

Within-group variation in the willingness to risk exposure to a predator: the influence of species and size

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The costs and benefits associated with feeding in the vicinity of a predator should vary within and among species, depending on an individual's vulnerability to a predator. In this paper, we investigate how willingness to risk exposure to a predator in order to gain access to food is expressed within groups of fish. We provided groups of six individually marked brook sticklebacks (*Culea inconstans*) and fathead minnows (*Pimephales promelas*) with the opportunity to feed in safety, or in the presence of a single predator (walleye, *Stizostedion vitreum*). Sticklebacks and fathead minnows are commonly found in the same locations at the same time, but sticklebacks also possess armour and spines that provide defence against some predators. Despite this morphological variation, patterns of individual behaviour were consistent between species. While feeding close to the predator, there was a positive relation between the size of the individual and the proportion of food consumed. No relation existed on the side farthest from the predator. These data suggest that fish may risk exposure to predators to exploit size-related differences in vulnerability to gain a competitive advantage for access to food.

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When animals forage under the risk of predation, they often forsake an increased feeding rate to reduce their probability of predation. For mobile animals, this usually means modifying behaviours to reduce the probability of encountering predators, or if predators are encountered, reduce the probability of death associated with the encounter. Behavioural options include altering the areas in which they forage, the types of food that would appear in their diet, and even the method by which they consume a particular food item (see review by Lima and Dill 1990). More recently, there has been growing interest in other consequences associated with predation risk, including its influence on relative competitive abilities (Persson 1991, Abrahams 1994), parental care (Magnhagen 1992, 1995, Mappes and Kaitala 1995, Svensson 1995), mate choice (Forsgren 1992, Hedrick and Dill 1993, Csada and Neudorf 1995, Briggs et al. 1996, Godin and Briggs 1996), and physiology (Gosler et al. 1995, Koskela et al. 1996).

All decisions involving the risk of predation are assumed to represent a balance between the benefits and costs of risking exposure to a predator. However, identifying those individuals most likely to risk exposure to a predator depends upon relative benefits and costs. For example, not all individuals will be equally vulnerable to a predator (i.e., the potential costs may not be equal). Those that are less vulnerable (e.g., larger, faster, etc.) should be the most willing to risk exposure to the predator as they pay less for an equivalent gain. Alternatively, the potential benefits associated with risking exposure to a predator may not be equivalent for all individuals. Those individuals that are competitively inferior may forsake a limited opportunity to gain access to food in safety for a much higher feeding rate while feeding in the presence of the predator. If relative competitive ability is inversely related to vulnerability to predators, then we make the opposite predic-

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tion that the most vulnerable individuals are the most likely to risk exposure to a predator to gain access to additional food.

The presence of predators can provide an opportunity that can be exploited by others. Here, we first determine whether there is individual variation in the willingness to risk exposure to a predator in order to exploit this opportunity. We then determine whether some individuals use the presence of a predator to enhance their foraging ability beyond what they are able to obtain in safety.

Methods

We examined differences in behaviour using two species of freshwater fish, brook sticklebacks (*Culaea inconstans*) and fathead minnows (*Pimephales promelas*). These two species share many similar life history characters, occupy similar microhabitats, overlap in diet, and are likely consumed by the same predators (Abrahams 1994). However, these two species are morphologically distinct. Brook sticklebacks possess lateral plates, and dorsal and ventral spines that reduce their vulnerability to some predators. Fathead minnows have no such antipredator morphology.

For these experiments, brook sticklebacks were obtained by minnow trap during May to July 1992 from the University of Manitoba's field station at Delta Marsh, located at the southern tip of Lake Manitoba. The fathead minnows were obtained in 1997. Fish were maintained by species in separate, 500-l flow-through fibreglass holding tanks in the animal holding facility at the University of Manitoba.

For these experiments, we used 30 sticklebacks and 18 fathead minnows divided into monospecific groups of six individuals. Within each group, the fish ranged in weight from approximately 0.8 to 1.5 g for the sticklebacks and 0.8 to 5 g for the fathead minnows. Each individual received a unique, colour coded tag that was a modified version of a tag developed by Chapman and Bevan (1990). These tags allowed individual identity to be determined throughout these trials. Colour combinations were randomly assigned to individuals within each group.

Trials were conducted in a 120-cm-long, 200-l aquarium that was divided into three chambers. The two end chambers were each 30 cm long and the central chamber was 60 cm long. Each chamber was separated by a transparent Plexiglas partition and illuminated by an overhead halogen light. At each end of the central chamber, automated feeders (Abrahams 1989) provided a constant flow of 75 brine shrimp (*Artemia salina*) over a 25-min period. This represents a maximum amount of 0.48 g (wet weight) of food provided to an average mass of 6.4 g of fish (an amount of food that

can easily be consumed without satiation). Food traps were located beneath each feeder to prevent unconsumed food from accumulating over the course of an experiment. As the majority of the fish were expected to feed in safety, any fish feeding in the presence of a predator should have fewer competitors and a higher feeding rate.

