the three different predator species used in this study. All predators were relatively motionless during experimental trials, positioned under the floating refuge provided in their containers, and made no attempts to attack guppies or to escape their containers.

Prey behavior (focal individuals)

Average distance from the predator

There was a significant difference in the average distance from the predator at which guppies spent their time for different predator treatments (one-way ANOVA: $F_{3,36}=3.779$ and $P=0.019$). Further analysis showed that while the average distance from the predator did not significantly differ between the three predator treatments, guppies spent significantly more time at a closer distance to the central

predator compartment in each of the predator treatments than they did in the control treatment with no predator present (independent *t* test: pike cichlid–no predator, $t=-3.293$, $df=18$, and $P=0.004$; acara–no predator, $t=-2.205$, $df=18$, and $P=0.043$; wolf fish–no predator, $t=-2.613$, $df=18$, and $P=0.018$; see Fig. 2a). Closer proximity to the predator was likely to be a consequence of the incidence of inspection behavior in predator treatments.

Time spent in the surface waters

Guppies spent significantly different amounts of time in the surface waters (upper third of the water column) with different predator treatments (Kruskall–Wallis test: $\chi^2=24.807$, $df=3$, and $P<0.001$). They spent significantly more time at the surface with a pike cichlid present than with an acara or wolf fish present (MCT: pike cichlid–acara, $Z_{10, 30}=14.75$ and $P<0.05$; pike cichlid–wolf fish, $Z_{10, 30}=24.35$ and $P<0.05$; see Fig. 2b) or when no predator was present (Mann–Whitney U test: $U_{10,10}=0.000$ and $P<0.001$; Fig. 2b).

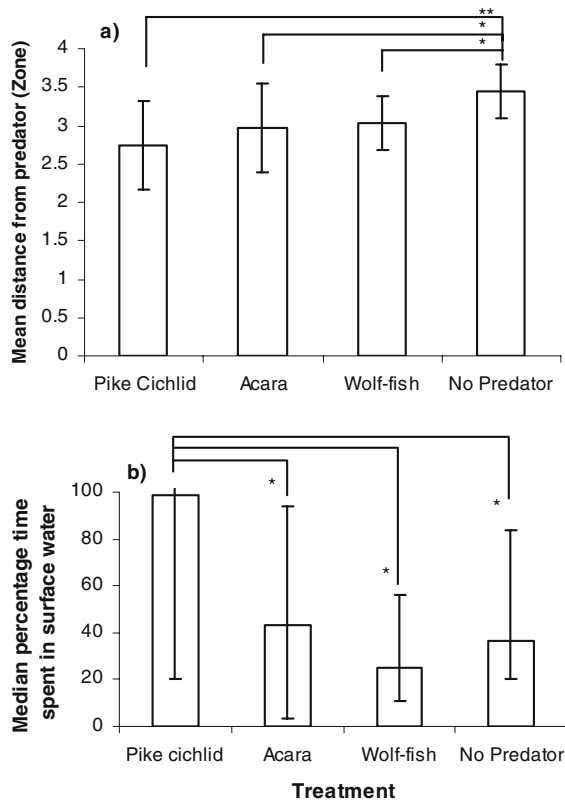


Fig. 2 **a** The mean distance from the predator (± 1 SD) in zones (where zone 1 is closest to the predator) spent by focal guppies under different predator treatments and a control treatment. **b** The median percentage time (\pm quartiles) spent at different positions in the water column ($*P<0.05$ and $**P<0.01$)

Shoaling (association with conspecifics)

There was a significant difference between the treatments in the time focal guppies spent shoaling (Kruskall–Wallis test: $\chi^2=8.550$, $df=3$, and $P=0.036$). They spent significantly more time shoaling in the presence of a pike cichlid than in the control treatment (Mann–Whitney U test: $U_{10, 10}=17.500$ and $P=0.011$; Fig. 3a) and when an acara was present (MCT: $Z_{10, 30}=10.75$ and $P<0.05$; Fig. 3a).

