CHAPTER 10
Social transmission of anti-predator behaviour in the rainbowfish, *Melanotaenia duboulayi.*

10.1 ABSTRACT

It is clear that social learning, the acquisition of a behavioural pattern through the observation of others, plays an important role in the acquisition of novel behaviours in many animals. In this experiment I attempted to discover if the anti-predator responses of the rainbowfish *Melanotaenia duboulayi* could be socially transmitted from predator-experienced demonstrators to predator-naïve observers. Having been exposed to their social role models for 20 minutes, naïve observers altered their behaviour away from the control naïve fish and towards that of the demonstrators. Although the average distance of observers to the predator was slightly greater than their untrained counterparts, they still differed significantly from the demonstrator fish. Variation in training and testing experience caused by differences in the level of predator activity is likely to have led to weak experimental contrast and a relatively conservative expression of the capacity for social transmission in rainbowfish.

10.2 INTRODUCTION

The predator avoidance behaviour displayed by prey often varies between geographical locations (Curio 1976, Magurran 1986, Magurran and Seghers 1990a,b). These differences presumably occur because of variations in habitat complexity and historically different predator regimes (Brown and Warburton 1997). In fish, schooling behaviour, predator inspection and the use of cover have all been shown to vary, but how are these differences maintained? While it has been demonstrated that many of these behaviours are at least in part genetically inherited (Seghers 1974, Giles 1984, Magurran 1990 and Chapter 3), many anti-predator responses improve with experience, indicating that learning also plays a large role in their development (Dill 1974, Patten 1977).

Learning is an example of phenotypic plasticity that enables animals to acquire locally adaptive behaviours (Galef 1996). The learning and memory capabilities of fish have not been widely studied by biologists, but, there is clear evidence that fish are capable of learning a number of tasks and retaining information for later use over extended periods of time (Csanyi *et al.* 1989, Marler *et al.* 1997 and Chapter 5). There are several ways animals may learn about their environment and how best to behave in certain situations. An individual may learn from its own experience via trial and error, experimentation and exploration (asocial learning, Heyes 1994). In some circumstances however, individual learning can be costly. Social learning (Giraldeau *et al.* 1994), on the other hand, enables animals to learn about their environment rapidly and efficiently (Laland and Williams 1997) by interacting with others. In this way, novel behaviour patterns or new information may be passed between individuals through social facilitation (Gochfeld 1980) or local enhancement (Waite 1982).

It is becoming increasingly obvious that social learning can play an important role in the acquisition of behavioural patterns displayed by animals. Mate choice (Dugatkin and Godin 1992, 1993), food choice and foraging behaviour (Laland and Plotkin 1992, Kawai 1965, Hinde and Fisher 1951) can all be influenced by observing others. Routes to foraging patches are transmitted socially among foraging guppies (Laland and Williams 1997, Lachlan *et al*. 1998) and coral reef fish (Helfman and Schultz 1984, Warner 1988). Data on fish behaviour suggest that shoaling tendencies in fish populations facilitate social learning, enabling naïve individuals to learn about the local environment swiftly and efficiently, without many of the costs associated with individual learning (Galef 1976). Other behaviours observed in shoaling fish, such as forage patch copying (Krebs *et al* 1972), are also likely to lead to the social transmission of food preferences, but these behaviours have yet to be fully explored.

Anti-predator behaviours, if carried out incorrectly, are likely to carry a heavy cost (death or serious injury). This argument has often been put forward to explain why so many aspects of anti-predator behaviour seem to be inherited genetically (Magurran 1990). However, such an argument could equally be used to support the prevalence of social learning in the development of anti-predator behaviours. Social transmission of predator recognition has been reported in a number of species of fish. Information about predators can be transmitted through shoals of minnows (*Phoxinus phoxinus*), zebra danios (*Brachydanio rerio*), salmon (*Salmo salar*) and sticklebacks (*Gasterosteus aculeatus*) (Pitcher 1986, Magurran and Higham 1988, Subuski *et al.* 1990 , Ryer and Olla 1991, Mathis *et al.* 1995) by social facilitation. It is suggested that this process also occurs in mixed species shoals (Krause 1993). Unlike studies with birds (Klopfer 1957, Curio *et al.* 1978) and primates (Mineka and Cook 1988), few studies involving fish have shown that naïve individuals can actually learn from this experience and alter their behaviour accordingly even in the absence of their “tutors”.

