

# Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey

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Foraging in animals is often associated with characteristic body postures, such as the head-down posture. When foraging conflicts with the ability to detect predators or to flee, individuals may incur a greater risk of mortality to predation than otherwise. Here we investigate the influence of different foraging postures (horizontal versus nose-down body posture) on the ability of individuals to respond to approaching predators and on the risk of mortality to predation in the guppy (*Poecilia reticulata*). Individuals engaged in nose-down foraging were assumed to be able to visually scan a smaller area for predators and to escape less effectively due to their body posture, and thus are more vulnerable to stalking predators than horizontally foraging ones. In a first experiment, we separately exposed nonforaging, horizontally foraging, and nose-down foraging guppies to an approaching cichlid fish predator model. Nonforaging guppies reacted sooner to and initiated flight further away from the approaching model than did foraging fish collectively, and horizontally foraging individuals responded sooner to the model than nose-down foraging ones. Comparing all test guppies, nose-down foraging individuals were the most likely not to exhibit any response to the predator model. When presented with a simultaneous choice of two guppies behind a one-way mirror, individual blue acara cichlid (*Aequidens pulcher*), a natural predator of the guppy, preferred to attack foraging guppies over nonforaging ones and nose-down foraging guppies over horizontally foraging individuals. In a final experiment with free-swimming cichlids and guppies, we demonstrated that individual risk of predation for guppies foraging nose down was greater than for guppies foraging horizontally, and both were at greater risk than nonforaging guppies. This latter result is consistent with the above differences in the guppy's responsiveness to approaching predators depending on their foraging behavior, and with the finding that cichlid predators preferred fish that were less likely to show any response to them. Our results therefore indicate that the ability to respond to approaching predators and the risk of mortality to predation in the guppy is strongly influenced by their foraging activity, and in particular their foraging posture, and that cichlid predators preferentially select less wary and more vulnerable guppies. **Key words:** cichlid fish, fleeing, foraging, foraging posture, guppy, *Poecilia reticulata*, predation risk. [*Behav Ecol* 7:264–271 (1996)]

Animals generally increase their visual scanning rates with increasing risk of predation (reviews by Elgar, 1989; Lima and Dill, 1990; Quenette, 1990), which suggests that predator detection and avoidance are the main functions of vigilance behavior (Elgar, 1989). However, individuals may be faced with trade-offs between antipredator vigilance and other behavioral activities when these are mutually exclusive (Lima and Dill, 1990). For example, birds tend to scan less frequently when feeding on dense food resources (Barnard, 1980) and when prey handling times are long (Popp, 1988). Similarly, fish under predation threat choose to feed on lower prey densities (Jakobsen and Johnsen, 1989; Milinski, 1984) and on smaller prey, with shorter handling times (Godin, 1990), than when there is no threat present. Recent studies (FitzGibbon, 1989, 1990; Godin and Smith, 1988) have shown that a decrease in vigilance due to foraging can indeed translate into higher individual risks of mortality to predation.

In most birds and ungulates, the difference in vigilance levels between foragers and nonforagers is commonly associated with differences in their body postures (i.e., head up and head down) (e.g., Dahlgren, 1990; FitzGibbon, 1989). In fishes, the buoyancy of the body allows individuals to feed in a variety of different postures: head up when foraging on surface food, head horizontal when foraging on plankton and on food located on vertical structures, and head down when foraging on

benthic food. However, the relationships between these and other fish foraging postures and individual vigilance are unknown.

In the current study, we experimentally investigated for the first time the effects of foraging behavior in general, and more specifically particular foraging postures, on the ability to respond to approaching predators and the risk of mortality to predation in individual prey fish. Since fishes do not have an unambiguous vigilance posture (as in most birds and mammals), it is difficult to assess the vigilance level of fish independently of their ability to detect and respond to predators. We therefore focused on the reaction (flight) distance of individual fish to approaching predators as opposed to vigilance. We also ascertained whether predators prefer to attack prey that are less likely to show an early reaction to their approach when given a choice. We used live blue acara cichlids (*Aequidens pulcher*) and guppies (*Poecilia reticulata*) as model predator and prey, respectively, as well as a cichlid fish predator model. Although the blue acara is not a specialist piscivore, it is a known natural predator of the guppy (Endler, 1978; Liley and Seghers, 1975).

