

RISK-TAKING BY THREESPINE STICKLEBACK (*GASTEROSTEUS ACULEATUS*) PELVIC PHENOTYPES: DOES MORPHOLOGY PREDICT BEHAVIOUR?

by

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Summary

The relationship between risk-taking behaviour and anti-predator morphology was studied in benthic threespine stickleback fish (*Gasterosteus aculeatus*) from Paxton and Priest Lakes on Texada Island, British Columbia, Canada. In general, Priest Lake benthics possess complete pelvic girdles and numerous lateral plates. In contrast, Paxton Lake benthics exhibit an apparent polymorphism in anti-predator morphology; some individuals possess complete pelvic girdles while others lack them entirely. Although phenotypes tended to differ in their willingness to risk exposure to a trout predator while foraging, the predicted positive relationship between risk-taking behaviour and anti-predator morphology was not observed. While 'girdled' Paxton individuals were more willing to forage in the vicinity of the predator than 'girdleless' Paxton individuals, the more heavily armoured Priest fish were intermediate in their risk-taking behaviour. These results suggest that the relationship between risk-taking behaviour and anti-predator morphology may be influenced by differences between phenotypes in predation regime and life history.

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Introduction

Many of the activities routinely performed by animals increase their exposure to predators (see Lima & Dill, 1990 for a review). Predation risk can be reduced by both behavioural and morphological defenses. Behavioural defenses are often used to reduce an individual's probability of being detected or captured by a predator (Lima & Dill, 1990 for examples). In contrast, morphological defenses typically reduce predation risk by making prey more difficult to handle and ingest, thereby increasing their probability of escape if captured (Edmunds, 1974; Endler, 1986; Sih, 1987). Due to the presumed energetic cost of producing and maintaining morphological defenses, it has been argued that the intensity of a prey's behavioural defenses should be inversely correlated with the effectiveness of its morphological defenses (Ydenberg & Dill, 1986; Sih, 1987; McLean & Godin, 1989). Thus, an individual's willingness to engage in apparently risky behaviour should increase with the robustness and effectiveness of its morphological defenses.

Much of the support for a positive relationship between anti-predator morphology and risk-taking behaviour comes from comparisons of closely related species (*e.g.* Hoogland *et al.*, 1957; Dodson, 1984; Kotler, 1984; Brown *et al.*, 1989; McLean & Godin, 1989; Abrahams, 1995); comparisons that may be confounded by concomitant differences in life history (but see Abrahams, 1995). Relatively few studies have compared populations of a single species or members of a single population, (but see Reist, 1980, 1983; Morgan, 1987; Andraso & Barron, 1995; Andraso, 1997), despite the prevalence of intraspecific variation in both defensive morphology and risk-taking behaviour. This is surprising, given the potential for such variation to influence patterns of habitat selection (Grand & Dill, 1999) and promote further diversification (Rice, 1987; Wcislo, 1989).

Substantial between-population variation in both anti-predator morphology and risk-taking behaviour has been reported for threespine stickleback fish (*Gasterosteus aculeatus*; see Reimchen, 1994 and Huntingford *et al.*, 1994, respectively, for reviews). Anti-predator morphology includes dorsal spines, bony lateral plates, and a pelvic girdle, which, when fully formed, consists of a pair of anterior processes with ascending branches, posterior processes, and pelvic spines (see Fig. 9.1, Reimchen, 1994; Fig. 2, Baker *et al.*, 1995). When locked erect, the dorsal and pelvic spines interact with the pelvic girdle to provide structural defense against vertebrate

predators (Hoogland *et al.*, 1957; Reimchen, 1983). Typically, populations derived from lakes containing native fish predators (*e.g.* cutthroat trout, *Oncorhynchus clarkii*; pike, *Esox lucius*) have longer spines and more lateral plates than those from lakes without predatory fishes (see Reimchen, 1994 and references therein). Behavioural responses to predators include schooling, remaining close to protective cover (or avoiding it in the presence of predatory dragonfly naiads), and predator inspection (Huntingford *et al.*, 1994 and references therein). In general, sticklebacks from lakes in which vertebrate predators are abundant tend to possess more well-developed anti-predator responses, and thus, appear less willing to expose themselves to predation risk than those from lakes in which predators are rare or absent (see Huntingford *et al.*, 1994 for a review).

