CHAPTER 4
Habitat and spatial predator association and avoidance in rainbowfish species.

4.1 ABSTRACT

Fish from all populations of rainbowfish tested appeared to be capable of avoiding dangerous habitats by remembering either the location and/or the microhabitat that a predator was last observed in. In all cases the rainbowfish tested had to rely solely on vision to orientate around the experimental arena. Reliance on different types of visual cues appears to vary between populations but the reason for this variation remains elusive. None of the ecological variables tested (flow variability, predator density or habitat complexity) correlated significantly with the orientation technique employed by each population. The level of predation threat at the collection sites, however, had a significant effect on habitat choice before, during and after exposure to a predator model. Therefore, population variation in the use of refuge structures could be related to variation in predation pressure encountered by the rainbowfish at each locality.

4.2 INTRODUCTION

Animals are able to recall the location of predators, food patches or territorial rivals. The ability to form a cognitive map of the environment is likely to have fitness benefits. While a lot of attention has been paid to orientation and migration in birds and mammals, few workers have considered orientation and cue use in fish.

4.2.1 Predator-habitat associations

Prey often face predators that can be found in certain areas (e.g. particular microhabitats) and/or at certain times. The risk of predation may be habitat specific, not only due to the behaviour of the predator, but also because some areas offer better refuge than others (Butler 1988). Many piscivorous fish species are often found in particular microhabitats. Individual cod and bass (Percichthyidae) for example, are often found at the same snag (i.e. fallen timber) that they defend rigorously and return to even after lengthy migrations (P. Kind pers. comm.). Mouth almighty (*Glossamia aprion*), a major predator of rainbowfish on the Atherton Tablelands, are always found in areas that are structurally complex, either in dense weed beds or among woody debris. One would expect therefore, that prey species would avoid specific locations or micro-habitats commonly occupied by predators in order to reduce the probability of encountering them. For example, minnows (*Pimephales promelas*) learn to associate alarm substances with high-risk habitats and later avoid such areas, even when the alarm substance is no longer present (Chivers & Smith 1994, 1995). Chivers and Smith suggest, however, that in clear water fish probably rely heavily on other senses such as vision to identify dangerous habitats. Huntingford and Wright (1989) showed that sticklebacks (*Gasterosteus aculeatus*) are capable of avoiding foraging patches associated with elevated predation risk, and that the ability to learn varies between populations, perhaps due to the level of predation risk experienced in their site of origin. In laboratory experiments, sticklebacks appeared to use one of two patterns of response. Individuals either used local visual cues (markers) or cues indicating the general location of a safe foraging patch (global cues).

4.2.2 Cue use in orientation

There is now a great deal of literature regarding how animals locate objects within their environment (for a review see Gallistel 1990). Insects use skylight patterns to navigate around the nest, but once close to the goal, they rely on local landmarks. Landmark snapshots are acquired during the individual's foraging life and are later used as a template for orientation (Wehner 1997). Similarly young pigeons learn local landmarks around the roost and use them for homing (Braithwaite and Guilford 1995). However, the cues on which pigeons rely may vary depending on the roost location (Wiltschko and Wiltschko 1989). The way in which ecology influences the learning and memory capabilities of animals has only recently begun to receive the level of attention it deserves (e.g. Giraldeau 1997). A number of techniques may be employed depending on the past history of the animal and the nature of the spatial problems it commonly faces (Braithwaite *et al*. 1996). It is conceivable that the types of cues used for orientation and navigation will depend on the level of stability in the environment (Girvan and Braithwaite 1998). Environmental stochasticity may affect cue reliability. Girvan and Braithwaite (1998) pursued this idea and found that sticklebacks from different locations (lake and river populations) relied on different cues to learn the location of a foraging patch. Fish from stream habitats relied on a behavioural algorithm (i.e. turn left, then right etc.) to navigate through a maze, whereas fish from ponds (a more stable/predictable environment) relied on local landmarks.

Warburton (1990) suggested that reliance on local landmarks for orientation may also vary according to the nature and complexity of the visual environment. It seems probable that fish derived from structurally complex environments may not rely on local landmarks since cues would be lost amongst the visual clutter. Fish from intermediate and perhaps low complexity environments are expected to rely more heavily on local cues.

4.2.3 Longevity of negative associations

Chivers and Smith (1995) were interested in how long the negative association between microhabitats and predator presence lasted, but they failed to investigate this. They suggest that if a predator is likely to be found in an area for only a short time, then it would not be beneficial for prey to retain the avoidance for very long. In their study, the prey fish were conditioned using just one trial four days before testing. In previous studies prey have shown conditioned responses to predators that may last from to six hours to 12 months (Csanyi *et al*. 1989, Miklosi *et al*. 1992). It seems that constant reinforcement would probably be necessary to enforce strict avoidance of a specific micro-habitat, particularly those habitats which offer some foraging reward. By recording the behaviour of the fish over an extended period after the encounter with the predator, we may be able to see how long it takes for the fish to return to their favourite habitat. The rate of return to the location/habitat where the predator was last seen may provide us with some index of the strength (decay rate) of the avoidance response.

4.2.4 Predation pressure and habitat utilisation

Predation may indirectly affect the fitness of individuals by confining them to sub-optimal micro-habitats. Many refuge habitats lack sufficient prey items so animals must find a compromise between remaining in cover and venturing out to forage. The use of complex structure as refuge may vary between populations of the same species (Brown and Warburton 1997) due to the level of habitat complexity (and hence refuge availability), the level of predation threat, or some combination of the two. The extent to which complex structures are utilised may depend on the level of risk sensitivity displayed by individuals. Populations originating from locations with intermediate levels of predation threat may show risk sensitive use of cover, while fish from regions of high predation may show hypersensitivity (Helfman and Winkelman 1997).

