

CHAPTER 11 General discussion

“..the most fundamental functional characteristics of animal design have been shaped by the very general properties of the physical world within which an animal lives, moves and behaves.” (Wehner 1997).

The research presented in this thesis set out to investigate a number of questions related to the behavioural ecology of predator avoidance using rainbowfish as model species. It is clear that the level of predation experienced at a population level is a vital ecological component shaping behaviour of rainbowfish (as it is with guppies, Table 1.1). However, other aspects of the local environment, such as stream flow (habitat variability) and habitat complexity may also influence inter-population variation in anti-predator behaviour. It is vital to consider all aspects of an animal’s environment if we are to fully understand behavioural responses towards certain stimuli. These responses must be analysed in the correct context, with an open mind and a view of obtaining a more holistic interpretation of the behaviour in question.

At first glance predator avoidance may seem to be a relatively simple phenomenon relying only on an animal’s instinct to survive. However, as this thesis has demonstrated, predator avoidance requires more than just an innate response to all things frightening. Rather it results from a complex web of cognitive pathways that may be influenced by a number of factors at many levels (Figure 1.1). The responses issued towards threat vary widely across different geographical populations of the same species. Broadly speaking, this variation may occur due to differences in the ability to detect threat, in threat recognition, and in responses to threat (Figure 11.1). Figure 11.1 may be thought of as a hierarchy with each step having flow on implications for the next. Variation in the ability to detect or recognise threat is likely to affect

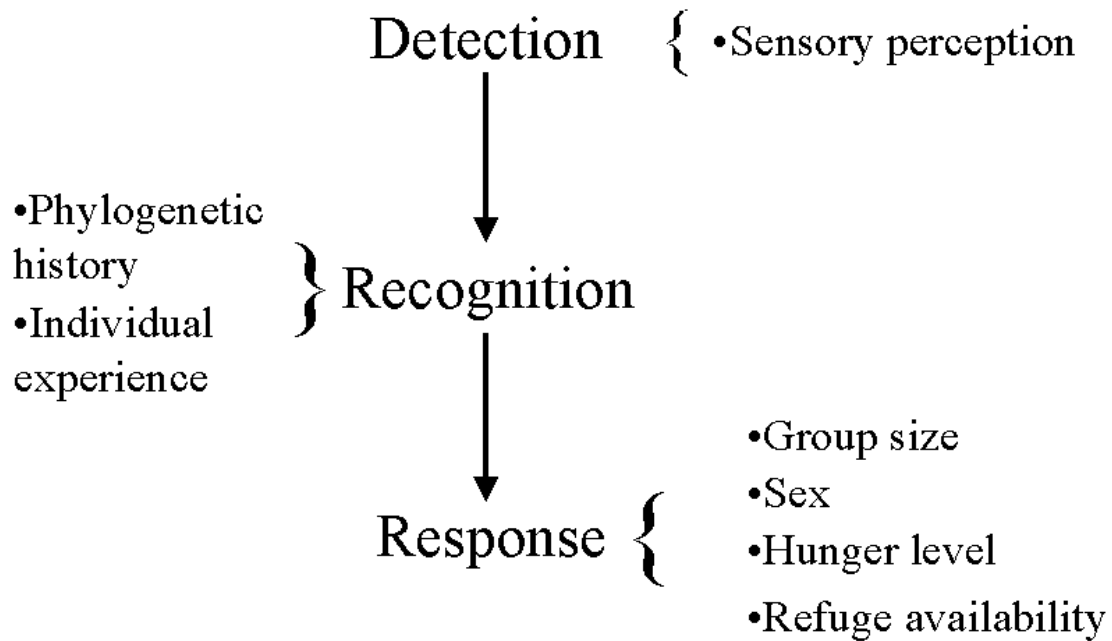


Figure 11.1. A theoretical hierarchical diagram showing some of the possible sources of population variation in anti-predator behaviour. Both phylogenetic history and individual experience may also influence responses directly.

the response issued. Threat detection has not been considered in detail within this thesis, however, it is assumed that the rainbowfish species studied have similar sensory perception capabilities. Threat detection in fish has been poorly studied in general, largely due to the underlying assumption that the absence of a response does not necessarily indicate a failure to detect a stimulus (Godin *et al.* 1988). Population variation in threat detection remains a challenging area for future research.