Within-population variation in anti-predator morphology is also frequently observed in stickleback fish. For example, three lateral plate morphs of the threespine stickleback (low, partial, and complete; Hagen & Gilbertson, 1972) are known to inhabit lakes that drain into the White Sea, Russia (Ziuganov, 1995). In contrast, two pelvic morphs (pelvic girdles and spines present and absent) of brook stickleback (*Culaea inconstans*) typically reside in North American streams and lakes (Nelson & Atton, 1971). Such variation in pelvic girdle morphology has also been observed among the 'benthic' threespine stickleback population of Paxton Lake, Texada Island, British Columbia (see Schluter & McPhail, 1992 for a description of the 'benthic'- 'limnetic' species-pairs). While much of this population appears to have lost the pelvic girdle and its associated spines, it is not uncommon to find individuals with fully expressed pelvic girdles (Steven Vamosi, pers. comm.). Thus, this apparent polymorphism provides yet another opportunity to study the relationship between anti-predator morphology and risk-taking behaviour within a single population.

As part of a larger study investigating the effects of intraspecific variation in anti-predator morphology on patterns of habitat selection (see Grand & Dill, 1999), I compared the risk-taking behaviour of three groups of stickleback with differing amounts of armour. In addition to the Paxton Lake benthic sticklebacks discussed above, I included benthic sticklebacks from nearby Priest Lake in the study. Typically, these fish are more heavily armoured than either of the Paxton Lake morphs (see Results). I predicted that an individual's willingness to expose itself to predation risk while foraging would be positively correlated with the amount of armour it

possessed and thus, that Priest fish would be the most willing to risk exposure to a predator to gain access to food and 'girdless' Paxton fish the least willing to expose themselves to predation risk.

I quantified willingness to risk exposure to a predator by calculating the energetic equivalence of predation risk for each phenotype (see Abrahams & Dill, 1989; Grand & Dill, 1997; and the Methods to follow) in the presence of a single, predatory trout. Because an individual's risk of predation, and hence, the relative efficacy of behavioural and morphological defenses may also depend on the structural complexity of the habitat (*e.g.* Savino & Stein, 1982, 1989; Schramm & Zale, 1985; Christensen & Persson, 1993), I quantified the risk of predation experienced by each phenotype in the two habitat types typically available to lacustrine sticklebacks; habitats with and without vegetative cover.

Methods

Experimental subjects and predators

I trapped adult benthic sticklebacks from Paxton and Priest Lakes, Texada Island, British Columbia, Canada, on May 21 and 22, 1998. Paxton Lake fish were separated into two groups; those who possessed a pelvic girdle ('Paxton+' individuals) and those without a pelvic girdle ('Paxton-' individuals). Eggs were collected from 6 females of each of three phenotypes (Paxton+, Paxton-, and 'Priest') and crossed with the sperm of one of 3 males of the same phenotype. Fertilized eggs were returned to the laboratory to hatch. Juvenile fish were maintained in 100-l aquaria at 16-18 °C on a 14 : 10 h light: dark schedule, and fed a mixture of live brine shrimp (*Artemia* spp.) and frozen bloodworm (*Chironomid* spp.) larvae until they were large enough to be used in the experiment.

Twelve cutthroat trout (*Oncorhynchus clarkii*; range 10-14 cm fork length) were captured by angling from Placid Lake in the University of British Columbia Research Forest. Trout were returned to the university, held in large, outdoor pens and fed a mixture of trout chow and juvenile sticklebacks between experiments.

Two days before each set of foraging trials was to begin, 10 sticklebacks of the same parental phenotype and similar mass (range = 0.49-0.69 g, $N = 240$; coefficients of variation: Paxton+ : $\bar{x} \pm SD = 0.031 \pm 0.018$; Paxton- : $\bar{x} \pm SD = 0.079 \pm 0.026$; Priest: $\bar{x} \pm SD = 0.027 \pm 0.0099$; $N = 8$ groups of 10 fish per phenotype) were chosen from one of the stock tanks. Groups were then transferred to one of the two aquaria in which experiments were to be conducted (see below). A single, cutthroat trout was netted and placed randomly in one of the two predator aquaria (see below). Sticklebacks were fed bloodworm larvae once daily during this acclimation period. After being transferred to the predator aquarium, no food was provided to the trout, ensuring that it was hungry and foraged actively when the experiment began. Experiments were conducted in random order (with respect to phenotype) over a period of 6 weeks, beginning November 3 and ending December 15, 1998.

