

# The interaction between antipredator behaviour and antipredator morphology: experiments with fathead minnows and brook sticklebacks

Mark V. Abrahams

**Abstract:** Prey species have two fundamental strategies for reducing their probability of being killed by a predator: behavioural modification and morphological defenses. It is hypothesized that prey species which possess morphological defenses should exhibit less behavioural modification in response to predation risk than species lacking such defenses. Experiments were conducted to examine behavioural modification by armoured (brook sticklebacks, *Culea inconstans*) and unarmoured (fathead minnows, *Pimephales promelas*) prey species foraging in the presence of a predator (yellow perch, *Perca flavescens*). Two experiments measured habitat avoidance and reactive distance to an approaching predator. The results of these experiments were consistent with the hypothesis. Compared with fathead minnows, brook sticklebacks exhibited relatively little behavioural modification in response to the presence of a predator, both in terms of avoiding dangerous areas and in their reactive distance to an approaching predator. Sticklebacks, however, graded their reactive distance to an approaching predator in relation to both their body size and group size. These data suggest that the morphology of brook sticklebacks and their behavioural sensitivity to predation risk may allow them to efficiently exploit habitats that contain predators.

**Résumé :** Il existe deux stratégies fondamentales par lesquelles des proies peuvent réduire leurs chances d'être tuées par un prédateur : des modifications de leur comportement ou des systèmes morphologiques de défense. Une espèce de proie qui possède un système morphologique de défense devrait hypothétiquement avoir moins recours à des modifications de son comportement en réaction aux risques de prédation qu'une espèce sans défenses morphologiques. Des expériences ont permis d'étudier les modifications du comportement chez une espèce de proie armée (Épinoche à cinq épines, *Culaea inconstans*) et une espèce non armée (Tête de boule, *Pimephales promelas*) cherchant leur nourriture en présence d'un prédateur (Perchaude, *Perca flavescens*). Deux expériences ont servi à mesurer la fuite loin de l'habitat et la distance de réaction à l'approche du prédateur. Les résultats des expériences confirment l'hypothèse. Comparativement aux ménés, les épinoches ont peu modifié leur comportement en présence du prédateur (fuite loin de l'habitat ou distance de réaction à l'approche du prédateur). Il a cependant été remarqué que les épinoches ajustent leur distance de réaction au prédateur en fonction de leur taille et du nombre de poissons dans leur groupe. Ces données semblent indiquer que la morphologie de l'Épinoche à cinq épines et sa sensibilité aux risques de prédation lui permettent d'exploiter efficacement les habitats où se tiennent des prédateurs.

[Traduit par la Rédaction]

## Introduction

It is now well recognized that predators can exert two negative effects on the fitness of individual prey animals: the direct effect of consumption and the effect of behavioural modification due to predator intimidation (i.e., the risk of predation). This latter effect has attracted considerable attention (for a review see Lima and Dill 1990) and can modify the manner in which prey engage in almost all activities important to their fitness (e.g., feeding, courtship, etc.).

However, recent experiments have demonstrated variation in the magnitude of different prey species' response to a common threat (Abrahams and Healey 1993; Werner 1991). This variation may be due to species differences in life-history characteristics and susceptibility to predators (Abrahams and Healey 1993).

The probability of being killed by a predator can be described by three parameters: the rate of encounter between predator and prey, the probability of death given an encounter, and the time spent vulnerable to encounter with a predator (Lima and Dill 1990). Prey can modify their behaviour to affect all three of these parameters, and it is generally assumed that the magnitude of this response will be positively correlated with a reduction in the mortality rate. Behavioural mechanisms that reduce mortality can be expen-

Received January 16, 1995. Accepted July 28, 1995.

M.V. Abrahams. Department of Zoology, University of Manitoba, Winnipeg, MB R3G 1J5, Canada (e-mail: abrahams@bldgduff.lan1.umanitoba.ca).