This study attempted to answer several questions using one protocol. Specifically the questions addressed were:

1) Can rainbowfish associate the presence of a predator with a particular microhabitat using vision?
2) Do rainbowfish avoid specific locations/habitats using different cues depending on the level of habitat stability or complexity encountered in the wild?
3) Does the level of predation threat experienced in the wild affect the ability to learn to associate micro-habitats and/or locations with predator presence (i.e. do fish from predator-wary populations show a stronger avoidance reaction compared with predator-naïve fish)?
4) Does the level of habitat complexity or predation at the collection site affect habitat use?

Three species of rainbowfish were chosen for this study, *Melanotaenia eachamensis*, *M. splendida* and *M. spp. nov.* (Utchee type). Each species was represented by three populations that originated from slightly different environments (Table 4.1).

Species	**Population**	**Flow Variability**	**Predators**	**Habitat Complexity**
M. eachamensis	Lake Eacham captive stock	Low	Low	Low
M. eachamensis	Dirran Creek	Moderate	Low	High
M. eachamensis	Upper Sth. Johnstone (USJ)	Low	Low	Moderate
M. splendida	Upper Nth.Johnstone (UNJ)	Moderate	Moderate	High
M. splendida	Lower Sth. Johnstone (LSJ)	High	High	Low
M. splendida / Utchee type	Ithica River	Moderate	Moderate	Moderate
Utchee type	Short Creek	High	Low	High
Utchee type	Utchee Creek	Moderate	Moderate	High
Utchee type	Fishes Creek	High	High	Moderate

Table 4.1. A list of the populations used in this study, their species identity and habitat information. See Methods section for further details.

4.3 METHODS

Rainbowfish were collected from 8 locations in the Atherton Tableland region of Northern Queensland during 1998 (see Figure 4.A.1 at the rear of the chapter for a map of the sampling localities). The captured fish were air freighted to the University of Queensland and placed in holding tanks (60 x 35 x 40 cm). Each tank contained approximately 40 fish and the water was filtered via under-gravel filters. Light conditions were 12L:12D, temperature was maintained at 24°C, and pH was close to neutral. A captive population of the Lake Eacham rainbowfish, which had been maintained in the laboratory, was also included in the experiment. All fish had adjusted to captive conditions for a month prior to the experiments and readily accepted flake food.

At each locality site proformas were filled out which included information on land use, habitat complexity/availability, water quality data and the level of disturbance (see Pusey and Kennard 1994 for further details). The relative levels of habitat complexity were calculated by adding up the total amount of refuge available at each site (a combination of 10 refuge types were scaled from 1-3, 3 being highly abundant). Predator density information was gained from a combination of seine net catches, visual observation (snorkeling) and personal communication with Dr Brad Pusey, Griffith University. Stream flow data were obtained from The Department of Natural Resources from 6 sites within the North and South Johnstone Rivers. These locations had between 30 and 80 years of flow data. Flow variability is highly correlated with catchment size ($R^2 = 0.811$, $N = 6$ and $P < 0.001$). A flow variability index was estimated by calculating the catchment area upstream of the collection sites. Sites with catchment areas over 120 km^2 upstream were considered to have low flow variability, as was the captive stock. Sites with catchment areas between 20 and 100 km^2 upstream were considered to have moderate flow variability. Sites with catchment areas under 20 km^2 upstream were considered to have high flow variability.

A large experimental tank (95 by 95 cm) was divided into 4 quadrants each containing a different habitat type (Figure 4.1). All sides of the tank were lined with white perspex and the bottom rested on white polystyrene. One quadrant contained fine branches made from plastic straws (snag), one contained artificial submerged aquatic weed (plastic strips of garbage bags attached to a plastic mesh), one contained rocks (cleaned and washed prior to use), and the other contained no structure. Water depth was maintained at 25 cm and the temperature 24°C. The tank was surrounded by white cloth on three sides and across the roof. The fourth side was a white wall to which a camera was anchored to an arm that extended over the top of the tank. Four fluorescent tubes provided the lighting directly overhead. The light was diffused through the cloth to provide even light conditions within the entire enclosure.

Only female fish were used during this experiment because they are thought to form the basis of many shoals and they exhibit a relatively low amount of inter-individual aggression (pers. obs.). Groups of five fish were selected at random from the holding tanks and placed into the experimental arena. The quadrants were numbered from 1 to 4 and allocated a habitat type based on a predetermined table. This eliminated quadrant/habitat biases. The fish were allowed 20 min to settle into the new environment. Every 5 min for 75 min (16 recordings) the location of the fish was noted. At the end of that time the preferred habitat type was determined and a model predator placed into that quadrant.

The predator model, *Glossamia aprion* (mouth almighty), was used as in previous studies (Brown & Warburton 1997). The model was attached to an overhead system of pulleys and elastic that allowed the observer to move the model toward any fish entering the quadrant. The model was introduced for 30 min (6 recordings), during which the behaviour and location of the fish was recorded. The model was then removed and the habitats rotated 90 degrees in the tank. The fish were then allowed to settle down for a further 10 min and their location recorded for another 75 min period (16 recordings). The procedure was repeated 8 times (using different individuals each time) for each population, making a total of 216 hours of observation.

The basic data (time (sec) spent in each quadrant/habitat, changes in habitat preferences before, during, and after the introduction of the model) were analysed using Kruskal-Wallis ANOVA by ranks. The rate of return to the preferred habitat or quadrant following the introduction of the model was analysed using Wilcoxon tests. The habitat – quadrant interaction was investigated using regression analysis. All statistics were performed using Satistica (Statsoft Inc.1999).