Following work by Subuski *et al.* (1990) on zebra danio, Chivers and Smith (1995) demonstrated that minnows were capable of associating alarm substances with chemical cues emanating from “risky” habitats and subsequently learned to avoid these areas. When naïve fish were placed in a tank with experienced fish (which displayed alarm responses in the presence of “risky habitat” cues) the naïve fish exhibited alarm reactions due to social facilitation. Later, when tested alone, the naïve fish also showed alarm reactions in the presence of “risky habitat” cues, indicating that social learning had occurred. Later studies (Mathis *et al.* 1996) showed that this fright response could also be transmitted to brook sticklebacks (*Culuaea inconstans*), which often occur in mixed species shoals along with minnows.

By associating with experienced fish, naïve fish may be alerted to the presence of potential predators, thus offering a short term benefit. In the long run naïve individuals also benefit by becoming conditioned to recognise predators in future encounters (Mathis *et al.* 1996). Importantly, conditioned individuals may then act as tutors for other naïve individuals, and so on.

There has been no work to date that indicates the importance of visual cues in the social learning of predator avoidance behaviour in fish. This study set out to determine if predator avoidance behaviours can be passed from predator-experienced fish to predator-naïve fish in *Melanotaenia duboulayi*, the crimson spotted rainbowfish. Unlike fish from the Superorder Ostariophysi, members of the Family Melanotaeniidae apparently lack any type of chemical warning system and subsequently must rely on vision to transfer information among shoal members.

10.3 METHODS

Two populations of fish were sampled using standard bait traps. The first population was from Amamoor creek at Amamoor (26E 21'S, 152E40'E), a relatively small, lowland stream dominated by large still pools and occasional riffles. Water depth varied greatly but averaged about 1m. Snags (fallen logs) and submerged aquatic vegetation provided habitat structure. The primary aquatic plant species were *Elodea canadensis*, *Potamogeton crispus* (curly pond weed), *Vallisneria gigantea* (eel-weed) and *Ceratophyllum demersum* (hornwort). A number of large predatory fish species were present including spangled perch (*Liopotherapon unicolor*), saratoga (*Scleropages leichardti*) and mouth almighty (*Glossamia aprion*). The rest of the fish community was comprised of hardy heads (*Craterocephalus stercusmuscarum*), firetail gudgeons (*Hypseleotris galii*), olive perchlets (*Ambassis nigripinnis*) and freshwater mullet (*Myxus petardi*). Rainbowfish and the olive perchlet were numerically dominant species. The second population was derived from the upper reaches of Obi Obi Creek near Maleny (26E45'S 152E 55'E). The headwaters of Obi Obi Creek were characterised by fast flowing waters with a number of waterfalls and rapids. There were several large pools of water that contained complex structure including snags and submergent vegetation. The fish used during this study were collected above a large waterfall in a pool containing dense stands of *E. canadensism* as well as small patches of *V. gigantea* and snags. The depth averaged around 1-1.5 m. 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 reinhardtii*). The dominant species was *M. duboulayi* but there was also a large number of Pacific blue-eyes (*Pseudomugil signifer*) as well as the ubiquitous firetail gudgeon. A different species of hardyhead, *C. marjouriae* (Marjourie□s hardyhead) was also present.

The fish were collected on four separate occasions in March 1997. They were transported to the University of Queensland and placed in large holding tanks for two days prior to experimentation. Obi Obi Creek fish were labeled as predator naïve (N) and Amamoor Creek fish labeled as predator experienced (E). The water temperature in the holding tanks and the experimental arena was 22EC. The fish were not fed for the period from capture to experimentation. Two types of groups were created; five groups of 10 (N control) and, 10 groups containing five (N observers) and five (E demonstrators). Half of the observer and demonstrator fish had the dorsal edge of the caudal fin clipped so the population members could be identified. The fish with clipped fins were randomised with respect to population. No change in behaviour was observed as a result of the fin clipping.