**Table 1.** Comparison of the life-history characteristics of fathead minnows and brook sticklebacks.

Character	Fathead minnows	Reference	Brook sticklebacks	Reference
Parental care	Male guards eggs that adhere to surfaces	Scott and Crossman 1973 Markus 1934	Male guards eggs that are laid in its nest	Wootton 1976
Mating system	Polygynous, repeat-spawning by females; sexually dimorphic when breeding	Scott and Crossman 1973 Markus 1934	Polygynous, repeat-spawning by females, sexually dimorphic when breeding	Wootton 1976
Egg size	Approximately 1.15 mm	Markus 1934	Approximately 1.3 mm	Weselowski 1974
Age at maturity	After 1 year	Scott and Crossman 1973	After 1 year	Scott and Crossman 1973
Mortality	High after spawning (approximately 80%)	Markus 1934	High after spawning	Weselowski 1974
Maximum age	3 years	Markus 1934	3 years	Weselowski 1974
Maximum size	83 mm	Scott and Crossman 1973	87 mm	Scott and Crossman 1973
Female gonado-somatic index	13–17%	Carlson 1967	10–20%	Braekvelt and McMillan 1967

sive, as they often constrain or compromise other activities that are important to individual fitness (Skelly 1992). Antipredator behavioural strategies therefore provide a range of options to prey species. At one extreme, prey may elect to not make any behavioural changes in response to the presence of predators. With this option, there would be little cost to antipredator behaviour but prey would suffer a high probability of mortality. At the other extreme, prey may devote substantial effort to avoiding predators. They would have a low probability of being killed by a predator but would pay a high cost for their antipredator strategy (including direct energetic costs and lost opportunities to pursue other activities; for examples see Lima and Dill 1990).

In addition to behavioural modification, susceptibility to predators will also be reduced by morphological traits. Cryptic camouflage can reduce the probability of being detected by a predator. Armour, spines, and chemical deterrents (both internal and external) can reduce the probability of an animal being killed by a predator once detected (Edmunds 1974). For most vertebrates, these traits are assumed to be fixed and can only be changed between generations through natural selection. However, Brönmark and Miner (1992) have shown that crucian carp (*Carassius carassius*) increase their body depth and consequently become less susceptible to gape-limited predators after only 12 weeks of exposure to piscivorous pike (*Esox lucius*). Some invertebrates (e.g., *Daphnia pulex*) are capable of cyclomorphic responses to the presence of predators (Dodson 1989). During periods of high predator density, many species adopt an antipredator morphology that renders them less susceptible to predators.

Everything else being equal, armoured species should have a reduced probability of mortality per encounter with a predator than would unarmoured species. Since significant costs have been identified with antipredator behaviour (Lima and Dill 1990), I predicted that armoured species should be able to benefit from their morphology by reducing the magnitude of their antipredator behaviour. I tested this hypothesis by examining two mechanisms whereby prey must modify their behaviour in response to predator intimidation: foraging in areas that contain a predator and their reactive distance to an approaching predator.

## Methods

The species used in this study were fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culea inconstans*). Both species are very common in the Atlantic watershed of North America and often occur together. For example, in southwestern Manitoba, at least one species is observed in 57% of surveyed streams and lakes and the two co-occur in 35% (data from the Manitoba Department of Natural Resources, Fisheries Branch). Sticklebacks possess armour and spines (for a description see Wootton 1984) that render them less susceptible to being consumed by a predator than fathead minnows, which lack these morphological defenses. In the presence of a northern pike (*Esox lucius*), brook sticklebacks had a survival time twice that of fathead minnows (Robinson 1989). In a similar experiment, Hoyle and Keast (1987) demonstrated that brook sticklebacks were less susceptible to predation by a largemouth bass (*Micropterus salmoides*) than similar-sized bluntnose minnows (*Pime-*

**Table 2.** Total lengths (mm) and wet masses (g) of the five different groups of fathead minnows and brook sticklebacks used in experiment 1.

Group	Fathead minnows		Sticklebacks	
	Length	Mass	Length	Mass
1	50.0±1.41	1.466±0.067	45.3±5.44	0.622±0.202
2	48.0±6.16	1.437±0.450	49.0±2.83	0.818±0.123
3	46.0±3.27	1.139±0.183	45.0±2.00	0.607±0.022
4	49.3±6.02	1.456±0.397	54.7±2.49	0.921±0.104
5	40.7±1.89	0.881±0.167	43.0±2.16	0.685±0.084

Note: Values are given as means ± SE.