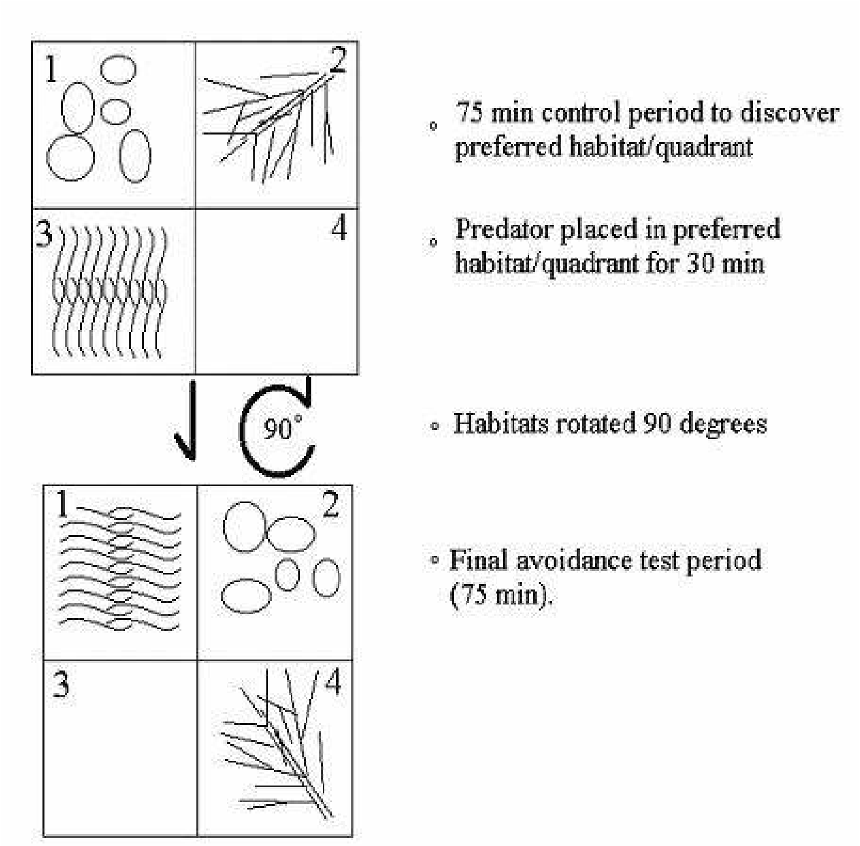

Figure 4.1. A diagram of the experimental tank setup and procedure. Numbers represent quadrant numbers. In the top half of the diagram quadrant 1 contains rocks, quadrant 2 contains a snag, quadrant 3 contains weed and quadrant 4 open water.

4.4 RESULTS

4.4.1 Cue use in predator/habitat avoidance

The results of the Kruskal-Wallis tests suggested that there was no effect of species identity, the level of habitat complexity, flow variability or predation pressure at the collection sites on the tendency of the fish to avoid the habitat or quadrant which was associated with the predator model in the first half of the trial. Nor were there significant differences between the nine populations (see Table 4.A.1 in the Chapter 4Appendix). However, fish from locations with low predator density tended to show the least avoidance of the habitat and quadrant containing the predator model: *M. eachamensis* showed the least difference in time spent in the favoured quadrant, followed by Utchee type and finally *M. splendida*. A similar pattern was true for the return to the favoured habitat. Fish from Dirran Creek showed the lowest level of avoidance of all nine populations.

Wilcoxon analysis of the amount of time spent in the preferred habitat and quadrant before and after the introduction of the model revealed that fish from all populations, with the exception of those from Dirran Creek, Upper South Johnstone River and Ithica River, showed significant avoidance of the habitat containing the predator model (Figure 4.2c). Four populations

(Lower South Johnstone, Ithica, Utchee and Fishes Creeks) spent significantly less time in the quadrant that previously contained the predator model (Figure 4.2d). Only the Lower South Johnstone, Utchee and Fishes Creeks fish avoided both the habitat and quadrant that once contained the predator (Figures 4.2c and d) (Table 4.A.2).

One can clearly see that the introduction of the predator to the initially preferred habitat/quadrant caused a significant decline in the occupancy of this habitat/quadrant (Figure 4.2b) (Table 4.A.3). Following the rotation of the habitats to test for avoidance after the removal of the predator model we can see a general trend to move back into the preferred habitat and quadrant (Figure 4.2c and d) (Tables 4.A.6 and 4.A.7). In most cases, however, the fish still avoided the habitat and quadrant. Fish from the Lower South Johnstone River and Utchee Creek rapidly reoccupied the habitat following the removal of the predator but still showed a significantly lower occupation than during the initial 75 min trial period. These same two populations plus the fish from the captive population also reoccupied the quadrant containing the predator. The captive population returned to an occupancy level similar to that prior to the model introduction.

Fish from all populations with the exception of Dirran Creek and Short Creek significantly avoided the preferred habitat during the period when the predator model was located in the tank (Table 4.A.3).

Figures 4.3a and b show the proportion return to original occupancy for each of the populations. Although the return to the preferred habitat and quadrant displayed by the populations varied over the range 50 – 80%, there were no significant differences between any of the populations, largely due to the high level of variation between replicates within each population.

Figure 4.2 (a-d). The amount of time fish from each of the nine populations spent in a) the preferred habitat before, b) the preferred habitat during, c) the preferred habitat after, and, d) the preferred quadrant after the introduction of the predator model. An asterix above a bar in (b) represents a significant difference between the time spent in the preferred habitat before and while the predator was present. An asterix above a bar in (c) and (d) represents a significant change in the time spent in the preferred habitat between the periods when the predator was present and after it was removed. The dollar signs in (c) and (d) highlight significant differences between the period before and after the introduction of the model predator.