In a first experiment, we tested the hypothesis that individual foraging guppies are less likely to react to a cichlid predator than nonforaging ones. We subsequently investigated the influence of different foraging postures of individuals on their ability to react to an approaching predator. Stream-living guppies commonly forage nose down on the substratum or scrape off algae and other food items from vertical rock surfaces with the long axis of their body horizontal (Dugatkin and Godin, 1992; Dussault and Kramer, 1980; Godin J-GJ and Krause J,

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unpublished data). Dussault and Kramer (1980) showed that benthic food is a major component of the diet of wild guppies and that their feeding apparatus is adapted for benthic feeding. We thus hypothesized that fish that forage in the nose-down posture are less likely to react to an approaching predator than fish that forage horizontally, because the visual horizon that can be scanned for predators is smaller and often obstructed when an individual has its head down (Lima, 1987, 1994; Metcalfe, 1984). In a second experiment, we presented individual cichlid fish with binary choices between either nose-down foraging, horizontally foraging, or nonforaging fish to test the hypothesis that predators preferentially attack individuals that are less likely to show an early reaction to their approach, owing both to their foraging activity and their particular body posture. In a final experiment, we investigated whether the combined effect of guppy foraging posture on their ability to detect and respond to predators and the preference of cichlids for guppies adopting particular body postures results in higher risks of mortality in foraging fish (compared to nonforaging fish) and, particularly, in ones that adopt a nose-down foraging posture. Addressing the above questions under laboratory conditions allowed us to experimentally control for potential confounding factors such as the distance between predator and prey and differences in sex, size, and condition among prey individuals that naturally occur in field studies.

## GENERAL METHODS

Ninety-five blue acara cichlids ( $X \pm SD$  total length =  $6.6 \pm 0.8$  cm) and about 400 nongravid female guppies ( $1.9 \pm 0.25$  cm) were obtained from a local aquarium fish retailer and kept in holding tanks at  $24^{\circ}\text{C}$ – $26^{\circ}\text{C}$  for several weeks before use in the experiments. Guppies were fed dry flake food (NutraFin) ad libitum thrice daily and cichlids were given freeze-dried euphausiid shrimps and chironomids twice daily. The cichlids were also regularly given juvenile guppies prior to the experiments to familiarize them with this prey and to ensure that they were able to capture and swallow juvenile guppies when used in the experiments.

In the three experiments described below, we compared the behavior of guppies foraging with their long body axis horizontal with those foraging with their nose down, and with those not foraging at all (see Figure 2 for illustrations of these postures). To get a fish into the desired foraging posture, we presented it with a glass microscope slide ( $2.5 \text{ cm} \times 2.5 \text{ cm}$ ) that was thinly coated with gelatin onto which a standard amount (about 6 mg) of NutraFin flakes was evenly sprinkled. The slide was then placed either against the tank wall (for horizontal foraging) or on the tank bottom (for nose-down foraging). Slides for nonforaging trials were not covered with either gelatin or flake food. Test guppies were given prior experience foraging on such glass slides in both the horizontal and nose-down postures before being used in the experiments described below. Preliminary trials ( $n = 12$ ) showed that the foraging posture of guppies (horizontal or nose-down) had no significant effect on the duration of their foraging bouts (independent  $t$  test:  $df = 10$ ,  $t = 1.09$ ,  $p = .30$ ; mean  $\pm 95\%$  confidence interval: nose-down posture =  $1.7 \pm 0.3$  min, horizontal posture =  $1.9 \pm 0.2$  min) or the number of bites per bout (independent  $t$  test:  $df = 10$ ,  $t = 0.31$ ,  $p = .76$ ; mean  $\pm 95\%$  confidence interval: nose-down posture =  $95.5 \pm 31.1$  bites/min, horizontal posture =  $87.8 \pm 16.9$  bites/min). Guppies and cichlids were deprived of food for 24 h prior to the experiments to standardize their respective hunger levels.

In experiments 1 and 3, nose-down foraging and nonforaging guppies were always oriented broadside or toward the

predator at the beginning of and throughout the predator model's approach to avoid the possibility that body orientation (nose-down foraging and nonforaging test fish could theoretically face away from the predator) rather than the foraging posture itself influenced the response of the test fish to the approaching predator model. In experiment 2, we included a series of additional trials to specifically test for the influence of prey body orientation with respect to the predator, while controlling for prey foraging posture, on predator attack behavior.

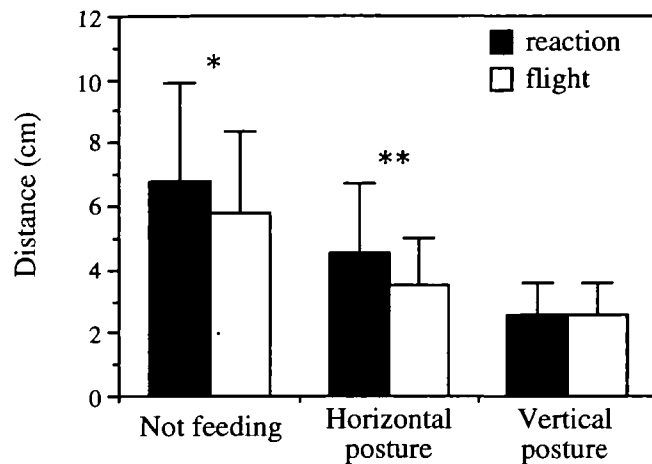
## Experiment 1: foraging posture and responsiveness to predators