Methods and apparatus

I conducted experiments in two large glass aquaria ($90 \times 30 \times 39$ cm; $L \times W \times H$), filled with dechlorinated water to a depth of 21 cm (see Fig. 1). 'Open water' and 'vegetated' patches were created by using silicon to attach small rocks (~ 1 cm in diameter), and rocks and 20 cm lengths of plastic aquarium vegetation, respectively, to heavy pieces of plexiglass. Thus, patch type could be randomly assigned to the left and right sides of the experimental aquarium. The back wall of each aquarium was covered with heavy, opaque cardboard to minimize disturbance of the fish. Water was aerated by a power filter suspended centrally along this wall.

Two smaller aquaria ($35 \times 20 \times 25$ cm; $L \times W \times H$; water depth = 21 cm) placed against the ends of each experimental aquarium (see Fig. 1) were used to house the predator during foraging trials. Predator aquaria were surrounded on three sides by heavy, opaque cardboard. The side of the predator aquaria closest to each experimental aquarium was fitted with a removable opaque plexiglass blind which prevented the sticklebacks and predator from interacting with one another between trials.

Throughout the experiment, sticklebacks were maintained exclusively on the frozen bloodworm larvae provided during the foraging trials. Prey were thawed, counted, and placed in two 4-l Erlenmeyer flasks filled with dechlorinated tap water. Prey and water drained from the flasks through 70 cm lengths of tygon tubing (7 mm diameter) fastened to glass spouts attached to the bottom of the flasks (after Abrahams, 1989; see also Fig. 1 of Grand & Dill, 1997). Each feeding tube emptied into one of two hollow, plastic cylinders attached to a length of plywood that spanned the length of the top of the experimental aquarium. A line down the centre of each aquarium's front face delineated the patches for the observer.

Prey in the flasks were kept in suspension by means of a stir bar constantly rotated by a magnetic stir plate, ensuring that prey left the flask at a relatively uniform rate throughout the trial. Flasks were sealed with a rubber stopper penetrated by a glass tube extending to the bottom of the flask, thereby maintaining a constant drain rate of water and prey. A length of tygon tubing was attached to the top of the glass tube and sealed at the other end with a hypodermic needle fastened to a syringe. Thus, the flasks could be operated simultaneously and remotely by simply removing the plungers from the syringes and allowing air to enter them. Water and prey were dispensed slowly over the course of the 20-min foraging trial.

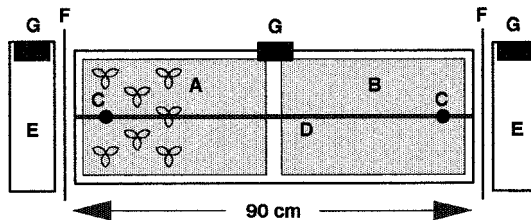


Fig. 1. Schematic top view of the experimental apparatus. Sticklebacks were placed in an experimental aquarium containing a vegetated (A) and open water (B) patch. Prey were dispensed through plastic tubes (C) attached to a length of plywood (D) that spanned the length of the aquarium. Predator aquaria (E) were separated from the experimental aquarium by opaque plexiglass blinds (F). Power filters (G) were used to aerate water in all three aquaria.

Trials were terminated by reinserting the plungers in the syringes. I counted the number of prey remaining in each flask and subtracted this number from the number originally placed there. Thus, for all trials, the actual number of prey available to the fish in each patch was known.

I conducted trials twice per day, between 0900 and 1100 h and again between 1500 and 1700 h, on each of two consecutive days. Experiments in the two aquaria were run sequentially. The first trial was used to teach the fish the locations of the feeding tubes. The second trial provided information on the distribution of individuals in the absence of a predator and as such, acted as a baseline to which subsequent trials could be compared. During the third and fourth trials, fish were exposed to the predator in each of the open water and vegetated patches in turn. Both the initial location of the predator and the side of the aquarium housing the vegetated substrate were randomized between groups. A VHS Hitachi video camera, mounted on a tripod, was focused on the open water patch during the second, third, and fourth trials, providing a continuous record of the number of fish foraging there.

