CHAPTER 1
General Introduction: The behavioural ecology of predator avoidance

The study of behavioural ecology is an attempt to understand why animals behave the way they do within the context of their surroundings. The behaviour of animals is particularly influenced by ecological variables such as refuge availability, the presence or absence of predators, and prey availability. Predators can act directly and indirectly on the reproductive fitness of prey and are therefore vitally important to the evolution of behavioural, physiological and morphological characteristics (Lima and Dill 1990, Kotler *et al*. 1994, Endler 1995). The interaction between predators and their prey often leads to an evolutionary arms race which may result in the development of costly traits (e.g. spines, avoidance responses etc.). While predation is an important component of the ecology of an animal, it is not the only one, and will often interact with other factors (such as the level of habitat complexity and prey availability) to shape the behaviour of animals (LaGory 1987, Savino and Stein 1989, Brown and Warburton 1997, Sih 1997).

In order to maximise reproductive output (fitness) animals must first survive to sexual maturity and then must gather energy for reproduction. To accomplish this they must finely balance the time devoted to energy acquisition (foraging) and predator avoidance (survival) (Smallwood and Carter 1996, Ryer and Olla 1998). While predation pressure may remain relatively stable over evolutionary time within a geographical region, on an ecological time scale (the lifetime of a prey individual) the risk may vary greatly from season to season or even minute to minute. For an animal to accomplish more in its lifetime than just evade predators, its anti-predator responses should show some degree of flexibility to facilitate response to variation in risk. Most behavioural ecology hypotheses are based on optimality models and assume that animals will behave in such a way as to maximise foraging efficiency while minimising predation risk. This is known as risk or threat sensitivity (Helfman 1989). A great many animals have found that one solution to this dilemma lies in the formation of groups (Elgar 1989).

1.1 PREDATION AND GROUP LIVING

Predation is considered to be a major selective force in the evolution of animal sociality (Godin and Morgan 1985, Lima and Dill 1990). Group living is a universal response to predation because it reduces individual risk, regardless of the cognitive abilities of the prey taxa. Upon encounter, the probability that a particular individual within a group will be attacked by a predator is reduced proportionately to the number of members in the group (Krause and Godin 1995). Prey derive other benefits from group living. As group size increases so to does the probability a predator will be detected (i.e. group vigilance or the many eyes hypothesis) (Hoogland 1979, Wawra 1988, Elgar 1989, Lima and Dill 1990, Pitcher and Parrish 1993, Lima 1995). Predators are detected earlier by groups (Lazarus 1979, Magurran *et al*. 1985, Godin 1988). Also, as group size increases, the amount of time spent scanning for predators per capita decreases while the time spent foraging or performing other behaviours increases proportionately. The flight response of the initial detector is socially transmitted to other members of the group (ca. the chorus line hypothesis; Potts 1984, the trafalgar effect; Treherne and Foster 1981, warning skitters; Magurran and Pitcher 1987, and collective detection; Lima 1995 and Lima and Zollner 1996). Moving prey have an additional benefit in the form of the confusion effect (Milinski 1977, Ohguchi 1981, Landeau and Terborgh 1986, Milinski 1990). When a predator approaches a group of animals, an individual is often targeted for attack. If a great number of similar targets are moving about randomly in a relatively small area, then the predator often becomes confused and is unable to focus on a particular target. Sick, injured or young animals are often targeted, not only because they may be easily run down but also because they are easily distinguished from other group members. This is known as the oddity effect (Pitcher and Parrish 1993) and explains why in shoals of fish for example, like will often shoal with like.

Animals with greater cognitive abilities obtain other benefits from grouping together. Co-ordinated group anti-predator responses such as flash expansions in shoals of fish (Pitcher and Wyche 1983), inspection behaviour (Pitcher *et al.* 1986, Pitcher 1992, FitzGibbon 1994) and mobbing (common amongst birds and mammals) (Curio *et al.* 1983, Hein 1986) also provide safety from predators. Schooling and flocking responses seen in fish and birds provide a mesmerising visual display of co-ordination between group members, but probably operate under strict rules and rapid (but passive) transfer of information between individuals. The selection forces governing the flight of individuals in a flock of birds for example must be immense, since one small mistake could end in a mid-air collision and the potential death of many group members. In shoals of fish, individuals that make mistakes during group avoidance manoeuvres are preferentially attacked (Parish 1992). Mobbing and inspection behaviour are more sophisticated and may require a degree of co-operation between individuals (Milinski *et al*. 1990).