### Materials and methods

To standardize the threat of predation, guppies were presented individually with a model of a slowly approaching (stalking) pike cichlid (*Crenicichla alta*). This cichlid is a major predator of the guppy in nature (Endler, 1978; Liley and Seghers, 1975). The model was constructed from body filler material using a mold made from a freshly killed 14-cm pike cichlid. Glass eyes were fixed into the model, which was painted realistically and coated thinly with fiberglass resin. The model was suspended in the water column (5 cm above the bottom) of the test tank ( $100 \text{ cm} \times 25 \text{ cm}$ ; water depth 15 cm) by two pieces of monofilament nylon line attached to an overhead track. Guppies respond to such predator models and live fish predators in a qualitatively similar way (Dugatkin and Godin, 1992; Magurran and Seghers, 1994). For each trial, a single guppy was introduced into a clear plastic container ( $10.7 \text{ cm} \times 13.3 \text{ cm}$ ; water depth 17 cm) containing a glass slide (with or without food) and given about 15 min to acclimate. The glass slide was placed on the bottom and midline of the container for nonforaging and nose-down foraging trials, and up against the container's side for horizontal foraging trials. In all three treatments, the slide was placed adjacent to the front side of the container. The container was positioned at one end of the test tank such that the glass slide was always in line with the path of the approaching predator model, which was initially located 60 cm away at the opposite end of the tank. When not moving, the model remained hidden among rocks. The predator model was then moved remotely toward the guppy container at 2.5 cm/s (thus simulating a stalking pike cichlid) by activating a stepping motor with a computerized controller. The predator model's stalk began only when the test guppy was stationary at the front of its container and facing or broadside to the model. The distance separating the model and guppy at the start of the attack was therefore constant for all treatments.

The behavior of the guppy in response to the approaching predator model was filmed with a video camera from above. Distances could be estimated from a grid on the bottom of the tank. Using frame-by-frame analysis of the tapes, we recorded (1) the distance separating the model and the guppy at the instant the latter reacted to the approaching model (reaction distance), as indicated by an abrupt change in the guppy's activity (e.g., freezing, interruption of feeding), and (2) the distance separating the model and the guppy at the instant the latter initiated a fleeing response (flight initiation distance; sensu Ydenberg and Dill, 1986), characterized by a rapid dart away from the approaching model. We used the fish's reaction and flight initiation distances as differential measures of the risk of being captured by a predator. In fishes, the risk of a prey being captured is generally greater when it is closer to the predator (Dill, 1973; Webb and Skadsen, 1980).

To investigate the influence of foraging and foraging posture on reaction and flight initiation distances, we compared



**Figure 1**

Mean (+SD) predator reaction and flight initiation distances for individual guppies that performed one of three different activities: (1) nonforaging, (2) foraging in a horizontal posture, or (3) foraging in a nose-down posture, while a model of a pike cichlid was approaching. Twenty-five fish were tested for each category. Significance of the difference between the distances within behavioral categories was determined using the paired *t* test (one-tailed) and is indicated by asterisks: \* $p \leq .05$ , \*\* $p \leq .01$ . Reaction and flight initiation distances varied significantly among the three treatments (one-way ANOVA: reaction,  $F_{2,72} = 21.30$ ,  $p < .001$ ; flight,  $F_{2,72} = 22.53$ ,  $p < .001$ ). All three treatments were significantly different from one another in pair-wise comparisons (Tukey's test, all  $p < .05$ ), except the comparison of flight initiation distances for nose-down and horizontal foraging fish.

guppies performing one of the three following behaviors: (1) nonforaging, (2) horizontal foraging, and (3) nose-down foraging. We carried out 25 replicates for each of the three behavioral activities. Individual guppies were used only once.

### Results

Foraging activity and body posture of individual guppies strongly influenced their ability to react to approaching predators and their risk of predation (Figure 1). More specifically, guppies foraging with their nose down reacted to the approaching predator later than nonforaging and horizontally foraging guppies (Figure 1). It thus appears that the nose-down (vertical) foraging posture reduced the likelihood of early reaction to an approaching predator more than any other posture.

Reaction distance in horizontally feeding fish was not significantly shorter than the flight initiation distance in nonforaging fish (Figure 1). Nevertheless, horizontally foraging fish allowed the predator model to advance a little closer before fleeing. The fact that flight behavior was delayed indicates that it is more costly (in terms of lost feeding opportunities) in the presence of food than in its absence. The difference between reaction and flight initiation distances was significant for those fish foraging in the horizontal posture. No such trade-off (between predator avoidance and foraging) was observed in nose-down foraging fish, probably because the predator had approached so closely in most cases that immediate flight was likely the optimal behavioral option. In fact, in 13 out of the 25 trials, vertically foraging guppies did not notice the predator at all until it stopped directly in front of them (closest distance about 2 cm).

