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Differences in Timidity and Escape Responses between Predator-naive and Predator-sympatric Rainbowfish Populations

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Abstract

Responses of rainbowfish (*Melanotaenia duboulayi*) from two populations towards a) an active and a passive predatory fish and b) a novel trawl apparatus, were compared. Predator-sympatric fish avoided the fish predators and showed stronger avoidance behaviour in response to the active predator. These fish used predator inspection excursions to rapidly assess the potential risk and their escape responses were consistently effective. In contrast the predator-naive fish ignored the passive predator but were continually drawn towards the active predator possibly due to generalized curiosity and the absence of significant negative feedback from the predator, which was restrained by a clear Perspex partition. Despite this attraction, the predator-naive fish did not display typical predator inspection behaviour and showed very poor escape performance when initially confronted by the trawl apparatus. Many of these fish, however, showed rapid improvement in their escape performance through learning. These results suggest that predator-sympatric rainbowfish have the capacity to assess the level of threat posed by a predator and predator-naive rainbowfish learn to implement appropriate escape strategies when forced to evade a threat.

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Introduction

Predation is one of the greatest selective pressures operating on populations of prey animals and can lead to substantial differences in morphology, physiology and behaviour of individuals from different geographical locations (Magurran 1990; Endler 1995). Animals which live sympatrically with predators should budget their time and alter their behaviour according to the perceived level of threat. For example, guppies alter their courtship behaviour from full display to sneak mating depending on the level of predator threat (Magurran & Seghers 1990). Scanning

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for predators and responding to them are costly in terms of time, which could be otherwise spent feeding or courting. Hence, predator-sympatric populations should utilize mechanisms which allow them to minimize the amount of time spent on antipredator behaviours in order to maximize fitness.

A number of studies have compared the behaviour of predator-sympatric populations of fish with 'predator-naive' populations and have uncovered several startling differences. Fish from areas of high predation are better able to recognize predators, detect predators earlier, inspect more readily, show attack cone avoidance, form tighter cohesive groups and display more appropriate escape responses compared with predator-naive fish (Seghers 1974; Liley & Seghers 1975; Magurran 1986; Licht 1989; Magurran & Seghers 1990; Gelowitz et al. 1993). Predator-sympatric fish are also much better able to determine the level of threat a particular predator represents. When faced with a predator, fish from predator-sympatric populations increase their vigilance but forage for longer periods of time before fleeing (Fraser & Gilliam 1987) and are quicker to return to postexposure behaviour (Magurran & Pitcher 1987). Fish from predator-sympatric and -naive populations also show variation in their ability to learn about predators (Magurran 1990; Mathis & Smith 1993).

Guppies are capable of determining the difference between satiated and hungry predators, presumably by responding to the movements of the predator (Licht 1989). This suggests that the behaviour of the predator may not only allow prey to determine what species the predator is (Coates 1980), but also something of its motivational state (Pitcher et al. 1986; Pitcher 1992; Huntingford et al. 1994). Hence, predator behaviour may be an important cue picked up by prey partaking in predator inspection and may determine the antipredator responses displayed by prey species following inspection visits (Magurran & Pitcher 1987).

Owing to ethical considerations, many investigators have used models in place of live predators to study antipredator responses. However, even the best predator models are likely to lack subtle behaviours displayed by particular predatory species, thus altering the prey animal's perception of threat. The use of models has another drawback in that it is much more difficult to assess the effects of predator experience over repeated trials because habituation rapidly sets in if little or no physical harm occurs (Csanyi 1986).

Nets and other fishing gear evoke responses in fish resembling that of predator avoidance (Francis & Williams 1995) and enable an experimenter to explore the learning and memory capabilities of fish, allowing the measurement of more realistic responses following repeated exposure to threat in comparison to predator models.

It is often difficult to distinguish the effects of predation pressure alone as a number of other habitat characteristics often covary with the presence of predators (Endler 1995). The rainbowfish populations in the present study varied in the level of predation experienced in the wild, while most other characteristics of their native streams (habitat complexity, light conditions, flow rate, depth, etc.) were similar. The study comprised two complimentary experiments. The first part compared the responses of members of two populations of rainbowfish (*Melanotaenia duboulayi*) to predatory fish that differed only in their level of activity. The live predators were placed behind clear Perspex so no negative feedback was forthcoming. A second experiment explored the abilities of fish from the two populations to solve a novel antipredator problem (escape from a trawl). In this experiment negative feedback was applied and allowed the learning rates of each population to be compared over repeated exposures.