Immediately preceding each trial, power filters were turned off, 30 bloodworm larvae were placed in each of the two flasks and the camera turned on. After leaving the fish undisturbed for an additional 5 min, I removed the plungers from the syringes and activated the foraging trial. At the end of each 20-min trial, the camera was turned off, the plungers re-inserted in the syringes, and the filter re-activated. During the third and fourth trials, the opaque plexiglass partition was removed from between the experimental and predator aquaria just before the camera began recording, allowing the fish to interact visually with the predator. The plexiglass partition was returned to its position once the trial was completed. Following the fourth trial, sticklebacks were removed from the experimental aquarium and replaced with the next group to be tested. Fish were sacrificed using MS-222, fixed for 7 to 10 d in 10% formalin, stained overnight with Alzarin red, and stored for 6 to 8 months in 40% ethanol.

Data analysis: Morphology

With the aid of a compound microscope and a digital stage micrometer, I measured (1) the standard length (to the nearest 0.5 mm) and (2) the length of the second dorsal spine (to the nearest 0.001 mm) of each fish. I also counted (3) the number of lateral plates and (4) the number of pelvic girdle components (pelvic spine, posterior process, ascending branch, and anterior process; see Fig. 1 of Bell *et al.*, 1994) present on each of the left and right sides. For each pelvic girdle component present, the fish was given a score of '1'. Thus, pelvic girdle scores ranged from 0 (no girdle) to 8 (fully expressed girdle).

Dorsal spine lengths of the three putative phenotypes were compared by performing an analysis of covariance (ANCOVA) with log-spine length as the independent variable, log-standard length as the dependent variable, and parental phenotype as the covariate. Differences between putative phenotypes in total plate number and pelvic girdle score were compared using Kruskal-Wallis one-way analysis of variance (ANOVA) and contingency tables, respectively.

Data analysis: Behaviour

To compare the observed distributions of fish to the distribution of food, and thus, quantify the energetic equivalence of predation risk, I determined the average number of fish in each patch at 1-min intervals during each trial from the videotapes. To avoid biasing the outcomes

of the comparisons with pre-equilibrium values, only data from the last quarter of each trial (*i.e.* minutes 16-20) were included. Because food was allocated stochastically to the patches, the actual number of prey arriving in a patch often differed slightly from the expected patch profitability (*i.e.* from 1 : 1). Therefore, I used paired *t*-tests to compare the mean number of fish in the open water patch to that predicted by the actual distribution of food. Because distribution data were homoscedastic and normally distributed, transformations were not required.

I used ideal free distribution theory (Fretwell & Lucas, 1970) to quantify the energetic equivalence of predation risk to the fish. IFD theory predicts that when food is the only variable contributing to fitness, individuals should be distributed across patches such that the proportion of individuals in each patch matches the proportion of food available there. At equilibrium, the mean foraging payoff per individual will be equal in the two patches. However, if one patch has a predator associated with it while the other does not, a smaller proportion of individuals is expected to use the high-risk patch than predicted by the distribution of food alone. Consequently, those individuals continuing to use the high-risk patch will receive higher foraging payoffs than those switching to the low-risk patch. Assuming that this new equilibrium distribution is also an ideal free distribution, individuals using the high- and low-risk patches will receive identical fitness payoffs, although foraging payoffs obtained in the two patches will differ. Those individuals in the high-risk patch are compensated by receiving more food. Thus, we can calculate the energetic equivalence of predation risk (E) as the difference in foraging payoffs between the patches:

$$E = \frac{R_h}{N_h} - \frac{R_l}{N_l} \quad (1)$$

where R_h and R_l represent the quantity of prey (items \cdot trial $^{-1}$) provided by the high-risk and low-risk patches, respectively, and N_h and N_l the mean number of individuals in those patches. Thus, E indicates how much food individuals are willing to give up to avoid the predator, and as such, is a measure of perceived risk of predation.