All fish underwent the following predator exposure: a group of 10 fish was placed in the experimental arena and allowed to settle for 15 min. The arena consisted of a 1.6m long tank divided in half longitudinally by opaque perspex. The width of each half was approximately 50cm. At one end a trap door could be raised to reveal a live predator (spangled perch) behind clear perspex (Figure 10.1). The two predators used in this experiment both had a standard length of 22cm. The rainbowfish were exposed to the predator four times for five min after 15, 30, 40 and 50 min. Each group of rainbowfish was then returned to separate tanks. Three hours later each group was divided in half, resulting in 10 groups of: five naïve fish having had no interaction with the experienced fish (naïve control), five naïve fish having had interactions with experienced fish (naïve observers) and 5 experienced fish having had interactions with naïve fish (experienced demonstrators). Each half was then placed on either side of the experimental arena and tested simultaneously (see protocol diagram, Figure 10.2).

After 15 min of settling the fish were exposed to the predator for five min. Every minute for five min the location of all fish and the elective group size was recorded. From these data a shoal dispersal index (SDI), inter-individual distances (IID), the mean distance from the predator, mean elective groups size (Allan and Pitcher 1986, Griffiths and Magurran 1997) and the amount of time spent in the front, the middle and the back of the arena was calculated. SDI was calculated as outlined in The Appendix. The data were analysed to compare the differences between each group of fish (control, observers and demonstrators) using a Kruskal-Wallis and Wilcoxon tests (SAS).

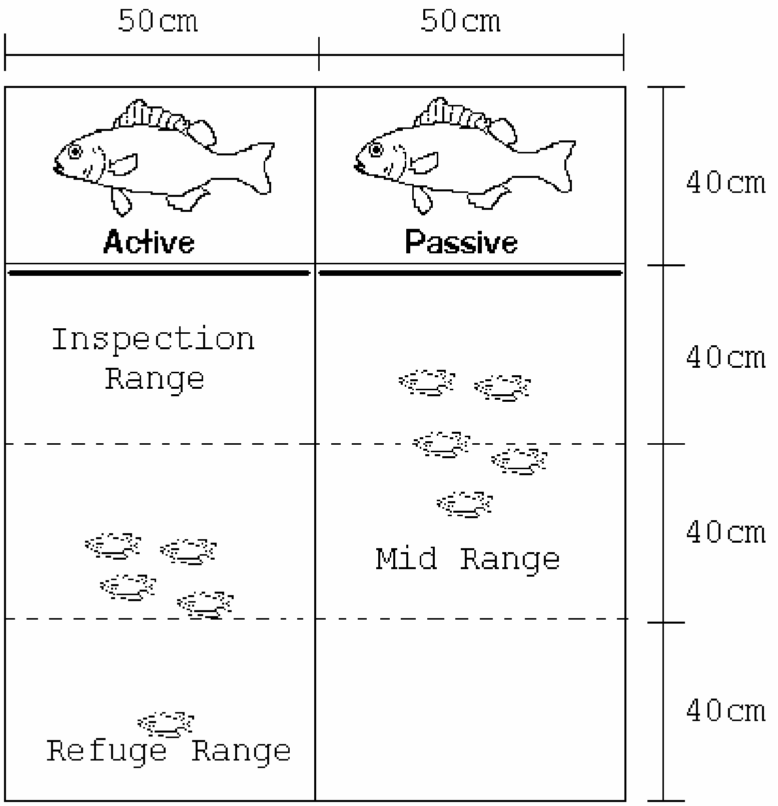

Figure 10.1. Diagrammatic view of the experimental tank used in this experiment showing the divisions into the three ranges (Inspection, Mid and Refuge). A clear perspex divide and an opaque division, which could be drawn up by a pulley system to reveal the predators to the prey, separated the predators from the rainbowfish.

