Predation Risk Influences Reproductive Behaviour of Iowa Darters, *Etheostoma exile* (Osteichthyes, Percidae)

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**Abstract**

In this study we tested the effects of predation risk on reproductive behaviour of Iowa darters (*Etheostoma exile*). We recorded the frequency of courtship behaviour (head shaking) and spawning acts for 30 min before and after removing an opaque barrier to expose groups of darters to (1) an empty tank (the before-pike treatment), then (2) a tank containing a pike (the pike treatment), and finally (3) an empty tank (the after-pike treatment). In response to the pike, darters performed significantly less reproductive behaviour than before exposure to the pike. Furthermore, darters performed proportionally less reproductive behaviour in the area in the immediate vicinity of the pike where risk of predation was highest. However, darters continued to occupy the risky area while exposed to the pike.

Removal of the barrier in the absence of the pike (the before- and after-pike treatments) had no effect on the overall level of reproductive behaviour, the proportion of reproductive behaviour performed in the immediate vicinity of the pike tank (the risky area), or use of the risky area.

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**Introduction**

Risk of predation influences a wide array of behavioural decisions made by animals. Many recent studies, for example, have focused on the way in which animals change their foraging behaviour in response to the presence of predators (Lima & Dill 1990; Milinski 1993). Such a trade-off occurs because animals cannot simultaneously maximize food intake and predator avoidance. Just as there are conflicts between foraging and predator avoidance, there are conflicts between reproduction and predator avoidance.

Recent reviews by Lima & Dill (1990) and Magnhagen (1991, 1993) show that reproducing animals are at a higher risk of predation than non-reproducing.
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animals. Reproducing animals generally increase their frequency of encounters with predators as a result of searching for (Gwynne 1987; Moore 1987; Hedrick & Dill 1993) or attempting to attract mates (Burk 1982; Ryan 1985). Egg carrying by males (Svensson 1988) or females (Winfield & Townsend 1983; Berglund & Rosenqvist 1986) may decrease manoeuvrability or increase conspicuousness to predators. Conspicuousness due to breeding coloration may also attract the attention of predators (Endler 1982; Wootten 1984). As well, duties associated with parental care may increase vulnerability to predators (Ainley & Demaster 1980; Matty et al. 1994).

Despite the large number of studies showing that reproduction increases the risk of predation, we know of only eight studies (Tuttle & Ryan 1982; Ryan 1985; Endler 1987; Shi 1988; Shi et al. 1990; Magnhagen 1990; Forsgren & Magnhagen 1993; Wisenden 1993) that have demonstrated the way in which reproductive behaviour is influenced by the presence of predators. Male tree frogs (Smilica sila) and tungara frogs (Physalaemus pustulosus) decreased their calling activity when a model bat was passed overhead (Tuttle & Ryan 1982; Ryan 1985). The presence of green sunfish (Lepomis cyanellus) significantly decreased reproduction by veliids (Microvelia australis) (Shi 1988) and water striders (Gerris remigis) (Shi et al. 1990).

Four studies have manipulated levels of predation risk to examine the influence of predators on the reproductive behaviour of fishes. Endler (1987) demonstrated that guppies (Poecilia reticulata) use fewer visually conspicuous reproductive displays in the presence of a pike cichlid (Crenicichla alta). Female convict cichlids (Cichlasoma nigrofasciatum) lay fewer eggs in areas where the risk of brood predation is high (Wisenden 1993). Magnhagen (1990) allowed sand gobies (Pomatoschistus minutus) and black gobies (Gobius niger) to build nests and spawn in the presence or absence of a cod (Gadus morhua). Black gobies, which reproduce during a single breeding season, did not decrease the number of nests built or the number of eggs spawned in the presence of the predator. In contrast, sand gobies, which potentially reproduce over several breeding seasons, did decrease their rate of reproduction. Subsequently, Magnhagen (1990) showed that old sand gobies (4–5 yr) spawned in the presence of cod while younger ones (2–3 yr) did not. These results suggest that the opportunity for future reproduction may affect whether animals trade reproduction for predator avoidance. A separate study has shown that male sand gobies decrease their reproductive activity when exposed to a cod while females do not (Forsgren & Magnhagen 1993).

In this study we examine whether Iowa darters (Etheostoma exile) decrease the frequency of their reproductive behaviour in the presence of a predator, the northern pike (Esox lucius). Male Iowa darters set up breeding territories in shallow water and females spawn with many males during a breeding season (Winn 1958, 1980). Given the low numbers of eggs deposited during each spawning act (generally 3 to 7, Winn 1958) and that darters may reproduce during successive breeding seasons, darters should be a good candidate to trade reproduction for predator avoidance. We quantify whether darters: 1. Decrease the frequency of reproductive behaviour in the presence of a pike; 2. Alter the
proportion of reproductive behaviour that is performed in risky areas (those closest to the predator's tank) versus safe areas in response to a pike; 3. Decrease use of risky areas in the presence of a pike.