I calculated E for each group of fish in each patch by comparing their distribution to the actual distribution of prey during the third and fourth trials. To investigate whether perceived risk of predation differed among putative phenotypes and/or with the location of the predator (*i.e.* in the open water or vegetated patch), I performed a single-factor repeated measures analysis of variance (ANOVAR) on the calculated energetic equivalence of predation risk in the two patches. Unless stated otherwise, reported *p*-values are two-tailed.

Results

Morphology

Although I attempted to match individuals for size within foraging groups (see 'Experimental subjects and predators' section), because the experiment was conducted over a period of 6 weeks, variation between groups and putative phenotypes could not be eliminated. Consequently, phenotypes differed in both mass and standard length (Table 1; $F_{2,237} = 20.781$,

TABLE 1. Mean (SE) wet weights, standard lengths, and second dorsal spine lengths of fish used in the experiment

Phenotype	Mass (g)	Standard length (mm)	Dorsal spine length (mm)
Paxton-	0.481 (0.006)	32.45 (0.152)	2.070 (0.029)
Paxton+	0.545 (0.008)	34.46 (0.145)	2.299 (0.032)
Priest	0.506 (0.007)	33.44 (0.162)	2.246 (0.027)

$N = 80$ fish per phenotype.

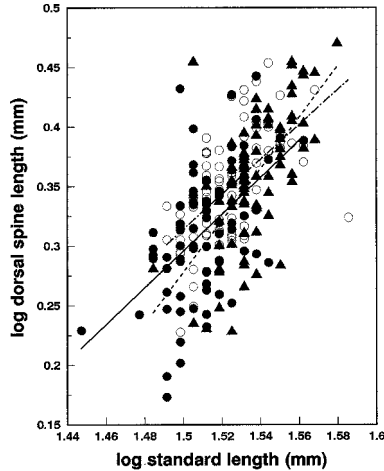


Fig. 2. The relationship between log dorsal spine length and log standard length for Paxton- (●, solid line), Paxton+ (▲, dashed line), and Priest (○, dotted line) fish. $\text{LogSpL} = -2.289 + 1.723 \times \text{logSL}$, $N = 240$, $r^2 = 0.42$.

$p < 0.001$ and $F_{2,237} = 42.837$, $p < 0.001$, respectively). Although the absolute length of the second dorsal spine also differed between phenotypes (Table 1; $F_{2,237} = 16.505$, $p < 0.001$), when corrected for standard length, such differences were no longer evident (Fig. 2; $F_{2,234} = 2.855$, $p = 0.159$). For all three phenotypes, spine length increased linearly with standard length (Fig. 2; $\text{logSpL} = -2.289 + 1.723 \times \text{logSL}$, $N = 240$, $r^2 = 0.42$).

Phenotypes, did however, differ in lateral plate number (Fig. 3; left side, K-W test statistic = 124.76, $p < 0.001$, $df = 2$; right side, K-W test statistic = 123.81, $p < 0.001$, $df = 2$; total, K-W test statistic = 128.49, $p < 0.001$, $df = 2$). In general, Priest fish tended to have the greatest total number of lateral plates ($\bar{x} \pm \text{SE} = 6.750 \pm 0.240$) and Paxton- individuals the fewest ($\bar{x} \pm \text{SE} = 1.338 \pm 0.172$). As expected,

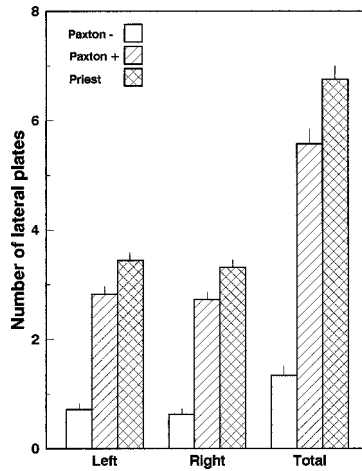


Fig. 3. Mean (+ SE) number of lateral plates (left side, right side, and total) characterising Paxton-, Paxton+ and Priest fish. $N = 80$ fish per phenotype.