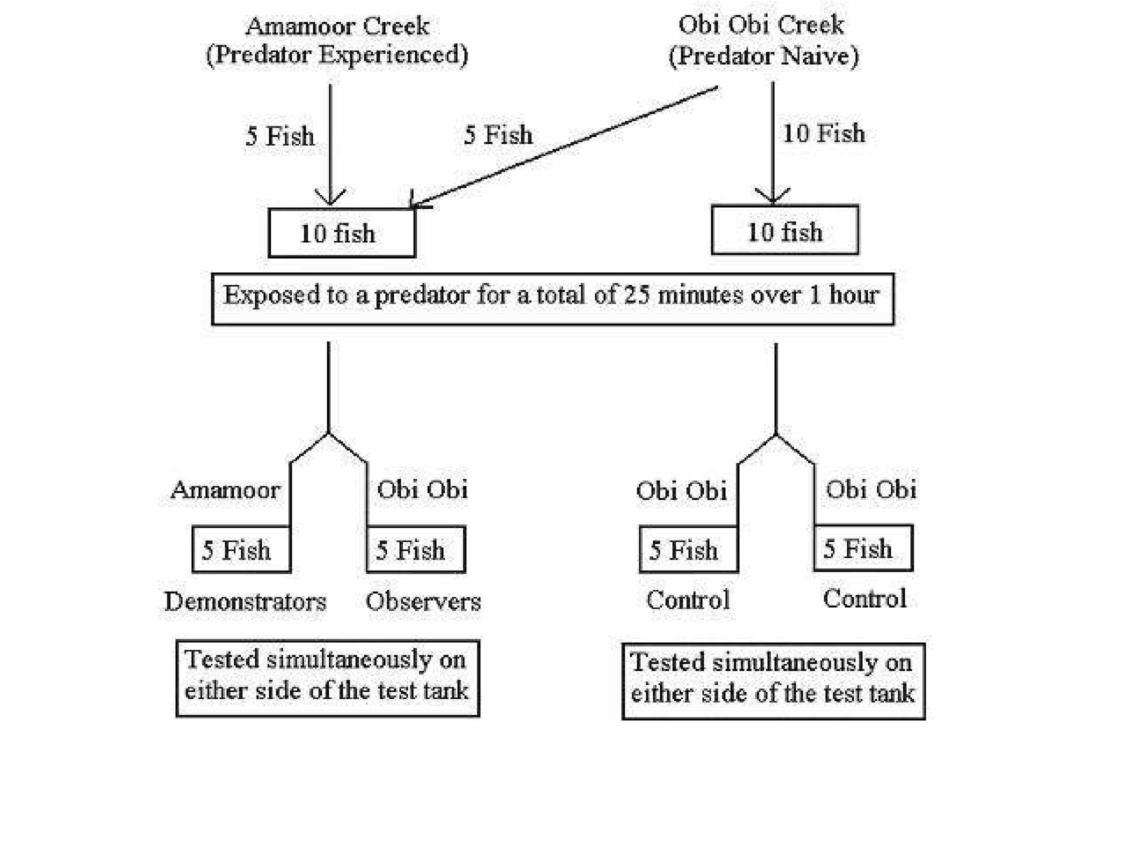

Figure 10.2. Diagram of the experimental protocol used to study social transmission of anti-predator behaviour.

10.4 RESULTS

The predators used were those described in Chapter 2 and the level of activity displayed by these two fish had a highly significant bearing on the results. When the experiment was performed using the less active predator, no significant differences were observed between treatments for any of the measures (e.g. Figure 10.3). The results will therefore be discussed in reference to the active predator only.