Methods

Collection and Maintenance

We collected northern pike from Pike Lake, an oxbow lake of the South Saskatchewan River in central Saskatchewan, in the fall of 1993. Pike were maintained in 300-l stream tanks at approximately 15 °C on a 14-h L:10-h D photoperiod, and were fed 1–2 fathead minnows every 5 d.

In early May 1994, Iowa darters were collected from a 1-ha pond located on the University of Saskatchewan campus. This population of darters originated from the South Saskatchewan River when the pond was filled in 1999 to provide water for agriculture. Prior to May 1993, this pond was free of piscivorous fish species, including pike. CHIVERS & SMITH (1995) introduced 10 pike into the pond in May 1993, and removed six of the pike in Jun. and Jul. 1993. Attempts to remove the remaining four pike were unsuccessful, therefore we cannot be certain if the pond still contained pike when the darters were collected. Nevertheless, the population of darters we tested was exposed to pike in the summer of 1993. Darters brought from the field into the laboratory were placed directly into the experimental tanks in order to minimize disturbance caused by moving the fish between tanks. We fed the darters ad libitum with live food (including copepods, fairy shrimp, and mosquito larvae) collected from local ponds. The darters acclimated quickly to the laboratory conditions, usually feeding and performing courtship behaviour within a few hours of being placed into the experimental tanks. Throughout our experiment we did not observe any evidence of separate male breeding territories as described by WINN (1958, 1980).

Experimental Protocol

We placed two male and three female darters into each experimental tank (75 × 30 × 25 cm). Each experimental tank contained a substrate of silica sand and four artificial plants placed along the middle of the long axis of the tank spaced at even intervals. We placed a second tank (50 × 25 × 30 cm), the pike tank, at one end of the experimental tank. The experimental tank and the pike tank were separated by a removable opaque barrier. We marked the front glass of each experimental tank with a grease pencil to divide the tanks in half, each section measuring 37.5 × 30 × 25 cm. The half of the experimental tank closest to the pike tank was considered to be the 'risky' area, while the half of the experimental tank furthest away from the pike tank was considered the 'safe' area. The experimental tank and the pike tank were each aerated with a single airstone located at the back of each tank.

As a standard testing protocol we quantified the number of darters present in the safe area and risky area every 30 s for a 30-min pre-stimulus period. We also recorded the total number of bouts of head shaking, the number of spawning acts, and the location (safe or risky) where each act was performed during the 30 min. Immediately after this 30-min observation period we removed the barrier between the experimental tank and the pike tank, and quantified the same behaviours for an additional 30-min post-stimulus period. A bout of head shaking was defined as a rapid lateral shaking of the head by either a female (estimated to be the performer of approximately 95% of all head shakes) or a male. In darters, females frequently initiate courtship (WINN 1980). Head-shaking bouts lasted for approximately 1–15 s, with a minimum of 2 s between successive bouts. Head shaking occurred prior to all spawning acts and usually when the darters came within about one body length of one another. Many hours of laboratory observations conducted outside of the breeding season failed to reveal any head-shaking behaviour. A spawning act occurred when a male moved over the female with his caudal region depressed against hers and the pair shook vigorously for up to 20 s.

Each group of darters was tested under three treatment conditions. In the before-pike treatment, conducted between 0830 and 1100 h, the darters were observed for 30 min before and 30 min after they were exposed to any empty pike tank. This controlled for any changes in behaviour that may result from the disturbance of removing the barrier. In the pike treatment, conducted 1 h after the end of the before-pike treatment, the darters were observed for 30 min before and 30 min after they were
exposed to a single pike in the pike tank. Four different pike (\(X \pm SD\) fork length = 24.0 ± 1.5 cm) were used in this experiment. In the after-pike treatment, conducted 1 h after completion of the pike treatment, the darters were again observed for 30 min before and 30 min after they were exposed to an empty pike tank. The after-pike treatment tested whether darters would remember the area where a pike was located previously and would consequently decrease their reproductive activity or avoid the area. We tested a total of 10 groups of darters (\(X \pm SD\) total length = 5.10 ± 0.41 cm) in each of the three treatments, with each fish being used only once. Each group of darters was considered as a single replicate. Tests were conducted at approximately 20 °C.

For each of the three treatments we used a Wilcoxon signed-rank test (SIEGEL & CASTELLAN 1988) to compare the change (post-barrier removal minus pre-barrier removal) in the total number of head-shaking bouts performed by all of the fish in the tank. For spawning acts, a similar analysis was conducted only for the pike treatment. The low number of spawning acts in the pre-barrier removal of the before- and after-pike treatments precluded testing for a reduction in spawning acts. For each of the three treatments we used a Wilcoxon signed-rank test to compare the change (post-barrier removal minus pre-barrier removal) in the proportion of head-shaking bouts that were performed in the risky area, and the change in the number of darters using the risky area. We did not compare the change in the proportion of spawning acts performed in the risky area before versus after the barrier removal for any of the three treatments because the low frequency of spawning acts precluded testing for a reduction.