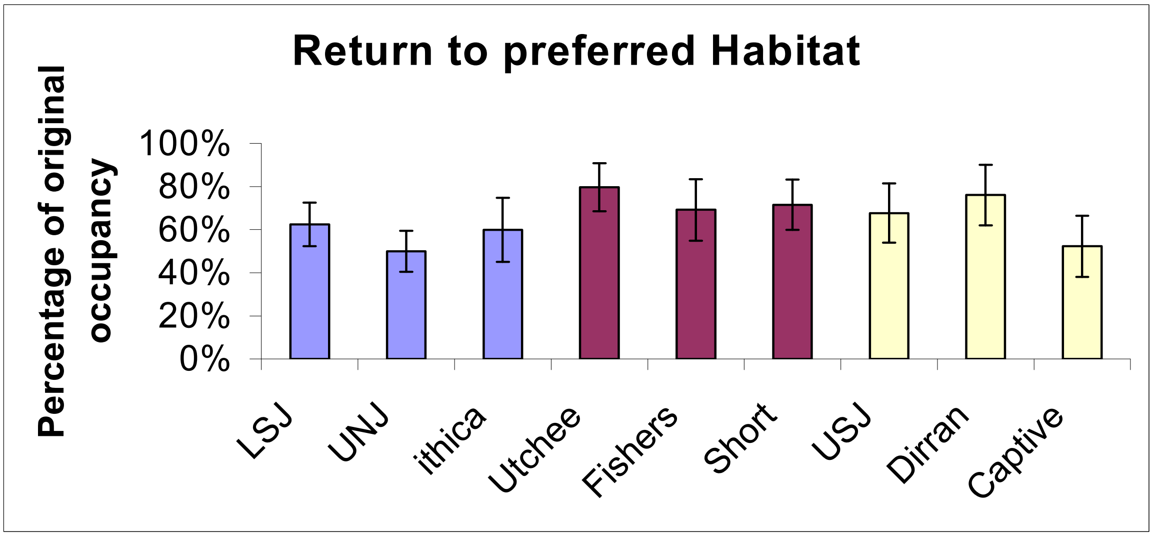

Figure 4.3a. Relative level of occupancy of the originally preferred habitat following exposure to the predator model. The colours highlight the three different species (*M. splendida, M.spp nov.* and *M. eachamsensis* from left to right).

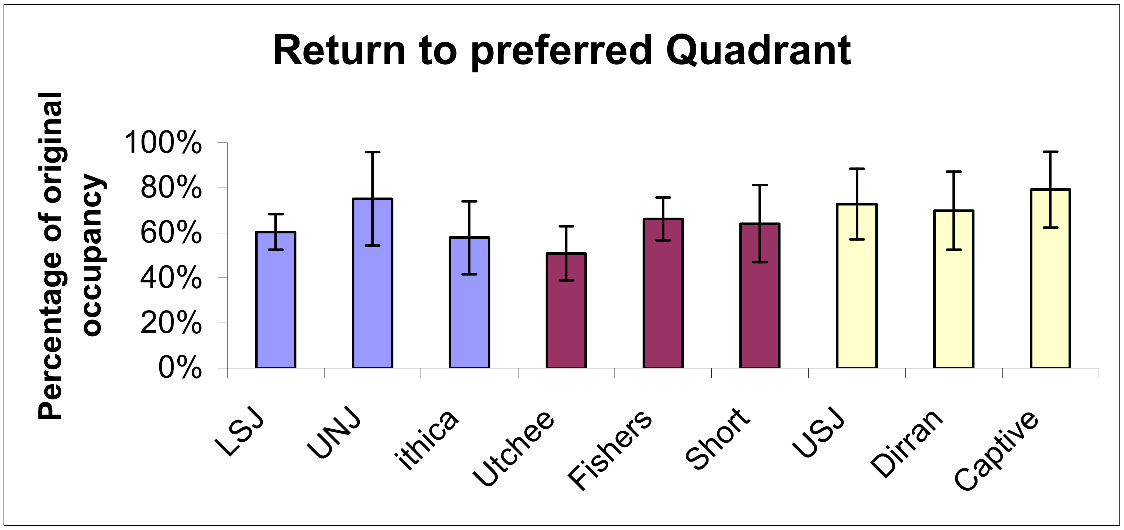

Figure 4.3b. The proportion of the original occupancy of the preferred quadrant following exposure to the predator model. Colours as in Figure 4.3a above.

4.4.2 Habitat preferences (irrespective of predator location)

4.4.2.1 Before predator exposure:

Kruskal-Wallis ANOVA revealed that the level of predator pressure at the collection site (high, medium or low) was significantly related to the preferences for habitats prior to the introduction of the model. Fish from areas of low predation spent more time in the weed compared to fish from both moderate or high predator areas. There was no significant effect of species identity, habitat complexity or flow variability (Table 4.A.8).

The data suggest that, overall, rainbowfish showed no specific preference for any particular habitat, but, rocks were the least favoured. Although not statistically significant, the populations exhibited differences in their affinity for the various habitat types. For example fish from the *M. eachamensis* captive stock showed a tendency to favour open water and avoided the snag. USJ preferred the weed, whilst fish from Fishes Creek preferred the rocks. Ithica Creek fish spent the greatest amount of time in the snag and avoided rocks; UNJ preferred the snag and avoided rocks and weed; Utchee fish strongly avoided weeds; Short Creek fish preferred the snag and avoided the open water.

In terms of the distribution of the fish within the tanks with respect to the four quadrants, there appeared to be no strong preferences for any quadrant.

4.4.2.2 During predator exposure:

Kruskal-Wallis analysis revealed that the level of predation experienced at the collection site was significantly related to the habitat choice of the fish while the predator was present (Table 4.A.8). Fish from areas subject to high predation spent less time in the rocks than did fish from moderate and low levels of predation.

Generally all the fish avoided the open quadrant when the predator model was present ($P < 0.001$, $n = 72$, $t = 6.706$), but there was no bias towards the other habitat types. Fish from the UNJ and Fishes Creek both went against the trend, spending the least amount of time in the weed and rocks respectively. There was no preference for any specific quadrant.

4.4.2.3 After predator exposure:

The results from the Kruskal-Wallis analysis suggested that both the level of predation experienced at the site of collection and species identity had a significant affect on the habitat choice of the fish after exposure to the model (see Table 4.A.8 for Ithica Creek listed as *M. splendida* and H statistic = 8.330, df = 2, $P = 0.016$ if Ithica is listed as *M.* utchee type). Fish from *M. eachamensis* populations spent more time in the weed than the other species (Figure 4.4).