Methods

Two populations of fish were sampled from two tributaries of the Mary River in southeast Queensland using standard bait traps. The first population was from Amamour Creek (26°21′S, 152°40′E), a relatively small stream dominated by large still pools and occasional riffles. A number of large predatory fish species were present, including spangled perch (*Liopotherapon unicolor*), saratoga (*Scleropages leichardti*) and mouth almighty (*Glossamia aprion*). The second population was derived from the upper part of Obi Obi Creek (26°45′S, 152°55′E) near Maleny. The headwaters of Obi Obi Creek were characterized by fast flowing waters with a number of waterfalls, deep pools and rapids. The fish community differed profoundly from that of Amamour Creek. Obi Obi Creek contained very few large fish species with the exception of the eel-tailed catfish (*Tandanus tandanus*) and the long-finned eel (*Anguilla reinhardti*). Both sites were characterized by submerged woody debris, submerged aquatic vegetation and a mean water depth of ≈ 1.5 m. The flow rates and light regimes were also very similar. Rainbowfish were the most abundant fish species at both sites. Random sampling established that the mean ($\pm$ SE) length of the fish was 51.9 ± 1.4 mm at Amamour and 53.8 ± 0.8 mm at Obi Obi ($n = 24$ in each case).

Experiment 1

Rainbowfish were collected on four separate occasions during Apr. 1987. They were transported to the University of Queensland and placed in large holding tanks for 2 d prior to experimentation. The water temperature in the holding tanks and the experimental arena was 22°C. The fish were not fed while held in captivity prior to experimentation.

The experimental arena consisted of a 1×1.6 m tank divided along its length by opaque Perspex. A trap door was located at one end and could be raised to reveal a predator (spangled perch) behind clear Perspex (Fig. 1). Lighting consisted of two overhead fluorescent tubes and another mounted on the wall over the predator end of the arena. All glass walls were covered with blue plastic to prevent fish shoaling with their reflection. The floor of the tank was white. The tank was surrounded by a curtain and a video camera was suspended overhead.

The two spangled perch used in this experiment both had a standard length of 22 cm and were of similar appearance. Spangled perch are a bland silver-grey colour with a light speckling of small, dark grey spots and lack any obvious bands or large spots. The two individuals used in this experiment differed greatly in their

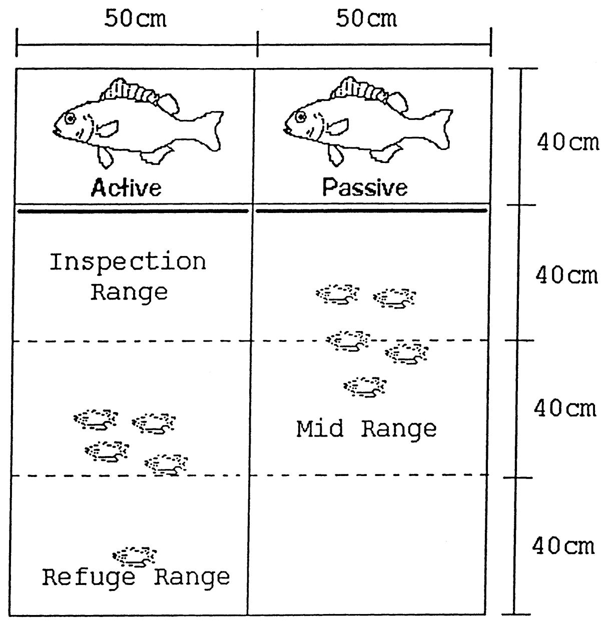

Fig. 1: Diagrammatic view of the experimental tank used in expt 1 showing the divisions into the three ranges (inspection, mid and refuge). A clear Perspex divide and an opaque division, which could be drawn up by a pulley system to reveal the predators to the prey, separated the predators from the rainbowfish