Having detected a threat, the threat must then be recognised and the relative level of risk established. The ability to recognise predators not only relies on an in-built recognition template (big things with large eyes represents danger), but also relies on the past experience (social and

asocial learning) of each and every individual (Chapters 2, 3, 4, 5, 6 and 10). It is becoming increasingly evident that fish utilise a number of very subtle cues to establish the level of threat a particular individual predator represents. Rainbowfish gain information about the intentions of predators during inspection visits which are characterised by a slow and cautious approach towards the predator and a limited time fixating on the predator before returning to safety. The results outlined in Chapter 2 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 and Crossman 1994). Predator inspection behaviour, while having its foundations in general curiosity, is a far more specific behaviour with a defined purpose of gaining information about a predator. It appears to be comprised of a number of psychological components namely; detection, *recognition*, approach, fixation, fine assessment and avoidance. Curiosity on the other hand may be best described as; detection, approach, fixation, *coarse assessment*, *investigation*, fine assessment, and habituation/avoidance (Figure 1.1). Curiosity lacks the recognition component seen in predator inspection behaviour and is sparked by novelty. Curiosity requires coarse assessment of the level of risk before closer investigation occurs. Curiosity could easily lead to predator inspection and it may well represent the origin of inspection behaviour. A naïve animal may approach a novel predator out of curiosity and, having had a negative experience, learn to recognise the predator and behave cautiously (i.e. not approach too closely) on future encounters.

Once the potential predator has been identified, the intentions of that predator may be established through inspection visits (Brown and Godin 1999, Fisherman 1999) or perhaps by observing the responses of others (Magurran and Higham 1988). Even at this stage each individual may independently weigh up the costs associated with continuing with its current behaviour or resorting to avoidance responses. An individual's, size, sex and hunger level may

all influence the ultimate decision (see Figure 1.1 and Chapter 6). Males and female rainbowfish have very different agendas and weigh up the costs and benefits of performing a behaviour independently. Females appear to be highly cautious and concentrate on avoiding predators, whereas males appear to be reactive and rely on last minute escape responses to evade predators. Even the sex ratios of shoals may effect the escape response observed in a shoal of fish. When single sex shoals are exposed to the trawl their initial escape latencies are far superior to when they are tested together (Chapter 5 and 6). This indicates that the social interactions occurring between males and females distracts them from achieving optimum escape responses.

Having decided to take evasive action, an appropriate response must be made. Responses vary between individuals, but, in rainbowfish, seem to be significantly dependent on the level of habitat complexity existing at the site of collection. Individuals from structurally depauperate locations rely largely on schooling techniques, whereas fish from structurally complex localities rely on refuge and crypsis (Brown and Warburton 1997). These two examples represent two ends of the response spectrum but are by no means mutually exclusive. A number of fish incorporate both aspects into their anti-predator responses. While the incorporation of cover into the anti-predator response is primarily inherited, the use of cover may vary depending on the environment within which an individual is raised (Chapter 3). This makes sense in terms of the local availability of complex structures that may be used for refuge. Many authors have overlooked the importance of refuge availability at the site of collection (see references in Table 1.1).

Until recently most studies have used either changes in schooling behaviour or the amount of time spent in cover to assess the relative levels of threat perceived by prey fish from various populations (e.g. Mugurran and Girling 1986). The two indices have rarely been combined to reflect the behavioural flexibility in escape responses that exist in the wild. Based

on these single index studies, it has been widely assumed that fish from areas of low predation threat show no or very poor escape responses. While this is true to some extent, the ability of predator-naïve individuals to avoid predation has probably been underestimated simply because they often rely on crypsis rather than schooling to avoid predators (Everett and Ruiz 1993, Brown and Warburton 1997).

Much of the variation we see in predator recognition and response is related to the learning and memory skills of individuals, both in terms of the variation in individual abilities and the decay of individual experiences. Individual variation is vital in maintaining population flexibility and acts as a buffer against environmental stochasticity. However, this variation is layered onto a background which is largely location (population) dependent. Natural selection acts strongly to create variation between populations, ensuring that baseline anti-predator responses are inherited (Magurran 1990). That is to say that the local environment dictates the gross response displayed by fish from distinct populations, but the response is fine-tuned by learning. Thus the behaviours displayed by individuals become locally adaptive and highly dependent upon prevailing ecological conditions.