The probability that no reaction to the approaching predator model nor flight behavior occurred was significantly different among the three treatments (independent *G* test (one-tailed): reaction,  $df = 2$ ,  $G = 14.02$ ,  $p < .001$ ; flight,  $df = 2$ ,

$G = 13.41$ ,  $p < .005$ ). The probabilities of no reaction ( $p = .44$ ) and no flight ( $p = .52$ ) occurring during a predator approach (and before the predator had stopped in front of the container) were highest for the nose-down foraging fish.

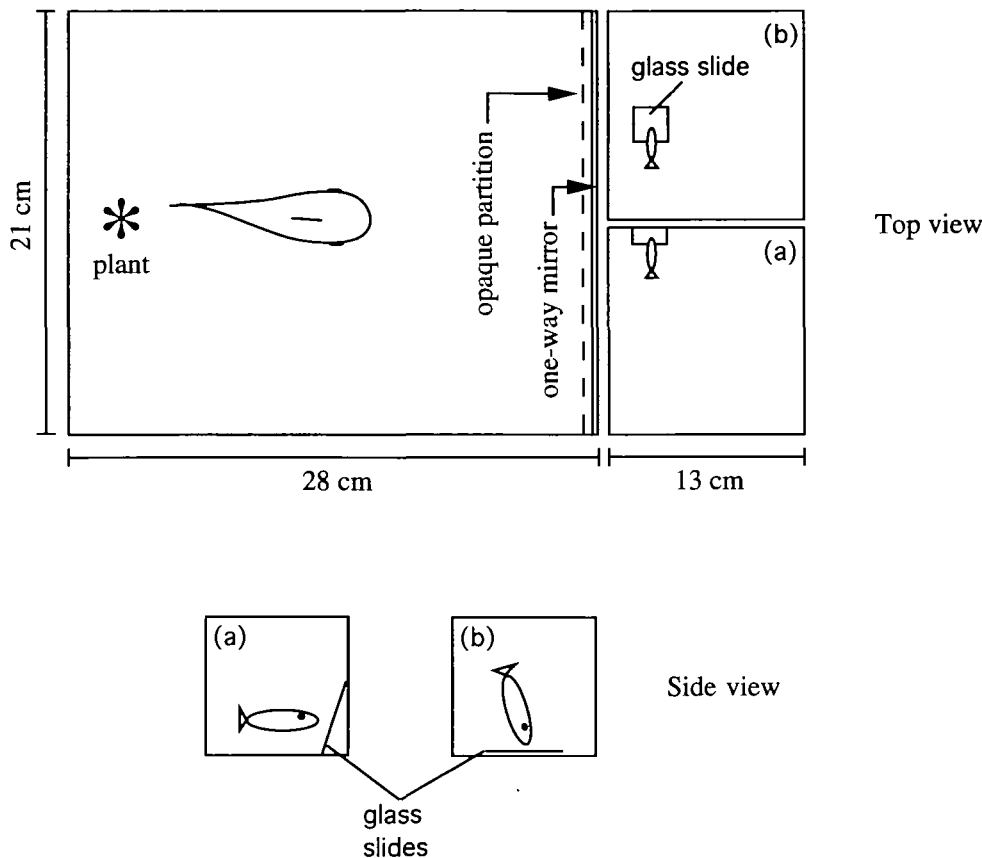
### Experiment 2: prey foraging posture and predator preference

The first experiment demonstrated that foraging guppies are less likely to react to an approaching predator than nonforaging ones, and that their particular foraging posture has a strong effect on their responsiveness to the predator. Nose-down foraging fish are less likely to react to an approaching predator than horizontally foraging ones. Based on these results, we tested in a second experiment the hypotheses that cichlid predators should prefer foraging fish over nonforaging ones as prey, and that they should prefer fish that forage nose down over ones that forage horizontally.

#### Materials and methods

The experimental apparatus (Figure 2) was similar to that used by Krause and Godin (1995) and comprised three separate clear plexiglass compartments, one which housed the blue acara cichlid predator (28 cm  $\times$  21 cm  $\times$  21 cm, L  $\times$  W  $\times$  H; 15 cm water depth) and two similar adjacent compartments (each 13 cm  $\times$  10 cm  $\times$  21 cm; 15 cm water depth), each containing one guppy. The bottom of all three compartments was covered with aquarium gravel, and water temperature was kept at 24°C–26°C. A one-way mirror was placed between the cichlid and the guppy compartments, and visual contact between predator and prey was prevented by an opaque plexiglass partition prior to the beginning of each trial. A piece of cardboard blocked visual contact between the two guppies. The cichlid compartment had a plastic plant on the bottom at the end opposite the mirror and was kept in dim light (about 2 lx), whereas the smaller guppy compartments were brightly illuminated overhead (about 1110 lx) by a SunGlo fluorescent tube (R.C. Hagen, Inc., Montréal, Canada) that simulates the energy spectrum of sunlight. The test cichlid in the larger compartment could see the guppies in the bright smaller compartments through the one-way mirror, but was not seen by the guppies. The one-way mirror thus prevented any predator-mediated change in the behavior of the guppies influencing the attack behavior of the cichlid (see Krause and Godin, 1995). The glass slides were placed on the bottom midline of the smaller compartments for nonforaging and nose-down foraging trials (Figure 2). For horizontal foraging trials, the glass slides were placed against the inner compartment wall. In all three treatments, the glass slides were 3 cm away from the one-way mirror (Figure 2).