TABLE 2. Number of individuals of each putative phenotype exhibiting girdle scores 0 (no pelvic girdle) through 8 (pelvic girdle fully expressed)

Pelvic girdle score	Paxton-	Paxton+	Priest
0	74	25	2
1	4	1	0
2	1	0	0
6	1	1	0
8	0	53	78

See text for details. Pearson $\chi^2 = 161.193$, $p < 0.001$, $df = 8$.

phenotypes also differed in pelvic girdle scores (Table 2; $\chi^2 = 161.19$, $p < 0.001$, $df = 8$). Almost all Priest individuals possessed complete pelvic girdles, while the majority of Paxton- fish were girdleless like their parents. Paxton+ fish exhibited the most variability in pelvic girdle score. Out of 80 Paxton+ individuals, only 53 possessed fully expressed pelvic girdles; the remainder tended to be girdleless, like their Paxton- counterparts.

Thus, phenotypes tended to differ from one another both qualitatively and quantitatively. Priest fish tended to be the most heavily armoured, possessing a greater number of lateral plates and pelvic girdle components than either Paxton phenotype. Paxton- fish tended to be the least heavily armoured, lacking pelvic girdles and possessing relatively few lateral plates.

Behaviour

Due to video camera senescence, behavioural data could not be obtained for the final group of Paxton- fish. The following results reflect this unavoidable reduction in sample size. Although fish were not marked for individual recognition and only foraging activity in the open water patch was captured on video, participation at the feeders never appeared to be less than one hundred per cent. Thus, deviations from an IFD are unlikely to be due to differences between actual and effective group size.

In the absence of the predator, distributions of the three phenotypes did not differ significantly from those predicted by the distribution of resources

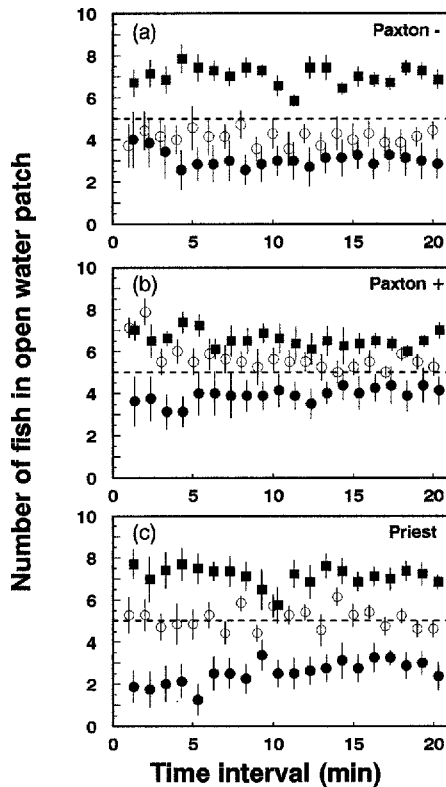


Fig. 4. Mean (\pm SE) number of (a) Paxton-, (b) Paxton+, and (c) Priest fish in the open water patch during the IFD trial (\circ) and with the predator present in the open water (\bullet) and vegetated (\blacksquare) patches. Dashed lines indicate the number of fish predicted to be in the open water patch according to the distribution of food alone. $N = 8$ groups of Paxton+ and Priest fish, $N = 7$ groups of Paxton- fish.

TABLE 3. A comparison of the observed number of fish in the open water patch to that predicted by the distribution of food alone during the IFD trial and when the predator was associated with the open water and vegetated patches

Trial	<i>t</i>	df	<i>p</i>	Power*
IFD				
Paxton-	1.426	6	0.204	0.68
Paxton+	1.177	7	0.278	0.68
Priest	0.534	7	0.610	1.0
Predator in open				
Paxton-	2.987	6	0.012**	—
Paxton+	1.154	7	0.143**	0.68
Priest	4.867	7	0.001**	—
Predator in vegetation				
Paxton-	7.759	6	0.001**	—
Paxton+	10.976	7	0.001**	—
Priest	4.934	7	0.001**	—

Student's *t* scores reflect paired comparisons (see text). Non-significant *p*-values indicate that fish distributions did not differ from the distribution of food across the two patches.

* As indicated by Cohen's *d*.

** One-tailed probability.

(Fig. 4, Table 3), indicating that individuals were indeed attempting to maximize their rate of energy intake. Thus, under these experimental conditions, Fretwell and Lucas' (1970) IFD theory appears to be a relatively good predictor of the distribution of three-spine stickleback fish (see also Milinski, 1979, 1984).