*phales notatus*) (a species similar to fathead minnows both phylogenetically and morphologically). Sticklebacks and fathead minnows overlap in their diet (both consume small aquatic invertebrates and filamentous algae; Scott and Crossman 1973) and are commonly observed in the same habitats at the same time (M.V. Abrahams, unpublished data). The two species are of similar size and are preyed upon by piscivorous fishes, birds, and insects (personal observation). They also have similar life-history characteristics (see Table 1).

The experimental fish were captured by seine net and minnow trap at the University of Manitoba's field station at Delta marsh, located at the southern tip of Lake Manitoba. Fish were transferred to the Animal Holding Facility at the University of Manitoba, where they were held in 200-L fibreglass flow tanks maintained at 15°C and fed a diet of frozen brine shrimp (*Artemia salina*), commercial trout chow, and Nutra Fin™ flakes. Prior to being used in experiments, fish were transferred to the laboratory and held in 80-L glass aquaria at 20°C.

The predators used in these experiments were yellow perch (*Perca flavescens*). They are a natural predator of both fathead minnows and brook sticklebacks and were also collected at Delta marsh. In the laboratory, these fish were maintained on a diet of live fathead minnows and brook sticklebacks.

### Experiment 1: interspecific variation in risk-taking

This experiment examined the relative willingness of fathead minnows and brook sticklebacks to risk exposure to a predator in order to gain access to additional food. A total of 10 groups of fish was used in this experiment: 5 groups of fathead minnows and 5 groups of brook sticklebacks. Each group consisted of three individuals that were randomly selected from a holding tank.

Trials were conducted in an 80-L aquarium that was divided into two equal-sized halves by a column of horizontal 5-mm glass rods, each at a distance of 1.3 cm from the next. These glass rods allowed the minnows and sticklebacks to pass freely between the two sides of the aquarium, while restricting a 175-g yellow perch (*Perca flavescens*) to one-half of the aquarium. (During experiments, the yellow perch was maintained on a normal feeding regime.) This partition rendered one-half of the aquarium dangerous and the other half safe. When trials were not in progress, a transparent Plexiglas partition covered the glass rods, preventing direct contact between the predator and prey.

Feeders were located 15 cm on either side of the divider

and delivered 0.5 g of previously frozen brine shrimp uniformly over a 25-min period (for details of the feeders see Abrahams 1989). The fish quickly learned to take food from these feeders and were completely trained after a 2-day learning period. During the 6 days required to complete the experiment, the feeders were the fishes' only source of food.

The level of predation risk is often affected by the behaviour of the predator (personal observation). As the behaviour of the predator can therefore generate significant variance in prey behaviour, groups of fathead minnows and brook sticklebacks were paired, allowing their behaviour to be observed at identical levels of predation risk. The fathead minnows and brook sticklebacks were paired so that they were of approximately equal length (Table 2).

The side containing the predator (left, right, or none) was randomly determined and this configuration was retained for 2 consecutive days. Trials were conducted three times per day, with the trials separated by at least 3 h. This provided 6 repeated measures for each of three different treatments on each of the 10 groups of fish used in this experiment. Trials began by placing 0.5 g of frozen brine shrimp suspended in 2 L of water in each feeder. Once the feeders were prepared, the transparent partition was removed and the fish were allowed access to both the safe and dangerous habitats. The feeders were then started and the spatial distribution of the fish was monitored remotely by a video camera placed in front of the aquarium.

The spatial distribution of all six fish was recorded every 30 s. The results were summarized as the mean spatial distribution for each species within the apparatus. Data from only one side of the aquarium were used (because of dependence between the two sides) and were analyzed as a paired, repeated-measures ANOVA using the PROC GLM procedure within SAS.

### Experiment 2: reactive distance to a predator

The distance at which individual fathead minnows and sticklebacks react to the presence of an approaching predator was measured using a model yellow perch. The model was constructed from a dead yellow perch (185 cm fork length) that was eviscerated and filled with 80 g of lead. The body was sutured, with the fins fixed in erect positions, and freeze-dried. The eyes were replaced with taxidermy eyes and the body was sealed with seven coats of transparent epoxy resin.