1.2 PREDATOR INSPECTION

Predator inspection is commonly observed in fishes although it has been reported in a wide range of animals (Curio 1976, Kruuk 1976, Lazarus 1979, Hirsch and Bolles 1980, Fitzgibbon 1994). Inspection is typically characterised by the cautious approach of a singleton or a small group of prey animals towards a predator (Pitcher 1992). At the end of the approach the prey fixate on the predator for some time before quickly returning to the safety of the group. The behaviour is thought to aid in predator recognition (Magurran and Girling 1986) and may provide up to date information regarding the predators' whereabouts and intentions (Pitcher *et al*. 1986, Magurran and Higham 1988, Murphey and Pitcher 1997). It may also cause attack abatement (i.e. the prey signals to the predator that it has been spotted and has therefore that the predator has lost the element of surprise) (Pitcher and Parish 1992, FitzGibbon 1994). Milinski (1987, 1990a, 1990b, 1997) described the situation whereby two individuals approach a predator as satisfying the requirements of the Prisoner's Dilemma in game theory. Tit for tat is often the best solution (or game plan) for such a problem. Tit for tat simply requires that an animal co-operates on the first move and then copies the last move of its opponent (Axelrod and Hamilton 1981). When fish approach a predator during inspection visits they often use a "kick and glide" approach each alternating turns at taking the lead. If both co-operate then they both receive equal information about the predator and share the cost (probability of being attacked). If, however, one lags slightly behind (i.e. does not co-operate) then the lead fish suffers an unreasonably high cost and the lag fish suffers no cost. Alternatively, the behaviour described as "tit for tat" could simply be an artefact of sociality in fishes. Fish commonly rely on a kick and glide motion when approaching an object and subsequently appear to take the lead in turns in an attempt to stay together.

While it appears that some fish may play the tit for tat game when paired off in the lab, it is still not known how such a tactic would work in the real world where groups may be comprised of hundreds of individuals (Pitcher 1973, 1992). Any number of these individuals could potentially pair off or approach as a small group. How then does an animal make its choice of partner? In this situation it may be reasonable to expect that animals are capable of recognising individuals and assigning values to them (Dugatkin and Alfieri 1991a, b). In other words, members within a group become familiar with one another and, therefore, can build an expectation of how an individual might react in a given situation. It has been shown, for example, that fish prefer to inspect with individuals who have not defected in past inspections (Milinski *et al*. 1990a, b, Dugatkin and Alfieri 1991a, b). Furthermore, fish generally prefer to shoal with familiar individuals (Brown and Colgan 1986, FitzGerald and Morrissette 1992, Magurran *et al.* 1994, Chivers *et al*. 1995, Griffith and Magurran 1997).

There are obvious limitations to the number of individuals an animal can remember and hence one of two possibilities present themselves. Firstly, it may be that members of extremely large groups only associate with a small proportion of the group. Secondly, there may be a critical group size above which recognition abilities decline significantly. In the latter case perhaps tit for tat is played every time an inspection visit occurs and partners are chosen at random.

1.3 SHOAL COMPOSITION

It is becoming increasingly evident that shoals of fish are not made up of a random selection of individuals, nor are the individuals randomly arranged in space (Jennings and Evans 1980, Pitcher *et al.* 1985, Parrish 1989, Pitcher and Parish 1993). Both in the wild and in the laboratory, individuals choose to join shoals that are made up of individuals that are relatively similar to themselves (Pitcher *et al*. 1985 Pitcher *et al*. 1986b, Ranta *et al*. 1992) and within a shoal they associate with individuals that are about the same size (Breder 1951, Pitcher *et al*. 1985, Milinski *et al*. 1990b). In some species, including rainbowfish, females tend to form the basis of the shoal while mature males cruise from shoal to shoal in search of mating opportunities (Grffiths and Magurran 1998). In mixed species shoals there may even be discontinuities in size at the breaks between monospecific layers of fish (Parish 1989a). Both minnows and sticklebacks may break into “sub shoals” segregated by size while foraging but rejoin larger individuals when under predator attack (Pitcher *et al*. 1986b, Ranta *et al.* 1992). By choosing to associate with similar individuals, the pool of individuals with which a fish commonly interacts with is dramatically reduced. Such a mechanism may increase the probability that small groups of fish within a shoal, may become more familiar with each other than other members of the shoal. In this way a fish may not only shoal with these individuals by default, but may preferentially seek them out as shoaling partners for activities such as predator inspection. Preferentially grouping with familiar animals also increases the flow of information between individuals (Lefebvre *et al.* 1996). Consequently shoals of familiar fish are more adept at predator avoidance. Compared with fish that are unfamiliar with one another (i.e. strangers), shoals of familiar fish are tighter and they show an increase in other behaviours that are known to be successful anti-predator responses (Chivers *et al*. 1995). Groups of animals containing familiar individuals are also more likely to display social learning (Galef 1976, Heyes 1994, Laland *et al*. 1996) and the rate of transmission of socially learned behaviours may be greater (Giraldeau *et al*. 1994, Laland pers comm.).