A significant population difference was detected only in terms of the distance to the predator and the distribution of the fish in the tank (proportion of time spent in the three ranges)(Table 10.1, Figure 10.4). None of the shoaling indices detected any significant differences in behaviour between treatments in the response to the predator. The average distance to the predator did not differ significantly between the observers and the control animals from the predator-naïve population (Obi Obi Creek). Both control and observers differed significantly from the predator-experienced, demonstrator fish (Amamoor Creek). It may be noted, however, that in terms of the distance to the predator, the time spent in the different parts of the tank, and shoaling indices, the Observer fish tended to be intermediate between the Control and the Demonstrator fish (Figures 10.3, 10.4 and 10.5). There was a large degree of variation present in both SDI (Figure 10.5) and IID (Figure 10.5) for both observer and demonstrator groups.

Naïve fish always differed significantly from the demonstrator fish. The observer fish differed significantly from the demonstrator fish in both the time spent in the refuge and inspection ranges. Both the naïve and the observer fish spent a very large proportion of their time within the inspection range (90% and 76% respectively). The demonstrator fish from Amamoor Creek, spent only 13% of their time within the inspection range (Figure 10.4).

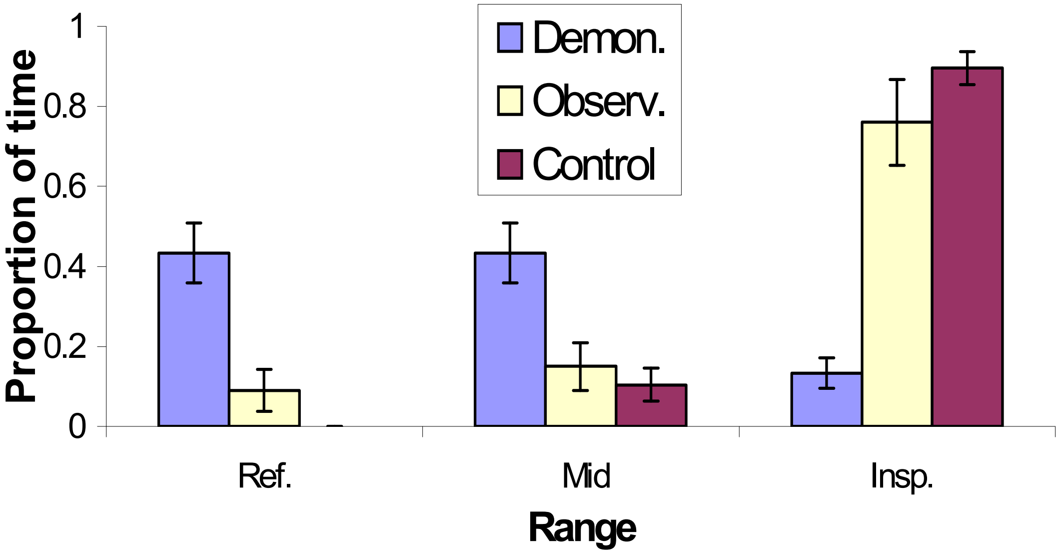

Figure 10.3. The mean distance (± se) to the predator when the fish were exposed to the active and passive predators.