The model was presented to the fish by means of a pulley system. An electrical motor pulled fine monofilament line through the aquarium towards the test fish. The model was attached to fishing leaders that were tied to this line. This system presented the model to the fish at a constant velocity of 4.24 cm · s<sup>-1</sup>.

Experiments were conducted in a long, narrow aquarium (200 × 30 cm). The back wall of the aquarium contained a grid of lines creating 2.5-cm squares. Fish were conditioned to react to an approaching predator by placing them in this aquarium with a live yellow perch (rather than the model). A column of horizontal glass bars located 30 cm from the end opposite the model provided a refuge from this predator, and the fish quickly learned to flee to this refuge when approached by a predator. The experimental fish were exposed to the live predator in this apparatus for 1 day prior to beginning a trial.

**Table 3.** Summary of the statistical results for experiment 1.

Source	df	F	P
Species	1,4	1.65	0.27
Group	4,4	1.67	0.32
Predator	2,2	4.56	0.18
Species × group	4,8	1.63	0.26
Species × predator	2,8	13.85	0.002
Group × predator	8,8	3.33	0.54
Species × group × predator	8,40	3.21	0.006

Note: The analysis employed a repeated-measures ANOVA with paired groups.

No fish were captured by the predator during this process. During a trial, the model predator was located at the far end of the aquarium.

Species were tested separately as solitary individuals or in a group of three (since susceptibility to a predator varies inversely with group size; Godin 1986). Regardless of group size, the protocol was the same. A feeder provided frozen brine shrimp to the fish at a rate of 0.5 g per 25 min. The food was presented to the fish 10 cm from the refuge and directly in line with the path of the predator model. The fish were allowed 1 day to learn to use the feeder (in the absence of the predator). Individuals that did not learn to use the feeder in that time period were not used in the experiment. Fish in the aquarium were monitored with a video camera. After they had consumed food from the feeder for 3 min, the model approached the feeding fish. Fish were considered to have reacted to the approaching predator when they ceased feeding and moved away from it.

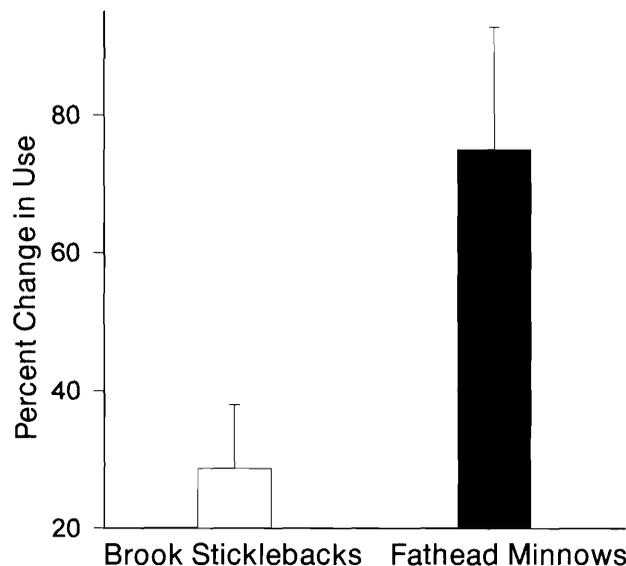
The test fish's reactive distance to the predator was quantified from video tape. The spatial point at which the fish reacted to the presence of the predator was determined, and the distance separating the nose of the predator from the nose of the prey as viewed against the grid system on the back wall of the tank, was taken as the reactive distance. Since the behaviour of fish in groups is strongly influenced by the behaviour of other individuals, I described the reactive distance of a group as the mean distance at which all three individuals reacted to the approaching predator. For statistical analysis, each trial (of either solitary fish or a group of three) represented a single independent observation. Six sticklebacks and 10 fathead minnows were used as solitary individuals and five groups of sticklebacks and six groups of fathead minnows were used. Fish were used only once in these experiments. Statistical analysis employed the SAS GLM procedure (SAS Institute Inc. 1985) using Type III sums of squares.