1.4 DIFFERENCES IN ANTI-PREDATOR RESPONSES

1.4.1 Between-population variation

The ecology of an animal partially shapes its behaviour. Many aspects of an animal’s ecology may change dramatically across the species’ range as a consequence of differences in habitat characteristics (including structural complexity, stream flow, and sympatric species, including predators). It is not surprising to find that predator recognition and anti-predator responses vary with geographical location (Curio 1976, Giles and Huntingford 1984, Mugurran 1986, Magurran and Seghers 1990a, b). The most marked differences exist between populations that live sympatrically with predators and those that do not. However, within predator-sympatric populations, predator diversity and abundance also vary. Differences in predator recognition and anti-predator response between predator-naïve and predator-experienced populations has been widely studied in a number of species, but none more so than guppies.

Guppies are native to the streams of north-eastern South America and the adjacent islands including Trinidad. Guppies show geographical variation in many different traits that co-vary with predation and other environmental factors (see review by Endler 1995). Table 1. is taken from Endler (1995) and shows the differences in predator related traits between populations of guppies which suffer either high or low predation. A similar table could be compiled for minnows (e.g. Magurran 1987) and sticklebacks (e.g. Giles and Huntingford 1984) although it would not be nearly as extensive.

Brown and Warburton (1997) have shown that the anti-predator responses displayed by prey fish vary with the habitat that they occupy (see also LaGory 1987, Savino and Stein 1989, Sih 1997). Rainbowfish derived from large open habitats, such as lakes, prefer to school in the presence of predators. They rely solely on the group to shelter them against attack. Prey from highly complex environments, such as upland creeks, have a tendency to flee and take cover amongst vegetation or other structures (Brown and Warburton 1997). In highly complex habitats the mechanisms for schooling (visual and/or lateral line communication between individuals) break down and schooling is no longer a viable anti-predator response.

Table 1.1 Traits in guppies that are affected by predation levels (modified from Endler 1995)

Trait	**High predation**	**Low predation**	**References**
Time spent foraging when predator present	Less	More	Magurran and Seghers (1994)
Feeding rate and tendency to feed when predator present	Higher	Lower or none	Fraser and Gilliam (1987)
Adult schooling size, cohesion and orientation (fish predator threat)	High	Low	Seghers (1974a), Magurran and Seghers (1994), Magurran and Seghers (1991)
Subadult schooling: parallel orientation	High	Low	Brenden et al. (1987)
Subadult schooling: nearest neighbour distances	Medium	Medium	Brenden et al. (1987)
Juvenile schooling: cohesion and orientation	High	Low – high	Magurran and Seghers (1994), Magurran and Seghers (1991), Magurran and Seghers (1990a), Magurran and Seghers (1990b)
Change in schooling of juveniles in the physical presence of a predators during tests: cohesion, orientation	Low (always school)	High	Magurran and Seghers (1991), Magurran and Seghers (1990a)
General anti-predator behaviour	Stronger	Weaker	Liley and Seghers (1975), Magurran and Seghers (1994), Magurran and Seghers (1994)
Response to bird predation threat	High	Low	Seghers (1974a)
Aquatic predator hunger assessment	Efficient	Weak	Licht (1989)
Reaction distance to potential predators	Long	Short	Seghers (1974a), Seghers (1974)b
Aquatic predator inspection and attack cone avoidance	High	Low	Licht (1989), Magurran and Seghers (1990a), Dugatkin and Alfieri (1992)
Apparent use of tit for tat strategy during aquatic predator inspection visits	High	Low	Dugatkin and Alfieri (1992)
Shallow or cover seeking in response to predator threat	High	Low	B.H. Seghers PhD Thesis University of British Columbia

1.4.2 Within-population variation

Much of the variation in anti-predator response within a population can be explained by the demography of the population: individuals vary in size, age and sex. The perception of risk differs between each demographic group and individuals are clearly capable of making subtle and adaptive behavioural decisions in response to this (Lima and Dill 1990). However, even within these subsets, the motivational state of individuals can change from moment to moment, thus changing their perception. Hungry individuals, for example, are more likely to take greater risk in order to access a food resource (Godin and Smith 1988, Morgan 1988, Pitcher and Parrish 1993).