For each trial, a single cichlid was introduced into the larger compartment and given at least 5 h to acclimate. During this period, the one-way mirror was blocked with the opaque partition to prevent the cichlid from viewing into the guppy compartments. The guppies were placed in their respective containers several hours prior to the trial. A glass slide was placed into each guppy compartment using long forceps, and the trial began when the cichlid was near the plant (its usual residence) and the guppies were foraging on the food-laden slides. The opaque partition was raised remotely, allowing the cichlid to view the guppies. We then recorded which of the two guppies was first attacked and subsequently how often each guppy was attacked by the cichlid during a 3-min period. An attack was defined as a rapid approach by the cichlid to within 2 cm of one of the guppy containers, typically culminating in a bite at the mirror in front of the selected fish. Usually the cichlid then returned to near the plant before launching a new attack. Additionally we measured the total

**Figure 2**

Top view of the experimental tank and apparatus used in experiment 2. The larger predator compartment, the smaller compartments containing one guppy each, and the one-way mirror and opaque partition separating predator and prey compartments are shown. The smaller inset illustrates a side view of the (a) horizontal foraging and (b) nose-down foraging postures of test guppies from the predator's perspective.

time spent by the cichlid within a 2 cm wide zone in front of each guppy container during the 3-min period. Observations were made from a hide to avoid disturbing the fish.

Cichlids were presented with three binary choices of two individual guppies, differing in activity and feeding posture. These are (1) nonforaging versus horizontally foraging fish, (2) nonforaging versus nose-down foraging fish, and (3) horizontally versus nose-down foraging fish. In the case of nonforaging guppies, we only analyzed trials in which the test fish was at about the same distance (3 cm) from the one-way mirror as the foraging fish after the opaque partition was removed. For each of the above three treatments, 20 replicates were carried out. Order of treatments and side assignments were randomized. Individual cichlids were used only once (i.e., a total of 60 cichlids were tested). Guppies were used repeatedly in subsequent trials (maximum of two) on the same day and were then returned to their holding tank, where they mixed with other fish.

To investigate whether the body orientation of stimulus guppies had a potential confounding effect in the above choice experiments, we presented cichlids with binary choices of guppies in two treatments in a separate series of trials (using the same apparatus and protocol described above): (1) nose-down foraging fish facing broadside or toward the predator versus nose-down foraging fish facing away from the predator, and (2) nose-down foraging fish facing broadside or toward the predator versus horizontally foraging fish (which are always broadside). In the first treatment, we controlled for body posture but varied body orientation (toward or away from the predator). In the second treatment, we controlled for body orientation but varied body posture. A problem with the experimental design is that we could not directly influence the body orientation of fish. Controlling for body orientation here therefore means that we selected those trials

(from a larger number of initial trials) in which the stimulus guppies were oriented as indicated above for treatments 1 and 2 at the instance of attack by the cichlid. A guppy's body orientation was defined as facing away if the angle formed by the long body axes of predator and stimulus fish was larger than  $90^\circ$ . Conversely, an orientation toward the predator was defined as any angle  $\leq 90^\circ$ . Since guppies continuously change their body orientation, we did not measure any additional predator attack parameters, such as number of subsequent attacks or attack duration (see above). For treatments 1 and 2, we obtained 11 and 10 replicates, respectively, using different fish.

Data on percentage frequency of attacks on, and percentage of time spent near, either stimulus guppy by the cichlids were normalized by arcsine transformation and analyzed using a two-way, repeated-measures ANOVA to test for the effects of experimental treatment and guppy activity (feeding posture) within treatments. We used such an ANOVA because the time spent near one guppy is strictly speaking not independent of the time spent near the other guppy for any given test cichlid. The *G* test (one-tailed) or paired *t* test (one-tailed) was used for comparison between guppies within a given experimental treatment.