Before the trials, the fish were trained to feed on the brine shrimp provided by the automated feeders. A neutral grey background allowed all individuals (and their identifying tags) at each feeder to be monitored by two video cameras. This procedure allowed us to accurately record how much food each individual at both sites obtained.

For these trials, a hatchery reared, 51-g walleye (*Stizostedion vitreum*) was used as the predator. This fish was selected because its aggressive behaviour provided a strong predatory stimulus. Three treatments were used in these trials, a predator located on the left side of the aquarium, the right side, or no predator in the apparatus. The order of these treatments was determined randomly. Trials were conducted two times per day for two consecutive days. During the trials, the food provided by the feeders was the fishes' only source of food. Opaque partitions were placed over the transparent partitions between trials to minimize exposure to the predator, limiting the chance of habituation occurring during the trial.

The protocol for all trials was the same. At 10.00 h, the feeders were loaded, the opaque partitions were removed from both ends, the cameras activated, and the flow of food from each feeder was started. The predator was placed in the appropriate chamber 16 h before beginning an experiment. Videotapes were analysed to determine individual patterns of habitat use and food consumption.

After the data had been obtained for one group, all individuals were sacrificed by an overdose of 2-phenoxyethanol. Their length and wet weight was determined, and they were dissected to determine sex. An average mass was determined for each group member, and relative mass was then calculated by subtracting the average group mass from each individual's mass.

Results

Both the groups of fathead minnows and brook sticklebacks avoided using the feeder located near the predator. Significantly more sticklebacks fed in the safe location than in the presence of the predator ($t_8 = 6.05$, $P < 0.001$). A similar result was observed for the fathead minnows ($t_4 = 4.32$, $P = 0.012$).

The presence of the predator exerted a significant influence on the relation between size and the proportion of food consumed for both the sticklebacks and

the fathead minnows (Fig. 1). When both the fathead minnows and the brook sticklebacks fed in the presence of the predator, relative size had a significant influence on the proportion of food that they obtained (Fig. 1). This result was not observed in the absence of the predator (Fig. 1). The mechanism responsible for this result was the behaviour of the smallest individuals. In the presence of the predator, there was general avoidance of this location by the smallest individuals. This allowed the largest individuals to obtain a relatively large proportion of the total amount of food at the dangerous location. It is important to note that without the presence of the predator, the larger fish in these experiments were unable to increase their access to food (Fig. 1).

To measure the influence of the predator on individual foraging decisions, we used a *t*-test to compare individual feeding rates in the presence of the predator to those in the control situation (no predator in the apparatus). Individuals were then categorized into three groups; those that preferentially fed in the presence of the predator (hazard-prone), those that avoided feeding in the presence of the predator (hazard-averse), and those that did not exhibit a significant change in their feeding behaviour. Using these criteria, eight sticklebacks were classified as hazard-prone, nine were hazard-averse, and twelve exhibited no significant change in their feeding behaviour in response to the presence of the predator. Only one individual never risked exposure to the predator (a male, 0.984 g from group 2). There was a significant difference in size between these three groups (ANOVA, $F_{2,27} = 4.08$, $P = 0.028$) with the hazard-prone group being significantly larger than the hazard-averse group (Bonferroni's test, $P = 0.026$). There was no difference in the sex ratio between these groups.

Of the 15 fathead minnows used in this experiment, four were never observed to feed in the presence of the

predator. Three of these were the smallest individuals used in these experiments. Using the same criteria as above, two individuals were classified as hazard-prone and nine as hazard-averse. The remaining fish reduced their feeding rate in the presence of a predator, but not significantly. The hazard-prone group had a greater mean weight (3.48 g) than the hazard-averse group (2.54 g), but there was no statistically significant influence of size on these groups (ANOVA, $F_{2,15} = 1.22$, $P = 0.32$).

Discussion

Our experiments demonstrated individual variation in decisions involving the risk of predation. In general, larger individuals of both species were more willing to feed in the presence of the predator, with some individuals preferentially feeding in the presence of the predator. Our data also demonstrate that the presence of the predator allowed these larger individuals to increase the proportion of food they were able to obtain from the feeder, a feat they were unable to accomplish while feeding in safety.

Previous studies have demonstrated that sticklebacks are more willing to risk exposure to a predator than fathead minnows (Abrahams 1994). This difference between species was attributed to the antipredator morphology of the sticklebacks and the subsequent reduced susceptibility to predators. Our data suggest that intraspecific variation in behaviour is generated by the same mechanism. Within a species, it is generally assumed that susceptibility to a predator is inversely related to body size (Werner and Gilliam 1984, Johnsson 1993). We believe that these relatively larger fish may exploit this difference in susceptibility to gain a competitive advantage while feeding in the presence