Fish from low predation areas spent significantly more time in the weed after exposure to the predator than fish from high levels of predation, which in turn, spent more time in the weed than fish from localities with moderate levels of predation (Table 4.A.8) (Figure 4.5). There was also a significant effect of population on the use of the weed (Table 4.A.8) and open areas (H statistic = 18.848, df = 8 and $P = 0.0157$).

4.4.2.4 Before-after comparison:

None of the populations showed significant changes in their use of habitat before and after exposure to the model (Table 4.A.9). This is not surprising considering the position of the model varied between replicates within each population. Most populations showed similar trends with decreased time spent in the open and increased time spent in the weed. A few of the populations went against this trend; fish from USJ not only increased the amount of time spent in the weed but also increased the amount of time in the open. Fish from UNJ increased the amount of time spent in the rocks. Fish from Utchee Creek and LSJ showed virtually no change.

All populations were combined in order to examine general responses to the predator model. Following exposure to the model, rainbowfish decreased the amount of time spent in the open (z- test; *P* = 0.013, n = 72, z = 2.491) and increased the time spent in the weed (z- test; *P* = 0.008, n = 72, z = 1.645).

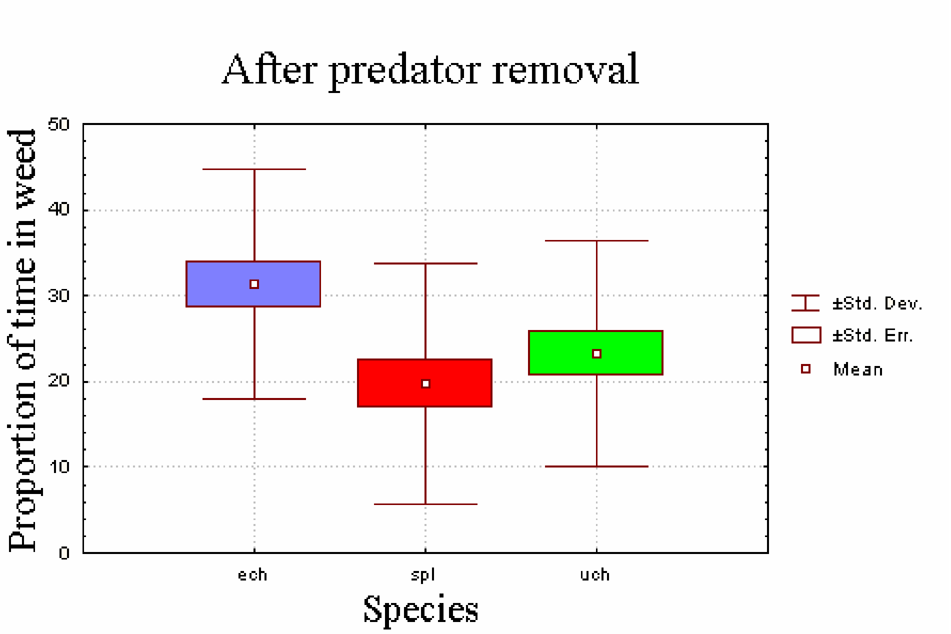

Figure 4.4. The amount of time fish from each of the three species (*eachamensis*, *spendida* and utchee type respectively) spent in the weed following the removal of the predator model from the experimental arena.

4.4.2.5 Quadrant/Habitat Interaction:

A quadrant/habitat interaction effect was expected to increase the avoidance response of fish to the originally preferred habitat or quadrant after exposure to the predator and the rotation of the habitat through 90 degrees. This was because the most preferred habitat could have been moved into the least preferred quadrant, and the least preferred habitat may have been shifted into the most preferred quadrant. Although there was some evidence for increased avoidance as a non-preferred habitat was moved into the most preferred quadrant, such interaction effects were statistically insignificant (β = -0.049, t(70) = -0.413, P = 0.681 and β= 0.221, t(70) = 1.897, P = 0.062 for the movement of the least preferred habitat and quadrant respectively).