In dynamic environments the learning ability of prey animals is important¹. Learning, resulting from variation in experience, is potentially the more highly dynamic of the two mechanisms resulting in population level behavioural differences (genetic inheritance being the other). Most importantly, learning is not bounded by the limits of vertical (i.e. parent-offspring) transmission (Figure 11.2). If phylogenetic history was the primary source of variation then we may well expect to see strong species-specific responses to predation. This is simply not the

¹ Surprisingly, a brief study comparing the learning abilities of fish from a stable environment (a lake) and an unstable / dynamic environment (upland stream) found no significant differences between the two localities. Lake fish showed higher schooling tendencies and retained a greater distance between themselves and a novel object. Lake fish also showed rapid habituation to novel stationary objects, but showed no habituation to a novel fish species. River fish showed moderate rates of habituation to both the stationary object and novel fish. (C. Brown unpublished data).

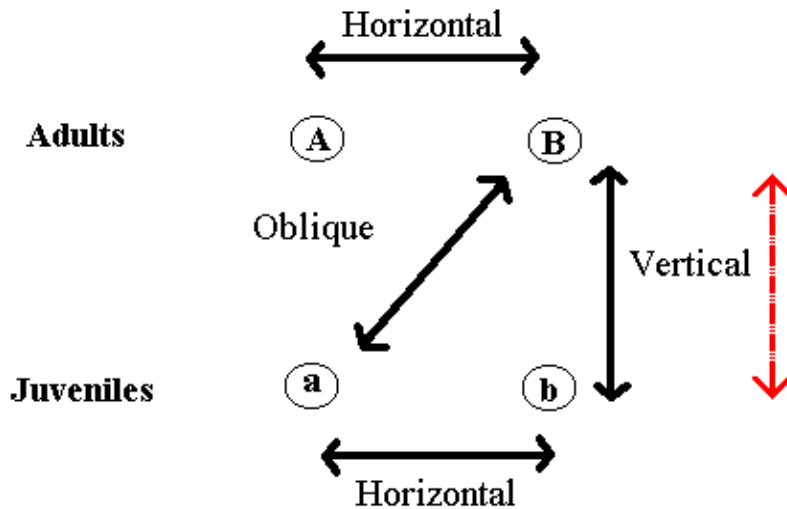


Figure 11.2. Transmission vectors. Solid dark lines represent social transmission of behavioural traits throughout the population, whereas the lighter dotted line represents genetic transmission.

case (Chapter 2). Much of the data presented here suggest that responses shown by fish towards predation vary from site to site and are independent of the species identity of the prey.

However, it may well be that anti-predator responses become rapidly fixed within a population (perhaps aided by the rapid diffusion of adaptive behaviours through the population via social learning), especially in areas of high predation pressure. That is selection is acting on a much smaller scale than the species level.

The ability of individuals to learn and remember may be genetically inherited but is also influenced by the local environment (Giraldeau 1997, Potting *et al.* 1997). Fish from predator-experienced populations are better at solving novel avoidance problems (i.e. avoiding trawls) than predator-naïve individuals (Chapter 2). Similarly, animals that actively forage for food, store caches of food for later use, lay eggs in distributed nest sites or navigate to specific home localities are much better able to solve spatial problems (Bingman 1992, Sherry *et al.* 1993, Sherry and Duff 1996). Closely related species with spatially less demanding lifestyles score comparatively poorly during tests on spatial memory (Day *et al.* 1999). It may well be that selection acts on behavioural flexibility rather than on specific skills, of which spatial memory

or problem-solving skills are only a subset. This hypothesis is further substantiated by the fact that animals that actively use environmental knowledge show an increase in other skills such as social transmission of food preferences (Eichenbaum 1996). It is likely that the hippocampus is the neurological focus for all these behaviours (Bingman 1992, Day *et al.* 1999) and upon which natural selection is acting.