In response to the addition of the predator, however, all three phenotypes tended to increase their use of the low-risk patch (Fig. 4), indicating that individuals were willing to give up food to reduce their risk of predation. In most cases, this shift resulted in the distribution of fish differing significantly from the distribution of resources (Table 3), as expected if individuals consider both foraging gains and predation risk when deciding where to feed.

The calculated energetic equivalence of predation risk varied markedly among groups of a single phenotype. For example, the number of prey items Paxton- fish were willing to give up to avoid the predator in the open water patch ranged from 0.85 to 20.87. Despite the magnitude of this

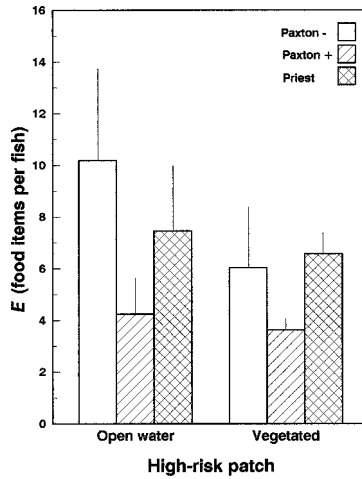


Fig. 5. Mean (+ SE) number of prey items Paxton-, Paxton+, and Priest fish were willing to give up to avoid using the open water and vegetated patch when associated with a predator (*i.e.* E , the energetic equivalence of predation risk). $N = 8$ groups of Paxton+ and Priest fish, $N = 7$ groups of Paxton- fish.

within-type variation, phenotypes tended to differ in their perceived risk of predation (Fig. 5; $F_{2,20} = 2.883$, $p = 0.079$, ANCOVAR). In general, the energetic equivalence of predation risk was highest for Paxton- fish and lowest for Paxton+ individuals. Because individuals of the three phenotypes differed significantly in both mass and length (see above and Table 1), and large body size itself is a potential defence against predation (see Lima & Dill, 1990), I reanalysed this data using group mass (*i.e.* the sum of the masses of all 10 individuals in a foraging group) as a covariate. As before, phenotypes differed in their perceived risk of predation ($F_{2,19} = 3.515$, $p = 0.050$, ANCOVAR). However, the energetic equivalence of predation risk did not co-vary with group mass ($F_{1,19} = 1.244$, $p = 0.279$, ANCOVAR), suggesting that differences between phenotypes in risk-taking behaviour were truly a consequence of phenotypic differences in anti-predator armour rather than merely an artefact of body size.

Although the energetic equivalence of predation risk tended to be higher in the open water patch than in the vegetated patch for all three phenotypes, there was no significant effect of predator location on perceived risk of predation (Fig. 5; $F_{1,19} = 0.582$, $p = 0.455$, ANCOVAR). Similarly, the interaction between phenotype and predator location was not statistically significant ($F_{2,19} = 1.015$, $p = 0.381$, ANCOVAR), although the risk of

predation experienced by Paxton– fish appeared to be most strongly affected by the location of the predator (*i.e.* the difference between E in the open water and vegetated patches was greatest for this phenotype).

Discussion

Threespine stickleback phenotypes were characterised by different amounts of anti-predator armour. Paxton– fish tended to be the least heavily armoured, possessing relatively few lateral plates and lacking pelvic girdles (see Fig. 3, Table 2). Priest fish tended to be the most heavily armoured, possessing more lateral plates and pelvic girdle components than either Paxton phenotype. Differences between phenotypes in pelvic girdle morphology are not surprising, given the moderately high heritability of girdle components in two related species, the ninespine stickleback (*Pungitius pungitius*; Blouw & Boyd, 1992) and the brook stickleback (*Culaea inconstans*; Nelson, 1977).

Phenotypes also differed in their willingness to risk exposure to a predator while foraging. However, the relationship between anti-predator morphology and risk-taking behaviour was not as predicted. While the least heavily armoured fish (Paxton–) had the highest energetic equivalence of predation risk (*i.e.* were willing to give up the most food to avoid the predator), the most heavily armoured fish (Priest) were intermediate in their risk-taking behaviour. Thus, although risk-taking behaviour and anti-predator morphology were positively correlated within a lake, the expected relationship was not observed across lakes (see Fig. 5). As suggested by Abrahams & Healey (1993), between-lake differences in risk-taking behaviour may reflect concomitant differences in life history, predation regime, or the efficacy of morphological defenses. Despite anecdotal evidence suggesting that predatory trout are more abundant in Priest Lake than in Paxton Lake (Steven Vamosi, pers. comm.), the abundance of predators and the relative efficacy of armour in the two lakes have yet to be quantified.