### Results

The cichlid predators generally preferred foraging over nonforaging guppies with respect to all three attack criteria (first choice, duration, and frequency of attacks; Figure 3). The predator's preference for foraging guppies over nonforaging ones was greater when the guppies were foraging in the nose-down (vertical) posture than in the horizontal posture (Figure 3). Within the category of foraging fish, nose-down foraging fish were significantly preferred over horizontally foraging fish with regard to all three attack criteria (Figure 3).



indicated by asterisks:  $***p \leq .001$ . There were no significant differences in cichlid attack duration (repeated-measures ANOVA:  $n = 40$ ,  $F_{1,38} = 2.55$ ,  $p = .12$ ) and attack frequency ( $F_{1,38} = 1.46$ ,  $p = .23$ ) when they were given a choice between nonforaging and foraging guppies (treatments 1 and 2). The cichlids preferentially attacked foraging guppies first ( $G$  test,  $df = 1$ ,  $G = 8.40$ ,  $p < .005$ ; panel a), subsequently attacked them significantly more frequently ( $F_{1,38} = 4.23$ ;  $p < .05$ ; panel b), and spent significantly more time ( $F_{1,38} = 14.60$ ;  $p < .001$ ; panel c) near them than nonforaging fish.

cichlids and guppies were used only once (i.e., a total of 30 cichlids and 30 guppies were tested; these fish were different from those used in experiment 2). Each cichlid was given 10 min to attack the guppy presented. Following the first attack, the cichlid was then allowed to chase and capture the guppy, but was prevented from launching subsequent attacks if it had failed to capture the prey on its first attempt. If the cichlid did not attack within 10 min, it was removed from the tank and the trial was discarded and subsequently repeated with another cichlid and guppy. From behind a hide we recorded (to the nearest centimeter) the distance from the approaching cichlid at which the guppy initiated its escape (rapid darting away from the predator), using a grid located on the bottom of the tank, and whether or not the guppy was captured. On average, the distance between cichlid and guppy was about 25 cm at the beginning of the attack. We observed in the field (Krause J and Godin J-CJ, personal observations in Trinidadian streams) that cichlids typically attack guppies from distances of  $\leq 40$  cm.

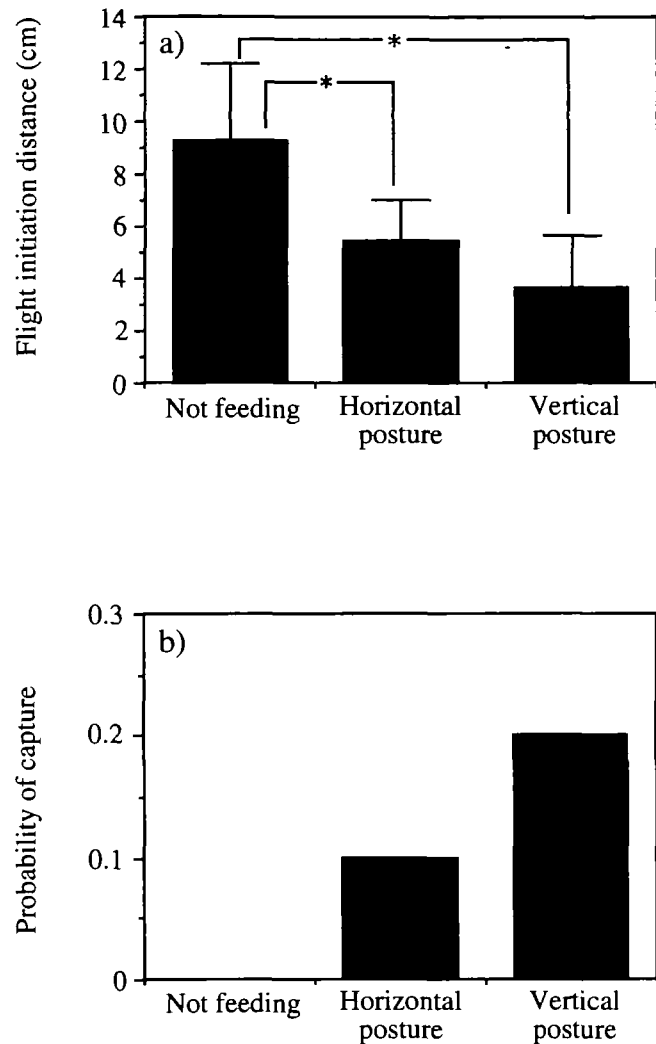
### Results

Guppies that were not foraging initiated flight furthest from the attacking predator, whereas fish that were foraging nose down showed the shortest flight distances (Figure 4a). Fish foraging horizontally had intermediate flight initiation distances. All of the nonforaging guppies successfully avoided capture, whereas some of the foraging ones were captured by the cichlids (Figure 4b). Individual guppies that were foraging nose down were more likely to be captured than those foraging horizontally, given that they were approached by the predator (Figure 4b).