**Results**

Darters did not show a significant change in the total number of head-shaking bouts (Wilcoxon \(T = 27.5, n = 10, p > 0.95\), Fig. 1a) or the proportion of head-shaking bouts performed in the risky area (Wilcoxon \(T = 24, n = 8, p = 0.461\), Fig. 2a) when exposed to the empty pike tank in the before-pike treatment. However, during the pike treatment, darters performed significantly fewer bouts of head shaking after barrier removal than before barrier removal (Wilcoxon \(T = 55, n = 10, p = 0.002\), Fig. 1b). In addition, during the pike treatment there was a significant decrease in the proportion of head shaking performed in the risky area (and a corresponding increase in the proportion in the safe area; Wilcoxon
Fig. 2: Mean (+ SE) proportion of head-shaking bouts performed in the risky area during 30 min pre- and 30 min post-barrier removal for (a) before-pike treatment, (b) pike treatment, and (c) after-pike treatment.

T = 48, n = 9, p = 0.012, Fig. 2b). During the after-pike treatment the darters did not show a significant change in their total number of head-shaking bouts (Wilcoxon T = 24, n = 10, p > 0.90, Fig. 1c) or the proportion of those bouts performed in the risky area (Wilcoxon T = 17, n = 7, p = 0.688, Fig. 2c).

During the pike treatment there was a significant decrease in the total number of spawning acts after barrier removal (Wilcoxon T = 21, n = 6, p = 0.031). Only 14 of the 57 spawning acts observed during the pike treatment were performed after the barrier removal.

There was no significant change in use of the risky area (post-barrier removal minus pre-barrier removal) for any of the three treatments (before-pike treatment, Wilcoxon T = 32, n = 10, p = 0.695, Fig. 3a; pike treatment, Wilcoxon T = 27.5, n = 10, p = 0.611, Fig. 3b; after-pike treatment, Wilcoxon T = 46, n = 10, p = 0.064, Fig. 3c).

Discussion

The results of this study demonstrate clearly that Iowa darters decreased their reproductive activity in response to an increase in predation risk. Furthermore, the reproductive behaviour that was performed in the presence of the predator, the proportion that was conducted in immediate proximity to the predator (the risky area) decreased. These responses reflect a compromise between the need to reproduce in order to increase fitness and the need to avoid predators in order to obtain future matings. Iowa darters should have many opportunities to spawn in the same season and in successive seasons, therefore lost opportunity costs may not be as prohibitive as for other species, such as black gobies, which reproduce during a single breeding season (Magnhagen 1990).
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![Graph showing mean (+ SE) proportion of time in the risky area during 30 min pre- and 30 min post-barrier removal for (a) before-pike treatment, (b) pike treatment, and (c) after-pike treatment.](image)

Fig. 3: Mean (+ SE) proportion of time in the risky area during 30 min pre- and 30 min post-barrier removal for (a) before-pike treatment, (b) pike treatment, and (c) after-pike treatment.

**Forsgren & Magnhagen (1993)** demonstrated that male sand gobies decrease their reproductive activity when exposed to a cod while females do not. In this study we did not separate the activity of males and females; however, because head-shaking bouts were performed almost exclusively by females (approximately 95%), our results reflect a decrease in reproductive activity by females when exposed to the pike. We are unable to conclude whether males also showed the same response.

In the after-pike treatment we tested whether darters would remember the area where a pike was located previously and would consequently decrease their reproductive activity or avoid the area. The darters did not decrease their reproductive activity or change the proportion of reproductive behaviour in the risky area following removal of the barrier in the after-pike treatment. In addition, the darters did not decrease their use of the risky area, but instead tended to increase their use of the risky area (although this was non-significant, p = 0.064). We observed that the darters appeared to be inspecting the area where the predator was previously seen. This inspection indicates that darters did remember the area where the pike was previously located, but did not avoid the area. Similarly, darters did not change their area use following exposure either to an empty tank in the before-pike treatment or to a pike in the pike treatment. When the pike was present, we predicted that darters would avoid the risky area closest to the predator. However, darters use freezing and crypsis as their antipredator strategy (Smith 1979) and are reluctant to flee their spawning territories (Winn 1980). Together, these factors may explain why darters did not avoid the end of the tank closest to the pike. We frequently observed that darters froze when in the immediate vicinity of a pike.

Our results demonstrate that Iowa darters, a species which has multiple mating opportunities within each of several breeding seasons, decrease their
reproductive behaviour in the presence of pike. Furthermore, the trade-off between reproductive activities and predation risk appears to be truly risk sensitive, as the proportion of reproduction decreases within the immediate vicinity of the predator.

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Literature Cited


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