All three stickleback phenotypes tended to perceive the presence of the predator in the open water patch to be riskier than its presence in the vegetated patch, (*i.e.* they were more willing to give up food to avoid the predator when in the open water patch; see Fig. 5), as expected if structural complexity reduces a predator's ability to detect and capture prey (see

Lima & Dill, 1990 and references therein). Such between-patch differences however, were not statistically significant. Similarly, although Paxton-fish appeared to be affected most strongly by the location of the predator (*i.e.* differences between the energetic equivalence of predation risk in the two patches were greatest for this phenotype; see Fig. 5), the interaction between phenotype and predator location was not statistically significant. In both cases, lack of statistical significance is most likely explained by the experiment's small sample size. Given the inverse relationship between anti-predator morphology and escape behaviour in brook stickleback (Andraso, 1997) and the well-documented predator-hampering effect of structurally complex habitats (*e.g.* Christensen & Persson, 1993), I had expected the location of the predator to have a differential effect on the behaviour of the three phenotypes. Depending upon the effect of vegetation on the relative swimming abilities of predator and prey, one might expect poorly armoured individuals to either avoid (vegetation hampers prey performance more) or aggregate in vegetated patches (vegetation hampers predator performance more) containing a predator more strongly than their more heavily armoured counterparts.

The practice of using ideal free distribution (IFD) theory to quantify the energetic equivalence of predation risk is a controversial one (see Moody *et al.*, 1996; Abrahams & Dill, 1999; Grand & Dill, 1999; Houston *et al.*, 1999). In using the distribution of fish across two patches to calculate how much food they were willing to give up to avoid a predator I made two necessary assumptions: (1) there is no dilution of predation risk and (2) the relationship between energy intake and fitness is the same for all members of a group. If an individual's risk of predation decreases as the number of conspecifics foraging in a patch increases ('risk dilution'; Foster & Treherne, 1981), we might expect fish to give up foraging opportunities to join larger groups. When patches provide similar quantities of food and differ only in risk of predation, full dilution of predation risk should result in all (or most) individuals occupying the same patch (see Moody *et al.*, 1996; Grand & Dill, 1999). Although sticklebacks increased their use of the low-risk patch in the presence of the predator, on no occasion did an entire group occupy a single patch. Furthermore, individuals were observed to switch between patches more or less independently of the other members of their group, suggesting that fish did not perceive their level of predation risk to be affected by the proximity of conspecifics, and thus, that risk dilution did not occur in

this experiment. Within-group differences in the fitness benefits of energy acquisition, and consequently, willingness to take risk, are often related to individual differences in energetic state (*e.g.* body size, parasite load, age; Houston *et al.*, 1993; Clark, 1994). Typically individuals who are smaller or more heavily parasitized benefit more from the acquisition of energy than their larger or healthier counterparts, and are thus predicted to be more willing to risk exposure to a predator to obtain food. Although I cannot verify that individuals within a foraging group perceived the fitness value of food to be identical, group members were of similar age, matched as closely as possible for size, and presumably parasite-free (all fish were reared in the same laboratory environment), thereby reducing within-group variation in the relationship between energy intake and fitness.

To date, investigations into the relationship between anti-predator morphology and risk-taking behaviour have consisted primarily of interspecific (*e.g.* Abrahams & Healey, 1993) and inter-population (*e.g.* Andraso & Barzon, 1995) comparisons. As evidenced by the intermediate risk-taking behaviour of heavily armoured Priest Lake sticklebacks in this experiment, such comparisons are likely to be confounded by differences in predation regime and/or life history. Given the recent interest in understanding how tradeoffs between morphology and behaviour might promote the maintenance of defense polymorphisms within populations (see Foster & Bell, 1994; Andraso, 1997), future studies on the relationship between anti-predator morphology and risk-taking behaviour should include information about the efficacy of the defense and potential life history differences between phenotypes.

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