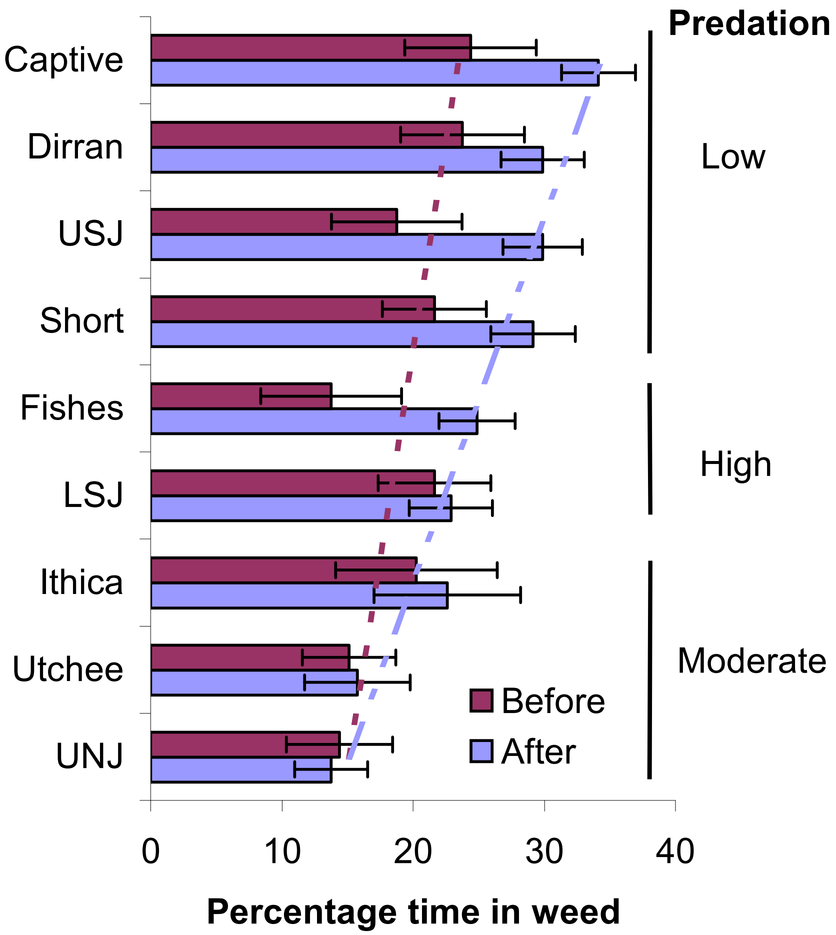

Figure 4.5. The percentage of time fish from each of the populations spent in the weed before and after the introduction of the model predator. The populations are listed down the left hand side and the level of predation at each locality is indicated on the right. Linear trend lines indicating a decrease in the use of the weedy area from the top of the figure to the bottom.

4.5 DISCUSSION

4.5.1 Use of visual cues for orientation

Fish from all but two test populations were capable of using visual cues to associate predators with either the location (global cues) or the microhabitat (local cues) that the predator was last encountered in. One of these two was the Dirran Creek population, which did not avoid the habitat the predator was located in even in the presence of the predator model. This poor avoidance response by Dirran Creek fish has been reported previously (Brown and Warburton 1997).

All but three populations showed significant avoidance of the habitat that once contained the predator model. The three 'odd' populations nevertheless decreased the time spent in that habitat following rotation of the arena. The populations had little in common and there was no apparent effect of species identity or any of the ecological variables tested on the tendency to avoid the habitat that previously housed the predator.

Four of the nine test populations showed significant avoidance of the quadrant housing the model following its removal. These populations had nothing consistent in common. Fish from three populations avoided both the habitat and the quadrant. These three populations again appeared to have little in common, except that they were the only populations that lived sympatrically with sooty grunter (*Hephaestus sp.*), a highly mobile predator. It may be that fish from these localities cannot rely on a single cue type alone to track mobile predators and must remember both the location and the type of habitat within which the predators was last located.

Unlike previous studies, the data presented here suggests that reliance on various cue types does not vary significantly with predation regime or habitat stability as proposed by Huntingford and Wright (1989) and Girvan and Braithwaite (1998) respectively. Nor was there any evidence to suggest that the level of habitat complexity played a role in cue reliance (cf. Warburton 1990). However, the data suggest that local landmarks (i.e. specific aspects of microhabitat structure) are utilised more often than global cues (i.e. cues indicating the general location) in orientation behaviour by most rainbowfish populations. At this stage there is nothing to hint at why some populations rely on global cues while others rely on local cues or a combination of the two.

One thing that all test populations do have in common is that they live in relatively clear water. All locations had a steady flow that should exclude the use of all objects above the water as landmarks owing to distortion created by currents. However, this does not exclude the possibility that rainbowfish can use such landmarks when they are available, as they would have been in this experiment. Studies conducted by Warburton (1990) suggest that goldfish (*Carassius auratus*) relied to some extent on cues outside the experimental tank to aid in forage patch orientation. Braithwaite *et al.* (1996) found that juvenile salmon (*Salmo salar*) use landmarks to help them track moving food resources using local cues. However, their experimental design did not allow the fish to utilise global cues. Sticklebacks (*Gaterosteus aculeatus*) have also been shown to use a variety of cues for orientation (Girvan and Braithwaite 1998). Recalling the location of a particular object is much easier if it can be associated with a single local cue, rather than a matrix of global cues (Zanforlin 1990) so we would expect the majority of rainbowfish to utilise local cues preferentially. This is especially the case when the only reliable global cues lie outside the experimental arena. It may well be that only a small number of fish were aware of objects outside of the arena and utilised them for orientation.

It is clear from this experiment that rainbowfish rely on visual cues for navigation but it is also likely that in the wild they would also use chemosensory cues associated with particular habitat types or localities. Chemosensory cues are widely used by other fish species (Huntingford and Wright 1989, Halvorsen and Stabell 1990) but were deliberately eliminated from this experiment. Future experiments could aim at establishing the relative importance of cue types in rainbowfish orientation since many animals use a hierarchy of cues for orientation, switching from one beacon to another as the need arises (Able 1993).

4.5.2 Memory decay

Rainbowfish are capable of making a strong negative association with specific microhabitats or locations, but return to those habitats over several hours. After 75 min the fish showed re-occupancy of the predator-associated habitat that ranged between 52 and 80% of their initial occupancy. A similar trend was evident for the return to the previously favoured quadrant (51 – 79% of the initial occupancy). It is likely that permanent or long-term avoidance of particular locations or microhabitats requires constant negative reinforcement, which would occur in the wild.

Returning to the location or habitat where a predator was once located seems like a risky venture, but it may make some sense in terms of patch exploitation. There is plenty of evidence to suggest that prey species exploit feeding patches based both on their level of profitability and how dangerous they are (see Krebs and McCleery 1984, Milinski 1986 for reviews). However, individual fish differ in their tendency to take risks and this is compounded by changes in hunger state (Morgan 1988, Godin and Crossman 1994). Although all the fish were fed just prior to testing, in the wild memory decay is particularly important in foraging activities such as prey and patch choice or switching (e.g. Milinski and Regelmann 1985). Some fish may have a greater tendency to return to a risky habitat in the hope of discovering prey items. The memory of foraging skills has been shown to vary between populations of sticklebacks. One possible explanation for this is the varying diversity of available prey at each sampling location (Mackney and Hughes 1995).

If memory and predator recognition vary phylogenetically, we would have expected *eachamensis* and *utchee* fish to have similar responses as these two species are very closely related in comparison to the *splendida* populations, which may represent a recent colonisation (Zhu *et al*. 1998, McGuigan and Hurwood unpublished data). This is not the case. One possible explanation for not observing a phylogenetic pattern in these data might be recent gene flow between the species groups as suggested by microsatellite data (F. Jones unpublished data). It seems much more likely, however, that variation in memory and avoidance abilities should be related to ecological conditions, as suggested in the Introduction to this chapter. However, such a trend was not apparent either.