An alternative method to reduce predation threat, as opposed to employing anti-predator responses, is to avoid locations or microhabitats that frequently shelter predators. This task obviously requires that animals remember where the predator was last seen or encountered. Animals are excellent at relating specific cues to positive or negative stimuli. Conditioning may only take a few exposures to the test conditions. Often, however, the cues used to remember the whereabouts of objects vary. Some individuals rely on local landmarks, such as the presence of a site specific marker (a rock or plant), while others rely on the spatial configuration of a number of cues (global cues) and determine where an object is in relation to those cues (Chapter 4 and references therein). Many animals rely on a hierarchy of cues so they may fall back on other methods if the primary method of orientation is lost (Able 1993). Thus, when chicks are trained to search for food at the base of a marker and the marker is moved, they automatically search for the food around the base of the marker irrespective of its location. However, if the marker is removed entirely the chicks recall the location of the marker and search for food where the marker was last seen (Zanforlin 1990). Zanforlin (1990) suggests that the colour and shape of an object are much easier to learn than its location since the location of an object requires that other objects, whose spatial relationship define the location, must also be recognised. The availability or reliability of local or global cues could dramatically affect the methods by which animals orientate or navigate within their environment (Braithwaite and Guilford 1995, Girvan and Braithwaite 1998). Wasps (*Sphecius speciosus*) for example incorporate wooden dowels into territorial boundaries because borders that are defined by a

single landmark are far easier to recall accurately (Eason *et al.* 1999). Environmental stability, the level of habitat complexity, cue availability and even perhaps the optical properties of the medium may all dictate the methods via which animals recall specific locations.

The formation of groups has many benefits, but quite possibly one of the more important is the ability to learn from one's fellows. Orientation, foraging and avoiding predators appear to be much more efficient when performed in groups (Grunbaun 1997, Pitcher and House 1987, Hagar and Helfman 1991, Chapters 9 and 10). Owing to the nature of shoals, information is rapidly transferred throughout the group either passively (by others observing the behaviour of their shoalmates engaging in an activity, e.g. foraging) or actively (where the attention of shoalmates is deliberately drawn to an object, e.g. skittering, inspection behaviour and head stands in rainbowfish). While rainbowfish are certainly able to learn on their own, the process appears to be accelerated when they are part of a group (Chapter 9). Not only does initial performance improve with increasing group size, but the rate of learning displayed by larger groups is far superior to that displayed by singletons or pairs of fish. A number of studies have found that animals perform better in groups due to the operation of social mechanisms such as social stimulation, social facilitation, local enhancement or social learning (Hale 1956, Thorpe 1963, Krause 1993, Giraldeau *et al.*, 1994, Laland and Williams 1997). However, in interspecific comparisons of fish training, Zhuikov and Trunov (1993) discovered that susceptibility to training was related to shoaling tendency. They proposed that shoaling species spend comparatively more time moving, which stimulates the development of the central nervous system. Zhuikov and Trunov (1993) suggested that mobility may be correlated with the rapidly changing external stimuli experienced by pelagic fish species. A constant flow of information requires rapid analysis and, while hippocampal mass was not measured, their data certainly suggest that their results may well be correlated with the size of the hippocampus.

Interestingly, more than 50% of rainbowfish shoals observed in the wild are comprised of singletons. Most tests in the laboratory situation indicate that fish will join a larger shoal if given the opportunity (Hagar and Helfman 1991). However, this choice may be altered if the fish is hungry, in which case it will choose the smallest shoal so as to reduce foraging competition (Morgan 1988). The existence of so many lone rainbowfish in the wild strongly suggests that competition for food often outweighs the threat of predation. Alternatively, this observation could simply result from a statistical conundrum since we are more likely to encounter singletons than any other group size by chance alone.

If rapid learning has fitness benefits then surely any mechanism that results in rapid learning also has some benefit. Choosing shoal mates becomes increasingly important since shoaling with familiar individuals may result in increased learning capabilities (Chapter 8). Shoals comprised of familiar individuals also show better escape responses and foraging efficiency (Chivers *et al.* 1995). This may stem from the ability of individuals within groups to learn from one another or a decreased level of stress that allows increased exploration.

It is clear that becoming familiar with one's environment also has multiple advantages. Knowing the location of suitable spawning habitats, foraging patches, refuge structures and locations commonly associated with predators have obvious fitness benefits. Knowing the layout of the environment enables an animal to better detect changes in that environment, such as the appearance of potential predator or prey items. The results presented here suggest that environmental familiarity increases problem-solving skills and predator avoidance responses because individuals can focus on the problem at hand (Chapter 5).