Activity

While there was no significant difference in the time spent stationary (Kruskall–Wallis test: $\chi^2=4.150$, $df=3$, and $P=0.246$), there was a significant difference in the time

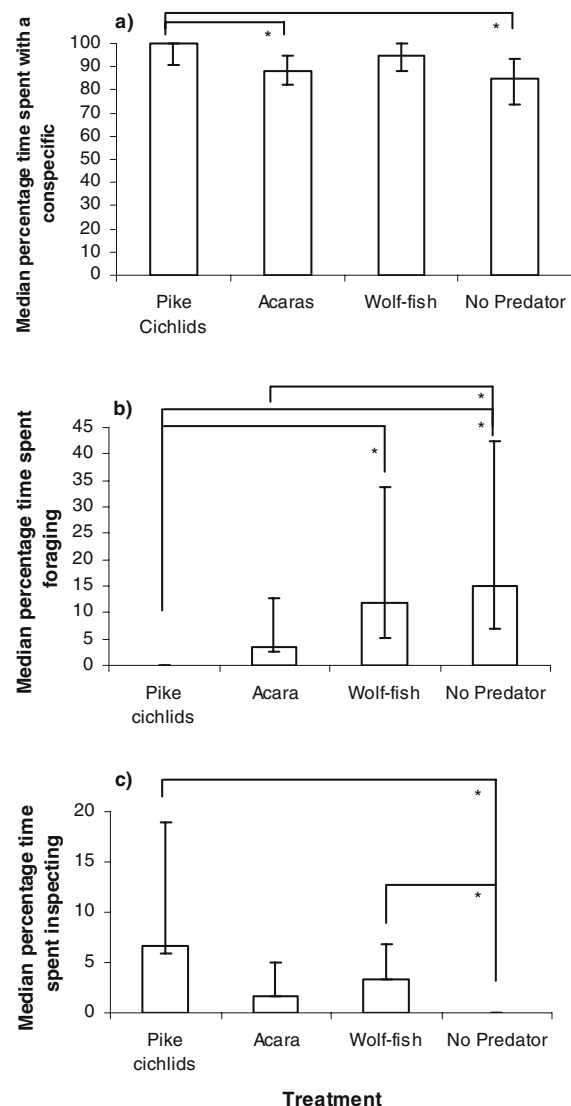


Fig. 3 The median percentage time (\pm quartiles) spent **a** associated with a conspecific, **b** foraging, and **c** inspecting the predator by focal guppies under different predator treatments and control treatment ($*P<0.05$)

focal guppies spent foraging and inspecting the predator under different predator treatments (Kruskall–Wallis test: foraging, $\chi^2=18.318$, $df=3$, and $P<0.001$; inspecting, $\chi^2=12.131$, $df=3$, and $P=0.004$). Though not statistically significant, we found a difference in the time spent swimming under different predator treatments whereby guppies spent slightly more time swimming with an acara present than in the other treatments (Kruskall–Wallis test: $\chi^2=7.585$, $df=3$, and $P=0.055$).

Focal individuals were rarely observed foraging with a pike cichlid present and they spent significantly less time foraging in both this and the acara treatment than in the treatment with no predator (Mann–Whitney U test: pike cichlid–no predator, $U_{10,10}=3.000$ and $P<0.001$; acara–no predator, $U_{10,10}=15.000$ and $P=0.007$; see Fig. 3b). Guppies also spent significantly less time foraging in the pike cichlid treatment than the wolf fish treatment (MCT: $Z_{10,30}=16.05$ and $P<0.05$; Fig. 3b).

In addition, guppies also spent significantly more time inspecting the predator in the pike cichlid and wolf fish treatments than the treatment with no predator (Mann–Whitney U test: pike cichlid–no predator, $U_{10,10}=15.000$ and $P=0.007$; wolf fish–no predator, $U_{10,10}=20.000$ and $P=0.023$; Fig. 3c).

Prey behavior (the shoal)

The mean shoal size significantly differed between predator treatments (one-way ANOVA: $F_{3,36}=9.050$ and $P=0.014$). Further analysis showed that the mean shoal size was significantly greater when a pike cichlid was present than when there was no predator present (independent t test: $t=2.281$, $df=18$, and $P=0.035$; see Fig. 4) and than when a wolf fish was present (Tukey's test: $T_{2,27}=0.1700$ and $P=0.020$; Fig. 4).

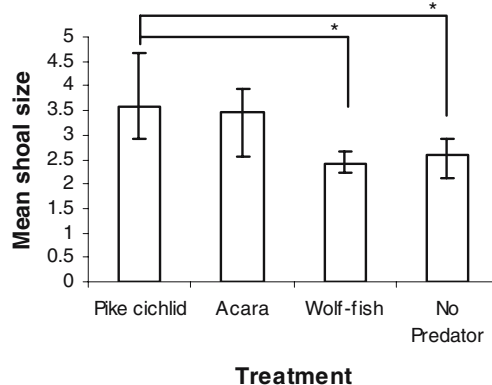


Fig. 4 The mean (± 1 SD) shoal size observed during trials under different predator treatments and control treatment (* $P<0.05$)