Males and females often differ in their perception of risks owing to different balances they achieve when weighing up costs and benefits associated with certain activities. Differences in behaviour, body size and conspicuousness can make one sex more vulnerable than the other (Magurran and Nowak 1991). Males often fight one other for access to females and in doing so put themselves at great risk both indirectly, through increased vulnerability to predation, and directly, due to any harm that may be caused during battle. The cost of gamete production to males is almost negligible. Females on the other hand, invest heavily in gamete production and are often the choosier sex. The females' prime objective is to find the best male (Parker 1983) while avoiding the unwanted attention of "low quality" males and predators.

1.5 DEVELOPMENT OF ANTI-PREDATOR RESPONSES

1.5.1 Innate Responses

A number of studies suggest that the anti-predator response displayed by prey are genetically predetermined (i.e. innate) and inherited from the parents (e.g. Seghers 1974, Giles 1984). When fry are bred and raised in the laboratory they show similar anti-predator abilities as their parents despite having had no personal experience with predators (Magurran 1989). Young are always at greater risk from predation than older individuals, both because they are inexperienced and because they are small. It makes sense to have at least some baseline defence against predation from the moment the young are born. Therefore, we might expect innate anti-predator responses to be adaptive. But what of populations where the local level of predation varies greatly and is unpredictable? In this circumstance animals require a mechanism that enables a degree of flexibility in response, particularly if anti-predator responses are costly to maintain. The mechanism for fine-tuning is learning.

1.5.2 Learned Responses

Increasingly, studies have shown that the learning abilities of animals are far greater than previously predicted. For example, even fruit fly larvae can learn to associate particular odours with predation (Dukas 1999). Animals are no longer viewed as mindless machines, responding to every situation by utilising a genetic template. Whilst animals may be genetically predisposed to perform particular behaviours, the form these behaviours eventually take on is determined by environmental influences (Huntingford 1986). Animals are capable of utilising a number of cues when making complex decisions (Blumstrein 1996). Further, many animals have excellent memory capabilities that enable them to recall past events in order to respond presently and to predict future events (Csanyi *et al*. 1989, Croy and Hughes 1991, Markel 1994, Miklosi *et al*. 1995).

The anti-predator responses displayed by animals change with ontogeny and experience (Dill 1974). Different responses are suited to different life-history stages (Brown and Colgan 1985, Magurran 1986). Offspring from both predator sympatric populations and predator naïve populations are capable of improving their anti-predator behaviours by learning through experience. However, an interesting interaction between population origin and the level of learning exits. For example, young from predator sympatric populations of minnows reach a greater level of competency in their anti-predator tactics than those derived from predator naïve populations (Magurran 1990). Perhaps the in-built, baseline genetic response provides juveniles from predator sympatric populations with a competitive edge over their naïve counterparts.

1.5.3 Social Learning

Animals can learn about their environment (including predators) in one of two ways; individual learning (trial and error) or social leaning (Giraldeau *et al*. 1994). In social learning the observer learns a behaviour by observing another individual. Watching other fish encounter predators, for example, may improve the predator avoidance behaviour of observers (Patten 1977). A novel behaviour may be adopted directly through imitation. More often, however, the observer's attention is guided or directed by the demonstrators' behaviour, the observer then interacts with the environment in order to learn the task. Hence, even in social learning there may be an element of individual learning (see Galef 1988, Laland 1992 and Heyes 1994 for reviews). When social learning has occurred the behaviour or information that was passed on is said to have been socially transmitted (Galef 1988).

Social transmission has been observed in many taxa ranging from fish to chimpanzees (reviewed by Robert 1990) and may lead to the development of animal culture, or the persistence of a novel behaviour in a local area through time (Mainardi 1980, Boyde and Richardson 1985, Heyes 1993). Social transmission is most likely to occur amongst social animals where there is a high degree of tolerance for others and, not surprisingly, is most commonly observed in troops of primates. Transmission may occur vertically (from one generation to the next) or horizontally (amongst individuals of similar ages). Learning may occur through key individuals in the group (indirect transmission), or via the majority of members (frequentcy dependent transmission)(Cavalli-Sforza and Feldman 1981, Boyde and Richardson 1985, Feldman and Laland 1996). Given the prerequisites for social learning (the tendency to form groups and social tolerance), it may be expected that individuals that are familiar with one another (i.e. those that frequently interact) are more likely to learn socially and the rate of transmission may be greater compared to groups of animals containing unfamiliar individuals.