## Results

### Experiment 1: interspecific variation in risk-taking

The statistical results from this experiment are summarized in Table 3. This analysis indicates that the spatial distribution of the fathead minnows and the brook sticklebacks did not differ significantly between the sides of the aquarium (the effect of species within Table 3), indicating that there were no differences in the way these species occupied the apparatus. No significant differences existed between groups, nor

**Fig. 1.** The mean ( $\pm 1$  SE) percent change in use of the dangerous feeder as a consequence of the presence of a predator on brook sticklebacks and fathead minnows. Larger positive values indicate increasing avoidance of a dangerous feeding area. Percent change in use was calculated as the difference in the proportion of fish using a specific feeder in the control treatment and the proportion of fish using the same feeder in the presence of a predator. This value was then divided by the proportion of fish using that feeder in the control experiment. The mean result for the left and right sides combined was used to represent a single value for each group.



did side of presentation of the predator have any influence on the results (the effects of group and predator, respectively, in Table 3).

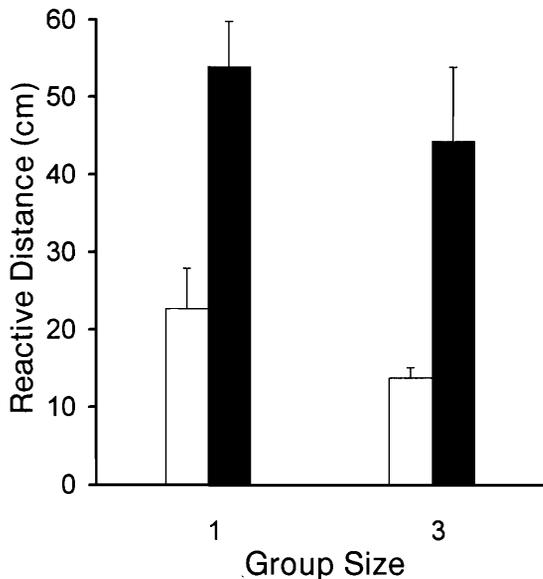
The presence of the predator resulted in reduced use of the dangerous side for both fathead minnows and brook sticklebacks (Fig. 1). Analysis of the results of this experiment indicated a significant species × predator interaction, indicating that the response to the presence of the predator differed significantly between species (Table 3). As illustrated in Fig. 1, the source of this difference is greater avoidance of the dangerous feeding area by the fathead minnows than by the brook sticklebacks. When both fathead minnows and brook sticklebacks are confronted by an identical threat, there is less avoidance of the dangerous area by the brook sticklebacks than by the fathead minnows.

Analysis of these data also revealed a significant three-way interaction between species, group, and predator. This result indicates that there was significant variation in the response of the different groups and species to the presence of a predator. It is likely that this variation was generated by temporal change in the behaviour of the predator during this experiment.

### Experiment 2: reactive distance experiment

In all trials, both individuals and groups fled the approaching predator in the opposite direction (towards the refuge provided at the end of the aquarium). There was a significant

**Fig. 2.** Mean ( $\pm 1$  SE) distance at which sticklebacks (open bars) and fathead minnows (solid bars) react to an approaching predator model by fleeing a feeder as a function of group size.



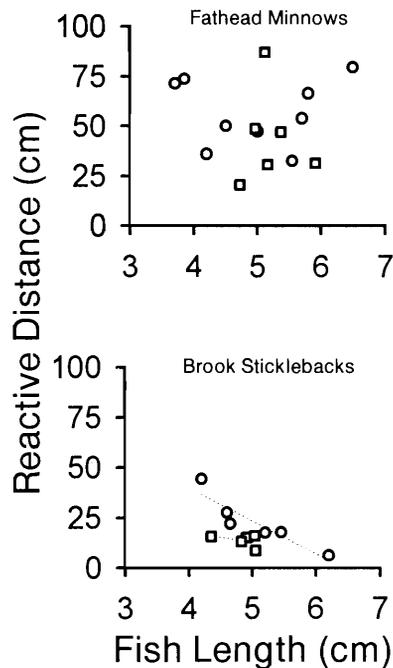
difference between the two species in their reactive distance to an approaching predator (Fig. 2; ANOVA,  $F_{[1,23]} = 20.23$ ,  $P = 0.0002$ ).