4.5.3 Indirect effects of predation: Habitat choice

The predator density at the collection sites was significantly related to the time fish spent in the four habitat types, before, during and after exposure to the model predator. Fish from locations with low predator densities spent more time in the weed than all other populations. This is perhaps indicative of the fact that at such locations weeds rarely (if ever) harbour danger. Indeed weeds are likely to provide more prey items than other microhabitats. Once the model was introduced nearly all fish strongly avoided the open habitat, irrespective of the position of the model. There was no consistent preference shown for any of the other three habitat types, although fish from regions of high predator density strongly avoided the rocks. Rocks and rubble probably provide few refuge opportunities and are unlikely to be favoured when other alternatives are available.

The correlation between habitat preference and the level of predation experienced at the collection site continued after the model had been removed and the habitat positions changed. In general, rainbowfish showed a similar trend in habitat preference to that displayed before the model was introduced, although fish from only two populations significantly altered their habitat occupancy distributions after the removal of the predator (Utchee Creek and Lower South Johnstone River). The fact that the strongest effect occurred with respect to the use of weed may have been due to weed providing the best cover available in the tank. But fish from locations with moderate predator abundance utilised this cover least which is perplexing since these regions contain complex cover. Both Ithica River and the Upper North Johnstone have an abundance of grass growing out over the water and the banks of Utchee Creek are dominated by root masses.

4.5.4 Summary

In conclusion, most populations of rainbowfish were capable of avoiding dangerous habitats by remembering either the location and/or the microhabitat that a predator was last observed in. Reliance on different types of cues appears to vary between populations but the reason for this variation remains elusive and does not appear to be related, at least in a simple way, to any of the ecological variables tested here. The avoidance of the predator habitat or quadrant began to decay virtually straight after the model was removed. Long term avoidance probably requires constant negative feedback. Predator densities at the collection site were significantly correlated with habitat choice before, during and after exposure to a predator model.

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4.A. CHAPTER 4 APPENDIX

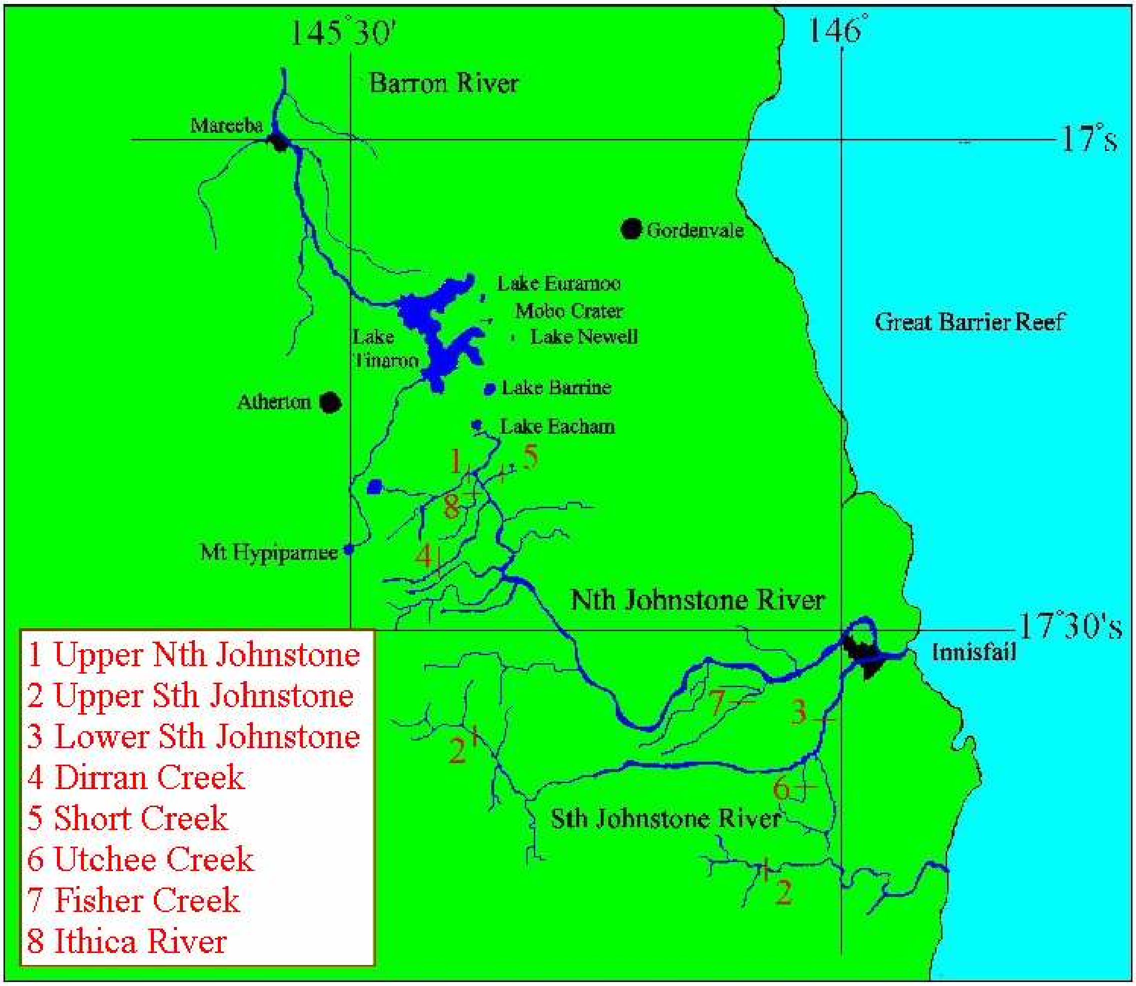

Figure 4.A.1. The location of the populations examined in this chapter.