Familiarity with both shoal mates and the environment may improve escape responses. Are the two connected in some way? When confronted with a novel problem, shoals of familiar fish appear to be more relaxed, show greater shoal cohesion and increased exploratory behaviour. Shoals of fish in a familiar environment show similar types of behaviour. Lowered

stress levels lead to increased rates of exploration or, at the very least, more efficient exploration. When escaping from the trawl apparatus, exploration was a key factor (Chapters 2, 5, 6 and 9). Escape required that fish focussed on the problem at hand to locate the hole in the net. However, fish in familiar shoals probably pay attention to one another, while fish in a familiar environment may focus on the novel features of the environment.

11.1 SUMMARY

The predator avoidance responses of rainbowfish are heavily influenced by site-specific environmental variables, including the level of predation threat, habitat complexity and habitat stability. Phylogenetic history seems to play little or no role in the behaviour of rainbowfish populations because selection at the population level occurs much over a much smaller time frame than the separation of species. Rather, local ecology strongly influences behavioural responses as well as the learning and memory abilities of individuals. In turn, learning provides the flexibility that enables responses to be locally adaptive, but these flexible responses are built on a deep-seated foundation that is genetically inherited. The formation of groups aids in the spread of new information through the population, enabling all individuals to adopt locally adaptive responses. Selective pressures differ between individuals (for example males versus females), and even within an individual (e.g. hunger level, reproductive status, etc.) resulting in variation at an even finer scale.

The results presented in this thesis are of importance in that few studies in the past have considered such a wide range of ecological variables and the impacts they may have on the behaviour of prey species. Predation has been the key factor in the past, and while it still remains highly important in determining escape responses and various other aspects of the

preys' behaviour, physiology and morphology, one must consider it within the broader context of an animal's ecology.

11.2 FUTURE DIRECTIONS

The wonderful thing about this area of study is that it is wide open to new possibilities. Environments and modes of interacting with them are so tremendously variable that behaviours vary over a very small spatial scale. How the level of habitat complexity interacts with the use of spatial (local and global) cues has only recently become the subject of investigation and will certainly provide some interesting results in the future. Similarly, the level of habitat stability may also influence both the reliability of local cues and the level of curiosity displayed by individuals. As an example, the stability of the environment probably affects the degree to which animals rely on social learning to discover the localities of foraging patches.

The question of why individuals choose to shoal with familiar individuals remains fairly open. In studies of this type a range of populations varying in predation pressure ought to be considered. Does the tendency to shoal with familiar individuals depend on the context (e.g. predation or foraging)? While my data suggest that Amamoor fish do not alter their preference when faced with a predator, it may well be that other populations are more sensitive in their response to predation. How long does familiarity take to acquire and how long does it last once the fish are separated? What cues are the fish relying on to recognise familiar individuals? And importantly, do groups of familiar individuals learn from one another more efficiently than a group of strangers? All these types of questions could be tested very easily using binary choice apparatus or the trawl apparatus used in earlier chapters. Finally, the role of familiarity in kin recognition is worthy of investigation. Offering fish choices between full sibs, half sibs and

non-relatives would help to elucidate the role of genetic relatedness and familiarity in individual discrimination. Further, what is the fitness benefit (if any) of kin recognition in the field?

A continuation of work on learning and memory would be rewarding, particularly with regard to group size. One may expect that as group size increases a plateau would be reached in terms of escape efficiency. Beyond this point increasing group size may cause interference and confusion. Optimal shoal sizes are likely to be context dependent. A similar plateau may be reached with social learning, since scrounging has previously been found to influence the flow of information through populations (Lefebvre and Giraldeau, 1994).

The relative importance of social learning in rainbowfish is yet to be fully investigated. Once again its importance is likely to vary not only from location to location (due to ecological differentiation) but also between tasks (e.g. foraging versus predator avoidance). One area of work that may well be worth investigating concerns the pathways of information transfer. That is who learns from who? Furthermore, how does social learning aid survival in the field? Are there certain conditions (e.g. resource limitation) where social learning becomes more important?

In terms of rainbowfish biology and ecology, we still know very little. Further work is required, particularly in the field, to establish shoal sizes and dynamics. Do individuals continually shoal with the same shoal mates? How far do rainbowfish move? Do they spend most of their time within the same pool? How does their use of microhabitats vary with predation pressure from location to location? How important is predation in relation to competition and food availability? It would be worth while to continue the work outlined in Chapter 7 using simulated predator attacks, but much greater control is required to gain reliable data.