### DISCUSSION

The body posture of foraging guppies strongly influenced their responsiveness toward approaching predators and their predation risk. Fish that were foraging in the nose-down (vertical) posture were the least likely to react to an approaching predator and the most at risk of capture by cichlid fish, which is analogous to gazelles grazing head down (FitzGibbon, 1989). These results were unlikely to have been confounded by the guppy's body orientation relative to the predator, because in the additional series of trials in experiment 2 we showed that the different body orientations (toward or away from the predator) in guppies did not influence the cichlids' choice, and the preference of cichlids for nose-down foraging fish (over horizontally foraging fish) was exclusively due to the difference in foraging postures (body orientation was controlled for). In addition, the presence of a food resource caused guppies (horizontally foraging ones only) to delay their flight compared to fish that were not given any food. This is consistent with studies on crayfish (*Procambarus clarkii*; Bellman and Krasne, 1983), house sparrows (*Passer domesticus*; Barnard, 1980), water striders (*Aquarius* (= *Gerris*) *remigis*; Ydenberg and Dill, 1986), and brook trout (*Salvelinus fontinalis*; Grant and Noakes, 1987), and likely reflects a trade-off between the expected benefits (continued foraging gains) and costs (greater risk of mortality) of delayed flight in animals (Ydenberg and Dill, 1986).

The observed preference of cichlid predators for nose-down foraging individuals indicates that they can differentiate among potential prey based on their foraging activity and body posture, and thus take advantage of the prey's decreased ability to react to approaching predators when choosing among those available. Despite the low levels of mortality in the third experiment, the results regarding flight initiation distances support our hypothesis that predation risks are higher for foraging fish, and particularly for those foraging nose



**Figure 4**

(a) Mean (+SD) flight initiation distance of individual guppies and (b) the hunting success of cichlids attacking them (as expressed by the ratio of the number of guppies captured to the number of predator approaches observed) in relation to the guppy's activity (i.e., not foraging, horizontally foraging, or nose-down foraging). Ten guppies and 10 cichlids were used for each category of behavioral activity. Flight initiation distance varied significantly among guppies that were performing different behaviors (one-way ANOVA:  $n = 30$ ,  $F_{2,27} = 14.07$ ,  $p < .001$ ; panel a). Significance in panel a was determined using a Tukey's test for multiple comparisons, and is indicated by asterisks:  $*p \leq .05$ . Although in the expected direction, differences in risk of mortality among the three treatments were not significant (independent G test (one-tailed):  $n = 30$ ,  $df = 2$ ,  $G = 2.99$ ,  $p > .15$ ; panel b).

down than for nonforaging fish. Relatively low mortalities in all treatments of experiment 3 may be due to a number of factors. First, the body size ratio between the blue acara cichlids and guppies (about 3.3:1) was rather small. Larger cichlids would probably have been more successful. Second, the raising of the opaque partition in the experimental tank may have alarmed the guppies to a certain extent, thereby rendering them more wary than otherwise. Third, the small dimensions of the tank did not allow the cichlid to attain high accelerations, which may be necessary for successful attacks.

The experimental cichlids were obtained from a local aquarium shop. We therefore do not know whether they had any previous experience with foraging guppies. The guppies

that were fed to the cichlids in their holding tanks prior to the experiments were typically consumed immediately and before the guppies could begin foraging. It is therefore unlikely that the cichlids gained any information regarding the effects of prey body posture on the ability of prey to react to approaching predators from such prior hunting experience which could explain their attack preference in the current study. An alternative to this learning hypothesis is that the cichlids simply attacked the most visually conspicuous prey when given a choice. Foraging guppies might have been more conspicuous to cichlids than their nonforaging conspecifics, owing to the continuous antero-posterior oscillation of the long axis of their body when picking food flakes from the slides. Preliminary trials revealed no difference in the duration of foraging bouts and in the number of bites per bout between nose-down foraging and horizontal foraging. This excludes the possibility that nose-down foraging fish were chosen for their potentially higher activity [predator choice of prey based on their activity level has been demonstrated by Kislalioglu and Gibson (1976) and Krause and Godin (1995)]. However, it has been shown for a different cichlid species (*Haplochromis burtoni*) that territorial males are able to clearly distinguish between nose-down and horizontal body postures of staged intruders (resident males attacked dummies in a nose-down posture more often) (Heiligenberg et al., 1972). Therefore, retinal receptors in cichlid fish may be more responsive to vertically oriented stimuli than to horizontal ones.