general behaviour. Both in the wild and in captivity, variation exists in the level of activity and aggression displayed by individuals of similar size. We were able to exploit this difference in behaviour by choosing animals that varied markedly in these characteristics. The aggressive perch's behaviour was characterized by constant patrolling of the holding tank and, when exposed to rainbowfish, it repeatedly charged at the Perspex divider. The other perch sat motionless in the water column and its fins moved only to maintain position. Throughout the period of the experiment both predators were permanently housed in the compartments at the end of the experimental arena. They were left undisturbed so that their normal behaviour was not disrupted by moving them between tanks. The results of a pilot study indicated that in the absence of predators, the distribution of rainbowfish shoals in the experimental tank did not differ significantly between the left and right sides (e.g. proportion of time spent in inspection range; ANOVA, $p = 0.910$; $n = 7$).

Fifty fish from each population (Amamour and Obi Obi) were divided randomly into 10 groups of five fish. Two groups from the same population were simultaneously placed on either side of the experimental arena and allowed to settle for 15 min. Following this adjustment period, the rainbowfish were exposed to a predator. Once a minute for 5 consecutive minutes the location of all fish was recorded on video. From these data the following indices were calculated; the mean distance of the shoal from the predator and the proportion of time spent in the front (inspection range), middle (mid-range) and back (refuge range) thirds of the arena (Fig. 1). Only the distribution data are reported here.

Because the mean distance to the predator tells us little about how the fish were distributed throughout the experimental arena, only the inspection range proportion was analysed using Mann–Whitney U-tests (Zar 1984). Because we were interested in interaction effects and used nonparametric statistics, the data were subdivided and analysed in two ways: 1) Each population was analysed separately to examine the effect of predator activity within each population; and 2) The response to each of the predators was analysed separately to determine how the level of predator activity affected our ability to distinguish between the two populations.

Experiment 2

An experimental tank measuring 200 × 30 × 30 cm was equipped with a pulley system which allowed a vertical net to be pulled along the long axis of the tank. The depth of the water in the tank was maintained at 20 cm and the temperature was 22°C. The net had a mesh size of 1 cm and completely blocked the tank with the exception of a small hole. The hole (2 × 2 cm) was placed directly in the centre of the net ≈ 10 cm from the bottom of the tank and 14 cm from each side. The fish could use the hole to avoid being trapped as the net was dragged from one end to the other.

Fish from each population were housed separately in large holding tanks containing 50 fish each. A group of five fish was randomly taken from either of the holding tanks, placed in the experimental tank and allowed to adjust to the new surroundings for 15 min. The net was drawn along the tank until it was 3 cm from the end, at which point it was held in position for 60 s. The time taken for the net to move from one end to the other was 30 s. Any fish that did not avoid the net became trapped. Fish which did not escape were allocated the maximum time limit of 90 s (= 30 + 60). The net was then removed and placed back in its original position. This constituted one run. The procedure was repeated at 2 min intervals in order to investigate the effect of negative experience (i.e. being trapped) on the learning ability of fish from each population. For each run, the time taken for each fish to escape through the hole and the number of fish that successfully escaped were recorded. From these data the mean escape time for each shoal was calculated for each run. Each group was exposed to a total of five runs. Six replicates from each population were tested. Owing to the nature of the data, nonparametric statistical analyses were conducted. Two-tailed Mann–Whitney U-tests (Zar 1984) were used to determine the effect of population origin and Kruskal–Wallis ANOVAS (SAS Institute) were performed to determine the effect of run number on escape latency and the percentage of fish escaping.

Results

Experiment 1

When exposed to a passive predator (n = 4) the Amamour Creek fish spent a large proportion (80%) of their time in the mid-region. When exposed to an active predator (n = 6) this declined to 48%, and the remaining time was spent in the refuge end of the tank. Therefore, high predator activity appeared to increase the wariness of the Amamour Creek rainbowfish as displayed by a movement away from the predator end of the tank. This change in distribution was reflected in the analysis of the refuge range data (Fig. 2) where the predator-experienced population (Amamour Creek) showed a significant difference in their response towards the two predators (Mann–Whitney test, $U = 24$, $n_1 = 6$, $n_2 = 4$, $p = 0.01$).