To determine whether the fish were sensitive to their susceptibility to an approaching predator, I analyzed the reactive distances for each species separately, using body length as a covariate. Fish should become less susceptible to predators as they become larger, owing to their increased swimming performance associated with size (Bainbridge 1958) and the predators' increased difficulty handling larger fish (Hoyle and Keast 1987). For the fathead minnows, the reactive distance of individual fish was unaffected by their length or group size (Fig. 3; ANCOVA,  $F_{[1,13]} = 0.76$ ,  $P = 0.39$ ;  $F_{[1,13]} = 0.04$ ,  $P = 0.85$  for the effects of group size and body length, respectively). However, both these variables had a significant influence on the reactive distance of the sticklebacks (Fig. 3; ANCOVA,  $F_{[1,8]} = 8.58$ ,  $P = 0.019$ ;  $F_{[1,8]} = 25.80$ ,  $P = 0.0010$  for the effects of groups size and fish mass, respectively). The reactive distance of sticklebacks decreased as individuals became larger (i.e., they allowed an approaching predator to come closer before they would stop feeding and escape). Similar-sized individuals placed in a group of three further delayed their response to an approaching predator.

## Discussion

The results of the current study are consistent with the hypothesis that possession of antipredator morphology results in less behavioural modification in the presence of a predator. When actively feeding, sticklebacks allowed a potential predator to approach closer before ceasing feeding than did fathead minnows. Furthermore, the reactive distance of the sticklebacks, but not of the fathead minnows, was sensitive to both group size and the size of the individuals. These data indicate that the fathead minnows' antipredator strategy may be primarily one of avoidance. If a

**Fig. 3.** Effect of species, length, and group size on the reactive distance of fathead minnows and sticklebacks. Open circles are the results for solitary individuals; open squares are the results for groups of three. Each point represents the result for a single individual or the mean reactive distance for a group of three. The dotted lines were fitted through the data by the least-squares method.



predator was present, they tended to avoid it regardless of their individual body size or the number in the group. Sticklebacks were more likely to feed actively in the presence of a predator, and modified their response to an approaching predator in proportion to their apparent susceptibility to predation.

The ability of sticklebacks, but not unarmoured minnows, to grade their behavioural response in proportion to the perceived risk of predation is counter to the results of McLean and Godin (1989), who observed that armoured prey species (threespine sticklebacks, *Gasterosteus aculeatus*, and two morphs of the ninespine stickleback, *Pungitius pungitius*) did not modify their reactive distance in response to variation in the distance to cover, but that unarmoured killifish (*Fundulus diaphanus*) did, as predicted by an economic model of fleeing (Ydenberg and Dill 1986). They argued that this result may be due to the armoured fish species not perceiving any variation in the risk of predation within the apparatus, or that these fish rely primarily on morphological defenses rather than fleeing to cover as an antipredator strategy. My data indicate that brook sticklebacks are sensitive to the level of risk based on their individual size or group size, and appear to respond accordingly. This suggests that brook sticklebacks do rely on behaviour, in addition to antipredator morphology, as a defense against predators. Similarly, Sweitzer and Berger (1992) have observed that porcupines (*Erethizon dorsatum*), despite their formidable antipredator morphology, exhibit sensitivity to the magnitude of predation risk associated with habitat use.

Both my results and those of McLean and Godin are based upon interspecific comparisons. It is therefore possible that factors other than antipredator morphology may account for some of the observed differences. In particular, the difference in morphology of the fathead minnows and brook sticklebacks may cause differences in their ability to escape a predator. However, the burst swimming speeds of these species show no detectable difference (M.V. Abrahams, unpublished data). Furthermore, intraspecific variation in antipredator morphology in brook sticklebacks is also known to affect their behavioural response to a predator (Reist 1983). As variation in antipredator morphology is known to affect behaviour, it is the parameter most likely to affect the difference measured between the species.