Although nose-down foraging is a common foraging posture in shoaling fish (e.g., Dussault and Kramer, 1980; Godin, 1986; Pitcher and Parrish, 1993; Wootton, 1990), the current study is the first linking foraging postures with an individual's ability to react to approaching predators and risk of mortality to predation in fishes. Our results strongly suggest that nose-down foraging is costly in terms of predation risk. This conclusion is supported by the observation that killifish (*Fundulus diaphanus*) reduce the duration of their nose-down posture when searching for benthic food in the presence of a fish predator (Godin, 1986). Since predation risk is also a function of group size (Pitcher and Parrish, 1993), it may be worthwhile to investigate whether nose-down foraging occurs more often (per capita) and over longer bouts in larger groups. The fact that nose-down foraging attracts hungry conspecifics (Krebs et al., 1972; Pitcher and House, 1987; Pitcher and Magurran, 1983) and predators (FitzGibbon, 1989; this study) further suggests that this behavior is costly in terms of both food competition and predation risk. Based on our results, we therefore expect fish to reduce the rate of nose-down foraging to a greater extent than their rate of horizontal foraging when under threat of predation.

Milinski (1984) demonstrated that sticklebacks (*Gasterosteus aculeatus*) foraging on high prey densities were less likely to react to an approaching predator than individuals foraging on low prey densities. This is consistent with the findings of Godin and Smith (1988), who reported that individual risk of mortality to predators was positively correlated with food density and the duration of prior food deprivation (both of which increased feeding rate) in the guppy. In conclusion, these studies show that predation risk increases the more an animal's attention is taken up by food searching and feeding. In the current study, we kept food density and the nutritional state of test fish constant. The observed differences in the ability to react to approaching predators between horizontally and nose-down foraging fish were assumed to be brought about merely by the different orientation of the body axis (i.e., foraging posture). This brings us back to the question: why should we expect nose-down foraging to be more risky than horizontal foraging? We suggest a combination of three determinants: (1) the visual horizon that an animal can scan

for predators is smaller, (2) the probability of obstacles obstructing the view is greater closer to the substratum, and (3) it might be more difficult for a fish to perform a fast-start escape (or any kind of predator avoidance behavior) in a nose-down posture. All of these factors should be amenable to experimental testing.

Previous studies have shown that proximity of prey to the predator (FitzGibbon, 1989), the spatial position of individual prey within a group (Krause, 1994), the sex, age, and general condition of the prey (FitzGibbon, 1989, 1990; Kruuk, 1972; Schaller, 1972), and factors such as prey color, body size and shape, and general activity (Ibrahim and Huntingford, 1989; Kislalioglu and Gibson, 1976; Krause and Godin, 1995) can determine which prey is attacked by a predator. Few other studies (e.g., FitzGibbon and Fanshawe, 1988; Godin and Davis, 1995) have shown prey selection by predators based on specific behaviors in prey other than general activity level. It is obvious, however, that the proximate mechanism of prey selection by predators, especially in the context of prey age and condition, is likely based on an assessment of prey behavior by predators (Kruuk, 1972). FitzGibbon (1990), for instance, pointed out that the head-down posture of prey animals could indicate two things to the predator. First, that the animal is less vigilant and therefore less likely to show any reaction to an approaching predator (than when in a head-up posture), and second, that the animal may be in poor condition (individuals in poor condition are likely to spend more time on foraging than on vigilance to regain their energy balance). Both reduced vigilance and poor condition of prey should increase the chances of a successful capture for the predator. An investigation of the relationship between condition factors and body posture (and vigilance, respectively) in the field, however, is complicated by the fact that body condition of free-ranging prey animals is difficult to visually assess at a distance.

Our study controlled for differences in predator-prey distance and for positional effects, body orientation relative to the predator, body size, body condition, and sex in prey individuals. The fact that the cichlid fish still preferred to attack nose-down foraging guppies over horizontally foraging guppies and nonforaging ones in the absence of the above differences indicates that body posture was likely the key determinant of prey choice in cichlid fish under the given laboratory conditions. Since guppies in nature forage in either the horizontal or nose-down posture (Dugatkin and Godin, 1992; Dussault and Kramer, 1980; Godin J-GJ and Krause J, unpublished data), they may well experience differential risk of predation from their cichlid fish predators depending on whether or not they are foraging and, if so, on which particular foraging posture they adopt.

Guppies adopting the horizontal posture (whether or not they are feeding) should benefit in two ways. They are more likely to respond to an approaching predator earlier (and therefore have more time to avoid it) and less likely to be selected by the predator than conspecifics that are foraging nose down. These benefits may have important implications for the evolution of vigilance patterns in groups. Packer and Abrams (1990) pointed out that any optimal strategy for vigilance strongly depends on the prey selection process of predators and on the extent to which nonvigilant individuals benefit from the presence of vigilant group members. Their models suggest that if predators can assess differences in the vigilance levels of their prey, then selfish groups (in which individual vigilance levels are independent of the vigilance levels of other group members) should always be more vigilant than cooperative groups. This is contrary to previous models (Grafen, 1979) that predicted individual vigilance levels to be higher in cooperative groups than in selfish ones.

Our data strongly suggest that individuals that detect and react to predators have a significant survival advantage over those that do not. This means that high levels of vigilance in groups could be explained without invoking cooperative vigilance among group members (see also Lima, 1994; McNamara and Houston, 1992).

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