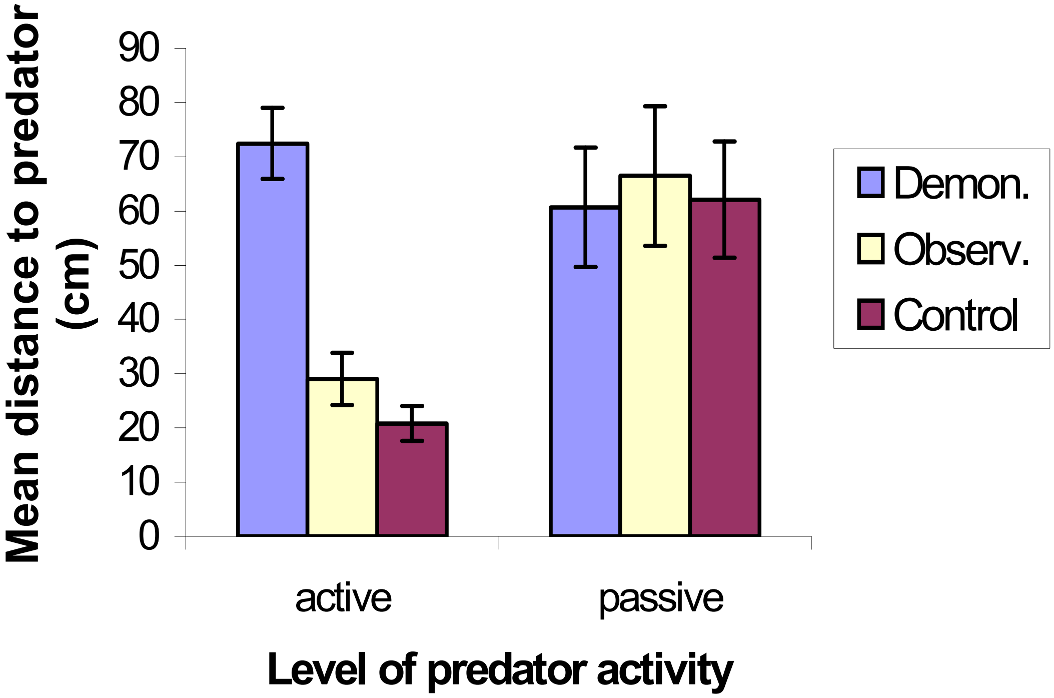

Figure 10.4. The proportion of time (± se) in the refuge, mid and inspection range by the three groups of fish.

Index	**$\chi 2$**	**df**	***P***

Distance to predator	10.688	2	0.005
Inter Individual Distance	2.056	2	0.356
Shoal Dispersal Index	2.173	2	0.337
Elective Group Size	2.025	2	0.363
Time in Refuge Range	11.556	2	0.003
Time in Mid Range	8.111	2	0.017
Time in Inspection Range	10.475	2	0.005

Table 10.1. The results of the Kruskal-Wallis Chi Squared Approximation on the difference between populations when the fish were tested with an active predator.

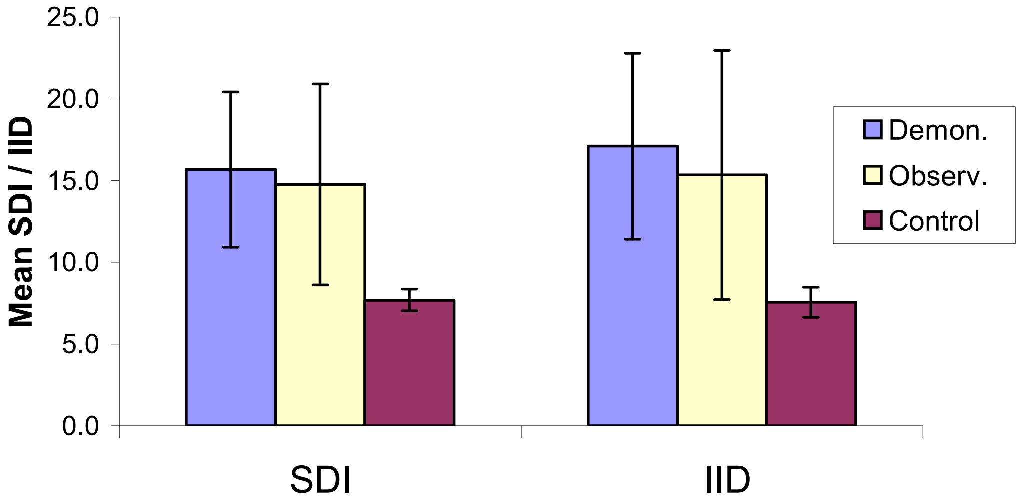

Figure 10.5. Mean shoal dispersal index and inter individual distances (± se).

10.5 DISCUSSION

This study investigated the anti-predator behaviour of two populations of fish that varied only in the level of predation experienced at each site. Obi Obi Creek fish lacked predator experience and could be distinguished from their experienced counterparts from Amamoor Creek primarily by considering their distribution throughout the experimental tank when faced with an active predator. Predator-experienced fish moved to the far end of the tank where they relaxed their schooling activities and resumed other social behaviours. In contrast to this response, fish from Obi Obi Creek maintained a high shoal fidelity and spent a large proportion of their time within 35cm of the predator. The predator-naïve Obi Obi Creek fish appeared to be attracted by the movements of the spangled perch. These starkly contrasting responses are interesting. Could they be altered by social interaction with other fish?