In contrast, when exposed to a passive predator, the Obi Obi Creek fish were distributed randomly throughout the tank. When exposed to the active predator, however, they spent 92% of their time in the inspection range (Fig. 3). The refuge range results (Fig. 2) suggest that the Obi Obi Creek fish significantly altered their response depending on the level of predator activity (Mann–Whitney test, $U = 25$, $n_1 = 5$, $n_2 = 5$, $p = 0.01$). Statistical analysis was not carried out on the inspection range data because the refuge and the inspection range data were not mutually independent.

The data for the active and passive predators were analysed separately to compare the differences between the two populations when faced with an active or passive predator. In the presence of the active predator the Amamour Creek fish spent significantly more time than the Obi Obi Creek fish in the refuge range (Mann–Whitney test, $U = 30$, $n_1 = 5$, $n_2 = 6$, $p = 0.005$), while in the presence of the passive predator the trend was reversed (Mann–Whitney test, $U = 20$, $n_1 = 4$,

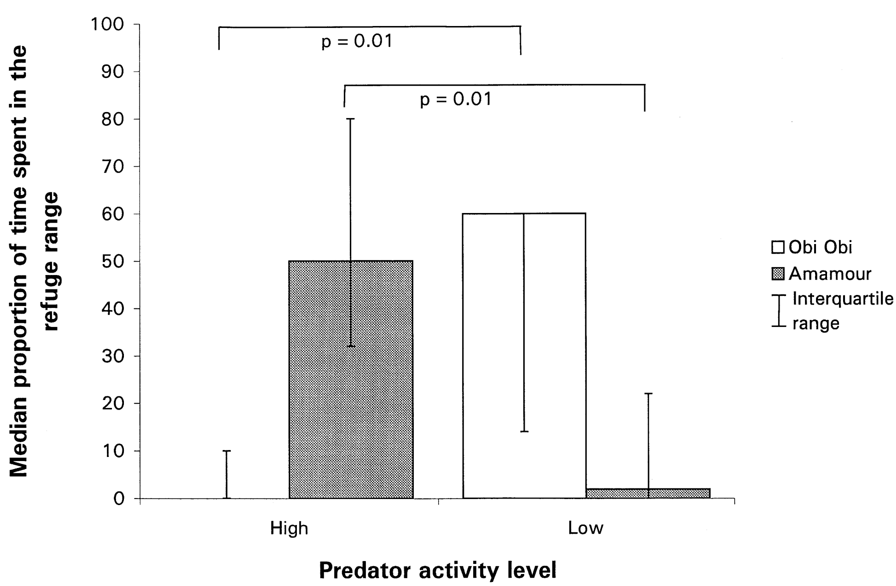

Fig. 2: The median percentage of time spent in the refuge range by both populations ± the interquartile ranges. Predator-experienced fish from Amamour Creek spent more time in the refuge range in the presence of an active predator. A significant and opposite trend for the predator-naive fish from Obi Obi Creek is evident

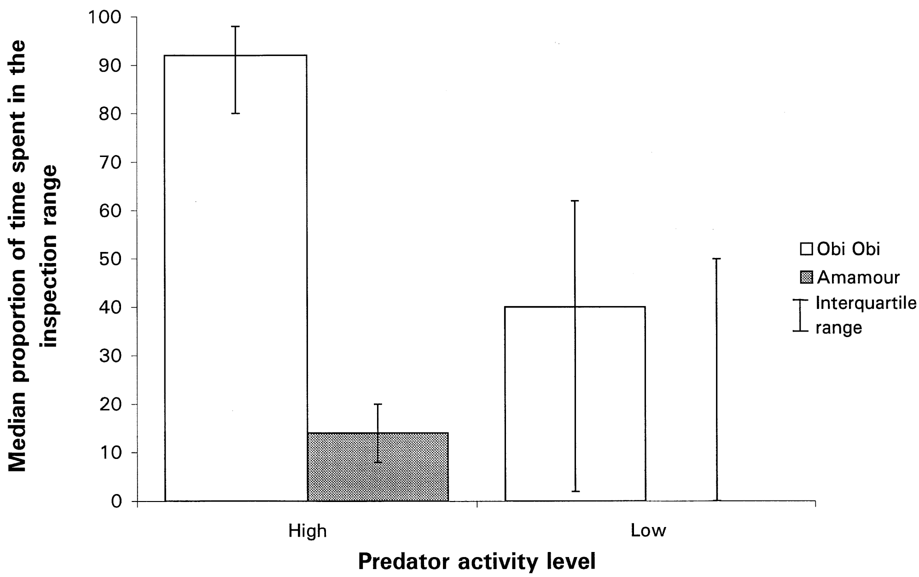

Fig. 3: The median percentage of time spent in the inspection range ± the interquartile ranges. Obi Obi Creek fish spent more time in the inspection range when an active predator was present compared with when the passive predator was present. Amamour Creek fish rarely entered the inspection range