4.A. Statistics appendix

Kruskal-Wallis ANOVA by ranks			
Habitat avoidance			
Variable	H statistic	n	*P* value
Species	3.851	2	0.146
Habitat	2.774	2	0.250
Flow	3.762	2	0.152
Predation	0.055	2	0.973
Population	6.792	8	0.559
Quadrant avoidance			
Species	1.211	2	0.546
Habitat	1.074	2	0.585
Flow	0.789	2	0.674
Predation	1.251	2	0.535
Population	3.791	8	0.876

Table 4.A.1 Results of a Kruskal-Wallis ANOVA by ranks on the effect of species identity, site locality (i.e. population), habitat complexity and the density of predators at the collection site on the ability to avoid dangerous microhabitats (Habitat) or locations (Quadrant). N = 72 in all cases.

Species	**Location**	**Predator Abundance**	**Habitat Stability**	**Habitat Complexity**	**Habitat P-value**	**Quadrant P- Value**
Eachamensis	**Captive**	Low	High	Low	0.017	0.161
Eachamensis	**Dirran**	Low	Med	High	0.141	0.069
Eachamensis	**USJ**	Low	High	Medium	0.069	0.091
Splendida	**UNJ**	Medium	Med	High	0.012	0.091
Splendida	**LSJ**	High	High	Low	0.036	0.012
Spl/Uch	**Ithica**	Medium	Med	Medium	0.069	0.036
Utchee	**Short**	Low	Low	High	0.017	0.093
Utchee	**Utchee**	Medium	Low	High	0.012	0.036
Utchee	**Fishes**	High	Low	Medium	0.025	0.012

Table 4.A.2. Results of a Kruskal-Wallis ANOVA testing avoidance of the preferred habitat and quadrant by each population. Significant results indicate an avoidance of that quadrant or habitat after having being exposed to a predator.

Population	T	Z	*P* value
Dirran	6.0	1.680	0.093
Captive	1.0	2.380	0.017
USJ	2.0	2.240	0.025
UNJ	1.0	2.380	0.017
Ithica	2.0	2.240	0.025
LSJ	0.0	2.521	0.012
Fishes	0.0	2.521	0.012
Short	5.0	1.820	0.069
Utchee	0.0	2.521	0.012

Table 4.A.3. P- values, T and Z statistics for a comparison of the amount of time spent in the preferred quadrant Before vs During the introduction of the predator model. N = 8 in all cases.

Population	T	Z	*P* value
Dirran	7.5	1.470	0.141
Captive	1.0	2.380	0.017
USJ	5.0	1.820	0.069
UNJ	0.0	2.521	0.012
Ithica	5.0	1.820	0.069
LSJ	3.0	2.100	0.036
Fishes	2.0	2.240	0.025
Short	1.0	2.380	0.014
Utchee	0.0	2.521	0.012

Table 4.A.4. P- values, T and Z statistics for a comparison of the amount of time spent in the preferred quadrant Before vs After (habitat) the introduction of the predator model. N = 8 in all cases

Population	T	Z	*P* value
Dirran	5.0	1.820	0.069
Captive	8.0	1.400	0.161
USJ	4.0	1.690	0.091
UNJ	4.0	1.690	0.091
Ithica	3.0	2.100	0.036
LSJ	0.0	2.521	0.012
Fishes	0.0	2.521	0.012
Short	6.0	1.680	0.093
Utchee	3.0	2.100	0.036

Table 4.A.5. P- values, T and Z statistics for a comparison of the amount of time spent in the preferred quadrant Before vs After (quadrant) the introduction of the predator model. N = 8 in all cases.

Population	T	Z	*P* value
Dirran	14	0.560	0.575
Captive	5.0	1.820	0.069
USJ	9.0	1.260	0.208
UNJ	5.0	1.521	0.128
Ithica	8.0	1.014	0.311
LSJ	0.0	2.521	0.012
Fishes	7.0	1.540	0.123
Short	10	0.676	0.499
Utchee	1.0	2.197	0.028

Table 4.A.6. P- values, T and Z statistics for a comparison of the amount of time spent in the preferred quadrant During vs After (habitat) the introduction of the predator model. N = 8 in all cases.

Population	T	Z	*P* value
Dirran	15	0.420	0.670
Captive	3	2.100	0.036
USJ	6	1.680	0.093
UNJ	6	1.680	0.093
Ithica	7	1.183	0.237
LSJ	1	2.380	0.017
Fishes	5	1.820	0.069
Short	13	0.770	0.484
Utchee	1	2.380	0.017

Table 4.A.7. P- values, T and Z statistics for a comparison of the amount of time spent in the preferred quadrant During vs After (quadrant) the introduction of the predator model. N = 8 in all cases.

Kruskal-Wallis ANOVA by ranks			
Use of Weed before predator introduction			
Variable	H statistic	n	*P* value
Species	4.498	2	0.106
Habitat	4.086	2	0.130
Flow	3.409	2	0.182
Predation	6.529	2	0.038
Population	11.336	8	0.183
Use of Rock during predator introduction			
Species	0.982	2	0.612
Habitat	2.200	2	0.333
Flow	4.384	2	0.112
Predation	8.728	2	0.013
Population	13.255	8	0.103
Use of Weed after predator removal			
Species	8.050	2	0.018
Habitat	2.505	2	0.286
Flow	3.483	2	0.175
Predation	13.740	2	0.001
Population	16.028	8	0.042

Table 4.A.8. Kruskal-Wallis testing the affects on the habitat preferences of rainbowfish irrespective of the location of the predator.

Kruskal-Wallis ANOVA by ranks			
Habitat preference			
Variable	H statistic	n	*P* value
Species	3.851	2	0.146
Habitat	2.774	2	0.250
Flow	3.762	2	0.152
Predation	0.055	2	0.973
Population	6.792	8	0.559

Table 4.A.9. Kruskal-Wallis test on the change in habitat selection before and after the introduction of the predator N = 72 in all cases.