It is also possible that differences in life-history characteristics between the species could account for these observations. In particular, theoretical work by Gilliam (1982) and Werner and Gilliam (1984) predicts that increased age-specific fecundity or reduced age-specific reproductive value between species could also generate differences in antipredator behaviour. As indicated in Table 1, the two species employ a similar mating system and have male parental care. Females of both species devote a similar proportion of their body mass to egg production. They mature at the same age and have the same maximum age. Growth in both species is seasonal, they are short-lived, and achieve similar maximum lengths. Since the groups of fish used in experiment 1 were matched by length, they were probably similar in age (i.e., offspring from the same year) and therefore should not differ in their future reproductive value. While it is possible that different life-history characteristics may affect antipredator behaviour, there are no obvious differences in life-history characteristics between these two species that would be consistent with the differences in observed behaviour.

An advantage of antipredator morphology is that it should allow animals to reduce their reliance on behavioural avoidance of predators as a primary means of dealing with predators. Behavioural avoidance of predators is known to be costly for aquatic vertebrates (Skelly 1992; McDonald et al. 1992) and often results in reduced growth rates (Lima and Dill 1990). The advantage of behavioural avoidance is that the costs should be flexible and proportional to the rate of encounter with predators (Sih 1987). Development of antipredator morphology involves fixed costs. For invertebrates, the development of antipredator morphology reduces feeding, growth, and reproduction rates (Dodson 1984; Riessen 1992). For vertebrates, it is likely that such morphological defenses carry similar costs.

Ecological data demonstrate that species which bear armour are not immune to predation, but that their occurrence in the diet of predators is relatively less than that observed for unarmoured species. Lyons (1987) observed that juvenile piscivorous walleyes (*Stizostedion vitreum*) consume more bluntnose minnows than spiny-rayed (i.e., armoured) young-of-the-year yellow perch. Northern pike selectively prey upon morphs of brook sticklebacks that have a reduced pelvic skeleton and spine (Reist 1980). Other piscivores are known to prefer soft-rayed prey over spiny-rayed prey (Beyerle and Williams 1968; Hoyle and Keast 1987). Furthermore, growth rates of aquatic piscivores are observed to be greater when soft-rayed prey are abundant (Tomcko et al. 1984).

In conclusion, the results presented in this paper are consistent with the hypothesis that there is an interaction between antipredator morphology and behaviour. It is argued that the change in behaviour by prey to avoid being killed by predators can be a major ecological force (Sih 1987). Proposed mechanisms include the concentration of different prey species into predator refuges (thereby amplifying interspecific competition) and changes in diet composition made by prey species to reduce susceptibility to predators (for a review of different mechanisms see Lima and Dill 1990). Prey species that possess effective antipredator morphology need to modify their behaviour less in the presence of a predator than unarmoured species do. This result has consequences for the nature of predator-prey interactions in aquatic communities. The indirect effect of predators should be less on armoured species than on unarmoured species, rendering predation risk a less important ecological force.

### Acknowledgements

I am grateful to Alvin Dyck for helping with these experiments and Ms. Llwellyn Armstrong of the University of Manitoba Statistical Advisory Service for assistance with some of the analyses. Jean-Guy Godin and two anonymous reviewers kindly provided comments on an earlier draft of the manuscript. Financial support for this research was provided by a research grant from the Natural Sciences and Engineering Research Council of Canada. This is Contribution No. 251 from the University of Manitoba field station at Delta marsh.

### References

- Abrahams, M.V. 1989. Foraging guppies and the ideal free distribution: the influence of information on patch choice. *Ethology*, **82**: 116–126.
- Abrahams, M.V., and Healey, M.C. 1993. A comparison of the relative willingness of four species of Pacific salmon to risk exposure to a predator. *Oikos*, **66**: 439–446.
- Bainbridge, R. 1958. The speed of swimming fish as related to size and to the frequency and the amplitude of the tail beat. *J. Exp. Biol.* **35**: 109–133.
- Beyerle, G.B., and Williams, J.E. 1968. Some observations of food selectivity by northern pike in aquaria. *Trans. Am. Fish. Soc.* **97**: 28–31.
- Braekveelt, C.R., and McMillan, D.B. 1967. Cyclic changes in the ovary of the brook stickleback *Eucalia inconstans* (Kirtland). *J. Morphol.* **123**: 373–396.
- Brönmark, C., and Miner, J.G. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science (Washington, D.C.)*, **258**: 1348–1350.
- Carlson, D.R. 1967. Fathead minnow, *Pimephales promelas* Rafinesque, in the Des Moines River, Boone County, Iowa, and the Skunk River drainage, Hamilton and Story counties, Iowa. *Iowa State J. Sci.* **41**: 363–374.
- Dodson, S.I. 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: morphological defenses and their cost. *Ecology*, **65**: 1249–1257.
- Dodson, S.I. 1989. Predator-induced reaction norms. *BioScience*, **39**: 447–452.
- Edmunds, M. 1974. Defence in animals: A survey of anti-predator defences. Longman, Harlow, Essex, U.K.
- Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. thesis, Michigan State University, East Lansing.