$n_2 = 5$, $p = 0.02$; Fig. 2). A significant difference between the populations could only be found when the fish were exposed to the active predator.

When exposed to the active predator the Amamour fish initially made several inspection visits. They approached the predator typically as singletons or in pairs and then returned quickly to their shoal mates. Later they moved to the far end of the tank, relaxed their schooling activities and resumed social activities, including courtship and dominance displays. The Obi Obi Creek fish gathered in a tight shoal and spent almost the entire time within 20 cm of the active predator. On many occasions the Obi Obi fish were repeatedly charged and harassed by the perch. The general response of the Obi Obi fish to this aggression was to wheel away from the predator for 1 or 2 s and then return to the Perspex divide. Several individuals elicited fast start responses to the activities of the active predator, but regardless of how many times the predator attacked, the Obi Obi rainbowfish always returned.

Experiment 2

The Amamour Creek fish escaped from the trawl more frequently than the Obi Obi Creek fish (Mann–Whitney test, $z = 3.66$, $n_1 = 30$, $n_2 = 30$, $p = 0.001$; Fig. 4). Escape latency times were significantly lower for the Amamour fish (Mann–Whitney test, $z = 4.024$, $n_1 = 30$, $n_2 = 30$, $p = 0.001$; Fig. 5). Both populations

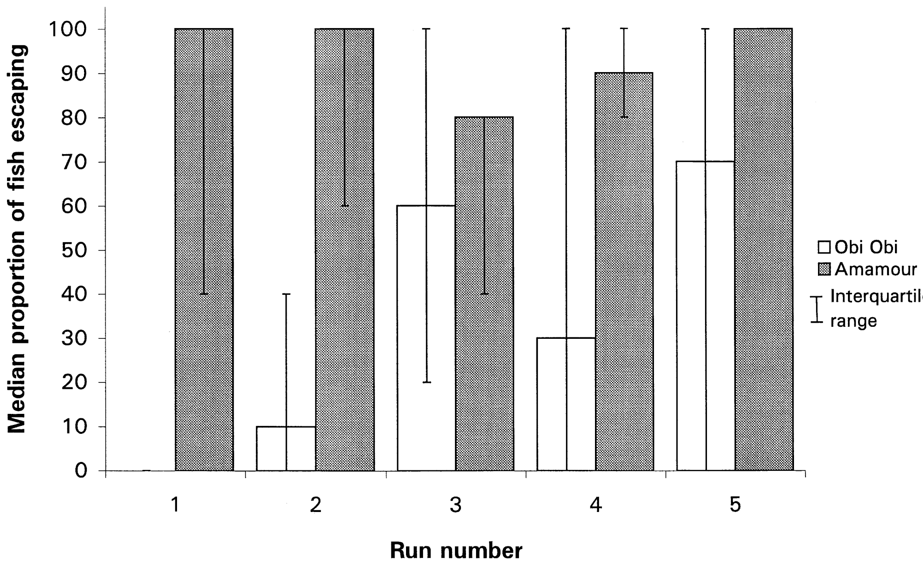

Fig. 4: The median percentage of fish escaping from the trawl (± interquartile range) for each population of rainbowfish and each of the five runs