Discussion

Graded antipredator responses

The results from our study provide evidence that pike cichlids may pose the greatest threat to guppies of the fish predators found in the northern mountain range of Trinidad because they elicited the strongest antipredator responses (for example, larger mean group size and most time inspecting). Our results also suggest that guppies were able to grade different aquatic predators from the same taxon and respond in a risk-sensitive manner (Helfman 1989) because they responded to acaras and wolf fish with similar antipredator behaviors, but less strongly and for a shorter duration to pike cichlids. Risk-sensitive behavior was demonstrated in guppies, for example, guppies moderate the intensity of foraging (Fraser and Gilliam 1987; Dugatkin and Godin 1992) and type of courtship behavior (Magurran and Seghers 1990) in the presence of predators. Risk-sensitive behavior is important for survival because antipredator behavior indirectly affects fitness through a reduction in the time and energy available for other activities important for their reproductive success. If certain predators pose less risk than others then prey should show a reduction in antipredator behavior in their presence, and increase the time dedicated to these other activities such as foraging and courtship (Lima and Bednekoff 1999).

Graded responses to different predators were observed in other animals. For example, the intensity of mobbing behavior in black-capped chickadees (*P. atricapilla*) varies with the size and species of predator present, whereby the intensity increases with the risk associated with each predator (Templeton et al. 2005). Similarly, acaras and pike cichlids attain much smaller sizes than wolf fish in the wild (Seghers 1973) and therefore guppies are likely to face differences in risk associated with predators of both different size and species. Predator size was kept constant in our study, suggesting that antipredator responses reflected the risk associated with the different species. Pike cichlids elicited the greatest responses in guppies as we had predicted because they are regarded as the major diurnal guppy predator in the northern mountain range of Trinidad (Seghers 1973). Guppies from localities with pike cichlids present were shown to exhibit greater levels of antipredator behavior than those from localities where they are absent (e.g., Seghers and Magurran 1995). Acaras elicited similar but weaker antipredator responses from guppies. We had also expected this because acaras are also diurnal, pursuit predators, but are less piscivorous, having more omnivorous diets commonly associated with disciform fish (Merigoux and Ponton 1998). Wolf fish, however, are highly piscivorous and were shown to greatly affect the behavioral time budgets of guppies (e.g., Fraser and Gilliam 1987; Fraser et al. 2004). Despite this,

guppies did not significantly reduce foraging time or increase time spent in the surface water in the presence of a wolf fish compared to the control, and the mean shoal size of guppies was lowest in the wolf fish treatment.

A possible explanation for the difference in behavior of guppies in the presence of wolf fish compared to other predators is that the guppies may not have had prior experience with wolf fish. Wolf fish density is highest in downstream localities and often relatively low in more upstream stretches of the river such as our study site (Seghers 1973). In contrast, pike cichlids and acaras are relatively abundant in more upstream stretches. In a field study carried out in the same location as where the fish used in this study were caught from, shoals of guppies were attacked by pike cichlids, acaras, and wolf fish (Botham et al. 2005). Pike cichlids and acaras were by far the most abundant predators responsible for attacks, though this may have reflected the time of day in which the study was conducted given that wolf fish are more active at night (Fraser et al. 2004). Experience through encounter rate with predators was shown to be important in developing antipredator responses. For example, squirrels from areas with high snake densities were more cautious than those from areas with low snake densities (Owings et al. 2001). Similarly, natal pool predator density results in a difference in the prevalence of schooling behavior in guppies (Magurran and Seghers 1991). However, Kelley and Magurran (2003) found that guppies from both high and low predation populations were able to discriminate between different predator models and that this persisted in future generations reared in the laboratory in the absence of predators. In addition, we found that guppies showed high levels of predator inspection behavior in the wolf fish treatment and the differences observed in shoal size and spatial position may reflect a difference in the hunting strategy of wolf fish compared to that of pike and acara cichlids.

The effects of predator hunting strategies

A more likely explanation for the differences in responses by guppies between wolf fish and other predator treatments is a difference in the hunting strategies of the different predators. Wolf fish are cryptically colored and often sit and wait until prey is close before launching short burst attacks (M. S. Botham et al., personal observation) whereas pike cichlids and acaras often actively pursue their prey. Teplitsky et al. (2005) found that pursuit predators induced a different morphology to sit-and-wait predators in anuran larvae, *Rana dalmatina*, which in turn affected their escape responses. In addition, certain behaviors, which reduce the likelihood of being caught by active pursuit predators, may be ineffective against sit-and-wait predators such as wolf fish. For example, the capture success of rock bass,

Ambloplites rupestris, using a sit-and-wait strategy was not affected by the shoaling behavior of creek chub, *Semotilus atromaculatus* (Krause et al. 1998). Because guppies showed high levels of predator inspection behavior in wolf fish treatments, it seems likely that they perceived wolf fish as predators (although guppies often show some inspection of novel objects (Kelley and Magurran 2003). However, there were large differences between the wolf fish treatment and other predator treatments for the time spent in the surface water and time spent foraging by guppies and their mean shoal size. Can these differences be correlated to the different hunting strategy of wolf fish?