- Godin, J.-G.J. 1986. Antipredator function of shoaling in teleost fishes: a selective review. *Nat. Can. (Que.)* **113**: 241–250.
- Hoyle, J.A., and Keast, A. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Can. J. Zool.* **65**: 1972–1977.
- Lima, S.L., and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Lyons, J. 1987. Prey choice among piscivorous juvenile walleyes (*Stizostedion vitreum*). *Can. J. Fish. Aquat. Sci.* **44**: 758–764.
- Markus, H.C. 1934. Life history of the blackhead minnow (*Pimephales promelas*). *Copeia*, 1934: 116–122.
- McDonald, M.E., Hershey, A.E., and O'Brien, W.J. 1992. Cost of predation avoidance in young-of-year lake trout (*Salvelinus namaycush*)—growth differential in suboptimal habitats. *Hydrobiologia*, **240**: 213–218.
- McLean, E.B., and Godin, J.-G.J. 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos*, **55**: 281–290.
- Reist, J.D. 1980. Selective predation upon pelvic phenotypes of brook stickleback, *Culaea inconstans*, by northern pike, *Esox lucius*. *Can. J. Zool.* **58**: 1245–1252.
- Reist, J.D. 1983. Behavioural variation in pelvic phenotypes of brook stickleback, *Culaea inconstans*, in response to predation by northern pike, *Esox lucius*. *Environ. Biol. Fishes*, **8**: 255–267.
- Riessen, H.P. 1992. Cost-benefit model for the induction of an antipredator defense. *Am. Nat.* **140**: 349–362.
- Robinson, C.L.K. 1989. Laboratory survival of four prey in the presence of northern pike. *Can. J. Zool.* **67**: 418–420.
- SAS Institute Inc. 1985. SAS® user's guide: statistics, version 5 ed. SAS Institute Inc., Cary, N.C.
- Scott, W.B., and Crossman, E.S. 1973. Freshwater fishes of Canada. *Fish. Res. Board Can. Bull. No.* 184.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. *In* *Predation: direct and indirect impacts on aquatic communities*. Edited by W.C. Kerfoot and A. Sih. University Press of New England, Hanover, N.H. pp. 203–224.
- Skelly, D.K. 1992. Field evidence for a cost of behavioural antipredator response in a larval amphibian. *Ecology*, **73**: 704–708.
- Sweitzer, R.A., and Berger, J. 1992. Size-related effects of predation on habitat use and behaviour of porcupines (*Erethizon dorsatum*). *Ecology*, **73**: 867–875.
- Tomcko, C.M., Stein, R.A., and Carline, R.F. 1984. Predation by tiger muskellunge on bluegill: effects of predator experience, vegetation, and prey density. *Trans. Am. Fish. Soc.* **113**: 588–594.
- Werner, E.E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology*, **72**: 1709–1720.
- Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.
- Weselowski, R.F. 1974. Comparison of populations of brook sticklebacks, *Culaea inconstans* (Kirtland) with and without predation by a piscivorous fish. M.Sc. thesis, University of Manitoba, Winnipeg.
- Wootton, R.J. 1976. The biology of the sticklebacks. Academic Press, New York.
- Wootton, R.J. 1984. A functional biology of sticklebacks. University of California Press, Berkeley.
- Ydenberg, R.C., and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Study Behav.* **16**: 229–249.