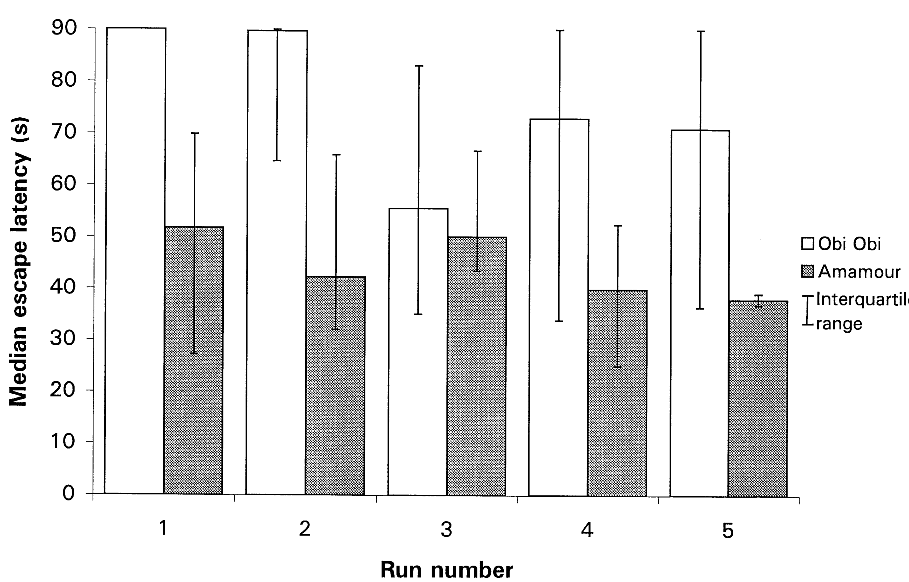

Fig. 5: The median (± interquartile range) time taken for shoals to make an escape from the trawl. Predator-experienced fish from Amamour Creek escaped significantly faster than fish from Obi Obi Creek (Mann–Whitney test, $z = 4.024$, $n_1 = 30$, $n_2 = 30$, $p = 0.001$)

showed improvement in their performance through successive exposure, but not significantly so (Kruskal–Wallis test, $\chi^2 = 4.541$, df = 4, p = 0.338 for Amamour and $\chi^2 = 9.258$, df = 4, p = 0.055 for Obi Obi fish). The improvement was more obvious for the Obi Obi Creek fish, which did not escape at all during the first trial (Fig. 4). There was a tendency for escape latencies to decrease with experience (Kruskal–Wallis test, $\chi^2 = 3.663$, df = 4, p = 0.454 for Amamour and $\chi^2 = 8.749$, df = 4, p = 0.067 for Obi Obi fish; Fig. 5).

A high level of variability was evident in the Obi Obi Creek data. Half the Obi Obi Creek fish groups performed equally well as the Amamour fish, while the other half failed to escape from the trawl altogether.

Throughout and between the runs Amamour fish were often observed approaching and inspecting the net in pairs or as singletons. However, fish rarely swam through the escape hole while the net was moving; rather they swam just in front of it and waited until it had stopped before turning and escaping. In the early runs the Obi Obi Creek fish often showed nervous, skittish behaviour towards the approaching net. In the final few runs, however, their behaviour was similar to that displayed by the Amamour fish.

Discussion

The data from the first experiment indicated that the level of activity displayed by the predators had a significant effect on the behaviour of prey individuals. The behaviour observed in the Amamour fish in response to the active predator would, under natural circumstances, allow them to maintain activities such as foraging and courtship (Godin & Crossman 1994). Indeed, a large number of social interactions were observed among the Amamour fish while they were at the refuge end of the tank far from the predator. Male fish showed clear hierarchical behaviour and continued to court females. Presumably if food had been available the fish would have also foraged. When presented with the passive predator, the Amamour fish primarily utilized the middle and inspection areas of the tank, indicating that the perceived threat was low. Amamour fish probably utilized information gained during early inspection visits to assess that the passive predator did not pose an immediate threat and continued with normal activities. Pitcher et al. (1986) suggested that minnows are able to predict when a predatory pike is likely to make a strike by observing the behaviour of the pike during inspection visits. This observation is indicative of the potential importance of subtle behavioural cues displayed by predators to inspecting prey.

In the second experiment, Amamour fish spent the time between runs, as well as during the early stages of the trawl, inspecting the net. These findings indicate that in the wild, Amamour fish may be able to quickly assess the level of threat a particular predator represents and respond appropriately, enabling them to exploit variations in predator pressure and thus lower their time and fitness costs. This type of behavioural flexibility may be selected for in regions of high predation pressure. In order to examine this possibility further, fish from a range of sites differing only in terms of predator presence would have to be tested. Such an experiment would avoid the problem of pseudoreplication present in this experiment caused by the limited number of populations represented, and would permit generalizations about differences in behaviours displayed by populations living sympatrically with predators and those that are predator naive.