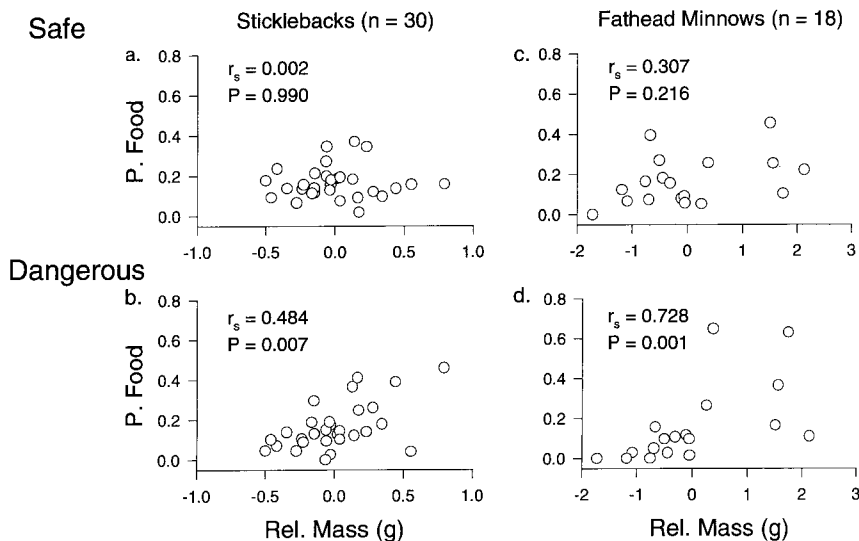


Fig. 1. The effect of predator position on the relation between the proportion of food consumed and the relative size of brook sticklebacks and fathead minnows. Data correspond to the mean result for individuals. Panels a and c summarize the results for the safe side, b and d summarize the results for the dangerous side. Numbers in the upper left hand corner of each panel are the Spearman correlation coefficient, and its probability. These data demonstrate that only in the presence of a predator is there a significant positive correlation between relative mass and the proportion of food consumed.

of a predator. The absence of this benefit in safety may not allow this size difference to translate into a competitive advantage.

Habitat selection decisions of the relatively large individuals were responsible for the negative correlation between body mass and feeding rate in the presence of a predator. The larger fish (both sticklebacks and minnows) tended to spend more time feeding at the dangerous location and due to the relatively small number of individuals feeding at that location, were able to effectively defend the site and obtain a disproportionately large share of the food. The large number of individuals using the safe feeders defeated any attempt to monopolize food at that location.

Utne et al. (1997) also investigated individual variation in perch (*Perca fluviatilis*) feeding in the presence of a predator. In their experiments, they observed that all fish in the absence of a predator achieved size-specific growth rates that were unaffected by intraspecific competition. However, when a predator was present, growth rates of smaller fish were reduced. They interpreted their result as being generated by variation in relative competition at the safe site. They argued that the presence of the predator increased the density of individuals at the safe site, and made it more difficult for the smaller fish to gain access to food at that location. They also did not observe any class of fish obtaining a growth benefit associated with the presence of the predator. A potential difference in their results compared to ours may have been that all fish in their experiment were unable to successfully exploit the dangerous location for extended periods of time. As a consequence, total food in their apparatus also declined with the presence of the predator. In our experiments, there was continuous use of the dangerous location throughout our observations, with some individuals preferring to feed at the dangerous location.

Our results are consistent with recent work by Coleman and Wilson (1998). They not only observed variation between individuals in their willingness to risk exposure to a predator, but also context-specific variation in their behaviour. They argue that natural selection may act to maintain a mix of reactions to a given situation. Relative abundance within a group can also affect the willingness to risk exposure to a predator. Using three-spine sticklebacks (*Gasterosteus aculeatus*), Peuhkuri (1998) demonstrated that larger individuals are more wary when there are few of them within a group. This result was not observed with smaller individuals. The explanation for this result is the "oddy effect" when individuals are distinct from others within a group because of their size, they are at greater risk when attacked by a predator. This result suggests that variation in susceptibility may be compensated by an increased probability of attack. As our groups were relatively small in size, and contained a range of body sizes, we did not observe the oddity effect influencing our results.

Previous work on group dynamics and risk of predation has suggested potential benefits for subordinate individuals. In a flock of great tits (*Parus major*), it is the subordinate individuals that return to feed the most quickly after being disturbed by a predator (DeLaet 1985). It is during this brief but dangerous time period that these individuals can feed at a rate unconstrained by dominant individuals. There is no reason to assume that there is any variation in vulnerability to predators between subordinate and dominant individuals, and thus this is a different situation compared to our experiments. The feeding opportunity provided the subordinate individuals likely provides information to the dominant individual on the relative risk associated with returning to a feeding location.

While competitively inferior individuals may periodically obtain a transient feeding benefit associated with the risk of predation, the most advantageous position is to be the dominant competitor within a group. As has been observed by Metcalfe and Thomson (1995), European minnows (*Phoxinus phoxinus*) are able to recognize the competitive abilities of other individuals and preferentially associate with poor competitors. The superior competitors should reap the rewards of the group's enhanced ability to locate food as well as its antipredator benefits, while also receiving more than its share of the resource. Our results are consistent with this interpretation.

So some of the individual variation in the willingness to risk exposure to a predator may be explained by the interaction between relative vulnerability and competitive ability. In the absence of a predator, differences in size are not sufficient to generate variation in competitive ability. Only in the presence of a predator do the size differences translate into differences in vulnerability. Larger individuals can then exploit these differences in vulnerability to obtain a competitive advantage for access to resources when feeding in the presence of a predator.

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