The data presented here suggest that social learning may play a role in the development of anti-predator responses. Although there was no single parameter that showed that the behaviour of naïve fish changed significantly following interactions with experienced fish, a general trend was evident in most parameters. The observers, having schooled with fish from Amamoor creek (Demonstrators) in the presence of a predator for a total of 25 minutes, displayed anti-predator responses that were intermediate between the control Obi Obi fish and the demonstrators from Amamoor Creek. Their shoaling indices more closely resembled that of the experienced fish but the average distance they maintained from the predator and their general distribution throughout the tank, was more similar to that of the control fish.

It appeared that the naïve fish that had interacted with the experienced fish (i.e. the observers) altered their behaviour to some degree. However, the results were complicated by the fact that the activity levels of the perch on either side of the test tank differed considerably. On the right hand side the perch remained still for most of the trials, while the perch on the left hand side moved around vigorously, frequently charging at the rainbowfish as they approached the perspex. The implications of this result are discussed in Chapter 2.

When the predator was slow or did not show any interest at all in the rainbowfish, all groups showed similar behaviours. Fish from all groups spent about the same time in the inspection range and tended to swim around 60cm away from the predator. However, when faced with an aggressive predator, the distribution of the demonstrator fish became statistically different from both naïve groups. The greatest difference occurred in the amount of time spent in the refuge. Demonstrator fish spent less time in the refuge when faced with a non-threatening perch, while the naïve fish spent more time in the refuge range. These data suggest that the behaviour of the rainbowfish towards predators is highly flexible and depends upon the level of activity displayed by the predator (Brown and Warburton 1999).

It is unfortunate that such a large difference in behaviour was due to activity of the two predators because in analysing the data independently the replicate size was reduced to 5. It is also unfortunate that half of the "training" of the observer groups occurred with the use of the less-active predator. It is clear that exposure to a more aggressive predator is likely to reveal differences between predator-naïve and experienced fish. One could propose, therefore, that Obi Obi fish trained with Amamoor fish in front of an active predator would have been exposed to true anti-predator behaviours. When the experiment was designed and performed it was not suspected that the level of predator activity would be such an influential factor. As noted in Chapter 2, this factor has rarely been considered when fish have been exposed to predators in experiments. Fish trained in front of the less active predator would not have been given the opportunity to learn anti-predator behavours given that the probability of learning a new behaviour is dependent upon the frequency at which it is performed in the group (Giraldeau *et al.* 1994). These factors may be responsible for some of the variation evident in the results. Furthermore, when the observers were trained, the training group consisted of 10 individuals, only half of which were naïve. This has several interesting repercussions. Firstly, it may well be that a group response that is suitable for a group of 10 fish is not suitable for a group of 5 (the group size in which the observers where eventually tested). Hence, while the fish may have learned a little during their training session, they may have struggled to apply what they had learnt in a new context (i.e. a group of five). Rainbowfish from all populations alter their behaviour considerably depending on shoal size, but the manner in which they do so varies between populations (Brown 1995). The experiment may have worked a little better if the testing shoal size was boosted to 10 by combining two groups. This course of action would have required twice as many fish. The second interesting repercussion stems directly from the proportion of observers and "tutors" in the training groups. Lefebrve and Giraldeau (1994) suggested that the number of tutors and observers present affects cultural transmission. The rate of transmission increases exponentially as the number of tutors increases and the number of observers decreases. Galef *et al*. (1990) found that multiple tutors allowed naïve rats to learn more quickly about a proper diet. Similarly, Sugita (1980) showed that the tendency to copy an avoidance response in guppies increases with the number of tutors available. Perhaps a larger number of tutors and fewer observers would have provided clearer results.

References

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