An unexpected result was the intense interest the Obi Obi Creek fish showed towards the active predator in expt 1. This is contrary to the widely accepted observation that predator-sympatric fish inspect predators more frequently than predator-naive fish (Magurran 1986; Magurran & Seghers 1990; Pitcher 1992; Huntingford et al. 1994). In the presence of a passive predator, the naive Obi Obi Creek fish ignored the predator and moved randomly throughout the tank. The increased level of 'predator inspection' observed in these fish during their exposure to the active predator would have probably led to the death of most school members were it not for the Perspex separating them from the predator. Huntingford & Coulter (1989) also observed that fish from low-risk sites spent more time inspecting a goldfish than did high-risk fish. Is this a case of predator inspection or fatal attraction? Predator inspection is generally carried out by small groups (typically pairs) of fish who approach and then stop at a relatively safe distance from the predator. The trip is often exceptionally short in duration with only a few seconds spent fixating on the predator. Obi Obi Creek fish approached as a tight shoal of five fish and were only a few millimetres from the predator on many occasions. Rather than quickly fleeing to a safer distance after inspection, they tended to stay within a few body lengths of the predator for most of the time.

The tendency to inspect and the minimum approach distance appear to vary greatly between different populations of fish (Magurran & Pitcher 1987; Dugatkin & Alfieri 1992; Huntingford et al. 1994; Magurran & Seghers 1994). Magurran & Seghers (1994) found that minnows from areas of low predation pressure showed high levels of predator inspection behaviour. They argued that this may be a remnant behaviour left over from the juvenile stage when fry have to avoid cannibalistic attacks. This may also be the case with rainbowfish. Similarly, Curio (1993) reported the retention of a minimal capacity to assess and evade predators in localities that no longer contained high numbers of predators. The behaviour of the Obi Obi Creek fish sometimes resembled classical predator inspection behaviour, but it was by no means well developed. Indeed, it appeared that occasionally the Obi Obi fish were attempting to school with the predator rather than inspect it.

Obi Obi Creek fish may have initially been investigating the active predator, but rather than fleeing, they rapidly habituated because they suffered no physical harm. Habituation to models and nonthreatening live fish has been shown to occur in many fish species but is often fastest in populations lacking high levels of predation (Huntingford & Coulter 1989). When confronted by the trawl apparatus, on the other hand, the Obi Obi Creek fish were forced to respond owing to the negative impacts of pursuit and physical confinement and showed marked improvements in their escape performance with repeated experimental exposure.

The results of our study highlight the importance and difficulty of distinguishing between general curiosity and predator inspection behaviour. It is widely accepted that predator inspection behaviour has a large curiosity component (Godin & Crossman 1994). It is not unusual for novel objects to attract the attention of rainbowfish in the wild. In many locations rainbowfish will inspect virtually any disturbance in their vicinity, even the body of a floating observer. This high level of curiosity is probably related to their generalized feeding habits and the variable environment in which rainbowfish live. In habitats which are dynamic in terms of food availability and habitat structure, such as creeks, it may pay to sample novel objects in the hope of uncovering and exploiting new resources.

Magurran & Seghers (1994) stated that a general tendency to investigate novel objects in the environment is a widespread and adaptive behaviour regardless of the level of predation risk, as such risk may fluctuate over the medium to long term. However, we believe from our results that the introduction of predators to an environment such as Obi Obi Creek would most likely be disastrous. Such a scenario seems to have already occurred in Lake Eacham in northern Queensland, where the disappearance of the Lake Eacham rainbowfish (*M. eachamensis*) from its type locality followed the introduction of predators (Barlow et al. 1987). Translocation of large predatory fish species in Australia for recreational angling is extremely common and represents a real threat to many smaller prey species. The trawl data suggest that with repeated exposure to predators, rainbowfish may be trained to avoid predators under controlled conditions, as is possible with hatchery-reared salmonids (Jarvi & Uglem 1993). This could be a useful tool for future conservation reintroductions should they ever be deemed necessary.

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