While an increase in surface area use was shown to be a common antipredator response in prey, fish faced with diurnal pursuit predators (e.g., Zhao and Chivers 2005), it is unlikely to be effective against predators employing sit-and-wait strategies where the proximity of prey is likely to be more important than its position in the water column.

Many prey reduce the time spent foraging in the presence of a predator to engage in antipredator behaviors (e.g., Dugatkin and Godin 1992). One way in which guppies are able to compensate for this reduction in foraging is by continuing to feed at night (Fraser et al. 2004). However, the presence of wolf fish prevents this and was shown to cause guppies to reduce their daytime courtship and increase their daytime foraging (Fraser et al. 2004). This may explain the relatively high incidence of foraging behavior in the wolf fish treatment compared to other predator treatments, rather than the suggestion that wolf fish may be perceived by guppies as low-risk predators.

As mentioned, shoaling behavior, like surface area use, may be ineffective against sit-and-wait predators (Krause et al. 1998). In addition, wolf fish often hunt nocturnally, where again shoaling may not only be ineffective, but may also aid detection by wolf fish through an increase in olfactory cues (Magurran 2005). Previous studies in both the laboratory and the field showed that shoaling guppies may receive greater attack attention from predatory fish, including the wolf fish, (Botham et al. 2005; Botham and Krause 2005b), which may further induce a smaller group size in guppies faced with sit-and-wait predators. Guppies still showed high levels of conspecific association when faced with a wolf fish. This may in part reflect the occurrence of inspection behavior (which is often performed in pairs or small groups; Croft et al. 2006) but may also reflect the maintenance of a social network in guppies (Croft et al. 2005). Social networks may facilitate the transfer of information between individuals regarding foraging sites and predators (Croft et al. 2005). This may be particularly important for the survival of guppies from populations faced with multiple predator species as predator recognition may be socially acquired through interactions

with individuals, which have experience with different predators (Vilhunen et al. 2005).

Multiple predator effects in the guppy system?

Clearly, further investigation is required to determine whether guppies respond to wolf fish with a different suite of antipredator behaviors to those recorded in the present study, whether their response to wolf fish and other predators varies temporally, or whether guppies simply perceive wolf fish as lower risk predators than pike cichlids and acaras. In addition, it would be interesting to conduct further studies, which manipulate both the densities and diversity of predators used to test for multiple predator effects given that the three predators used may elicit both different levels and types of antipredator responses. Studies showed that particular predator-specific behaviors in prey might make them more susceptible to predation by other types of predators (Soluk 1993). Alternatively, preys may adopt more general antipredator behaviors that serve to lower their risk to a wide range of different types of predators (Crowder et al. 1997). Shoaling behavior in guppies may be such a general behavior because many predators attack using visual cues and are therefore likely to be affected by the “confusion effect” incurred when attacking groups of preys (Neill and Cullen 1974). Crowder et al. (1997) found that juvenile spot suffered a lower mortality rate in the presence of avian and aquatic predators than that calculated by adding the mortalities imposed by each predator alone, together. In the presence of only southern flounder, spot moved to shallow waters to minimize predation, while in the presence of only avian predators they moved to deeper waters. With both types of predators present spot stayed in the shallower waters but exhibited strong shoaling behavior. Guppies experience similar behavioral conflicts between avian and aquatic predators (Templeton and Shriner 2004). The density of predators is also important when investigating predator–prey interactions. When *Stenonema* mayfly larvae were subjected to multiple predators of either the same species or two different species, the mortality rates were equally reduced compared to those predicted by a multiplicative risk model (Vance-Chalcraft et al. 2004). This was attributed to similar levels of inter- and intraspecific interference between the predators. In previous studies investigating the effects of both intra- and interspecific competition on the prey choice in acaras, Botham and Krause (2005a) found that odor cues from both con- and heterospecifics resulted in the loss of the original preference of acaras to attack shoals over single guppies.

In conclusion, our results show that guppies are able to discriminate between different predators within the same taxon and respond appropriately in what is likely to be a

risk-sensitive manner. They also highlight the importance of considering the effects of different predator species separately and how traditional methods of measuring antipredator responses may be insufficient. The hunting strategies of some predators may not be affected by common antipredator behaviors such as grouping and may elicit entirely different responses. In addition, our results also provide support to previous studies, which have suggested pike cichlids are the most dangerous aquatic predator of guppies in rivers in the northern mountain range of Trinidad.

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