There is much debate about the role of social transmission in the evolution of behaviour (Maynard-Smith and Warren 1982, Laland 1992). The so called gene-culture evolution models (e.g. Feldman and Laland 1996) examine the interaction between the social and genetic inheritance of behaviours and their persistence through time (i.e. over several generations). These models suggest that the pattern of evolution in populations with socially transmitted cultural traits differs from that in acultural populations because; 1) Cultural transmission can modify selection pressures, 2) Culture can generate new evolutionary mechanisms, 3) The interaction between genetic and cultural inheritance can produce time lags in selection, 4) Non-random associations between genes and cultural traits can occur and significantly affect the genetic response to selection, and finally, 5) Culture may generate exceptionally strong selection pressures (Feldman and Laland 1996).

A behaviour that has been adopted by an individual or a population is by no means fixed in the behavioural repertoire. Galef (1996) stated that "there is no reason to assume that behaviour patterns learned socially will persist when they are no longer differentially rewarded any more than will individually learned behaviour patterns". Socially acquired behaviours are under the same selection pressures as behaviours acquired via other means. Therefore, like individually learned behaviours, socially acquired behaviours may be regularly picked up and discarded providing a level of behavioural flexibility.

In many animals there appears to be a critical point in life where the ability to learn new things is reduced or lost entirely. Imprinting in water foul is a classic example (Lorenz 1970). In rainbowfish, both habitat preference and anti-predator responses are probably, at least in part, genetically inherited. Although anti-predator responses can almost certainly improve via learning, few people (if any) have considered whether habitat preferences can also be influenced by learning. Individuals living in fast flowing rivers or streams must cope with sudden alterations in their surroundings. This may occur either when an individual is swept down stream, or when structural habitat is removed by scouring during floods. In upland creeks for example, weed beds may be entirely removed during severe flooding. If prey rely on cover as a food source or to evade predation, they must adapt quickly or die. The juveniles and eggs of fish are particularly susceptible to being washed downstream (Beumer 1979) and it would be advantageous if these individuals could rapidly alter their behaviours to suit their new surroundings. In many species it appears that young are the most likely individuals to experiment and learn new behaviours (Fragaszy and Visalberghi 1996). If habitat preference is flexible in any way, then we are likely to observe this flexibility in juveniles.

1.6 THREAT RECOGNITION

Naïve animals often have an inherent ability to determine whether an object represents a threat or not. It seems likely, therefore, that a number of basic cues are used to identify threat and that recognition may be genetically based. In fish, predators are often identified by large eyes and upturned mouth (Karplus *et al*. 1982). Movement and larger size also seem to be fundamental cues for threat (Brown and Warburton 1997). Learning may enable animals to recognise site-specific predatory species or even particular predator individuals (Edge *et al.* 1993, FitzGibbon 1994). This fine-tuning through experience (including social experience) may enable prey to learn about colour patterns and subtle behavioural and chemical cues emitted from potential predators (Karplus *et al.* 1982, Guthrie 1983). Once a particular threat is recognised an appropriate response can follow.

In Brown and Warburtons' study (1997), rainbowfish intensified their avoidance responses to a predator model with increasing predator realism. While the shape and colour of the predator model had an impact on response, movement was by far the most important indicator of threat. Other studies have obtained similar results. Minnows showed the greatest response (and least habituation) to a realistically marked model pike over a plain pike, a marked cylinder and a plain cylinder (Mugurran and Girling 1986). Other authors have found that live predators provide better threat stimuli than moving models, which are in turn more threatening than stationary models (e.g. Godin and Crossman 1994). Moving objects may represent a greater threat than stationary ones because predators in motion are more likely to attack (Pitcher *et al.* 1986). It seems likely that subtle movements displayed by predators may provide prey with further information on the likelihood of attack (Licht 1989).

Predator inspection behaviour almost certainly provides prey with the type of information required to make a judgement about the level of threat a predator represents. Figure

1.1 represents a model of how a prey animal may respond to a disturbance. First, a disturbance is detected. Disturbance detection is most likely to occur if an animal is familiar with its surrounding environment. Any novel cues can be quickly separated from background noise and the full attention of the individual can be devoted to investigating the disturbance. In the case of visual detection, the prey animal usually fixates on the object for some time and uses an open cue assessment to identify the object. If the object cannot be identified, then curiosity generally leads to an approach response. The object is then cautiously investigated at close range and a risk assessment is undertaken. When determining the level of threat that an object represents a number of factors may be taken into consideration, for example: a) the feedback emanating from the object, b) distance to refuge, c) distance to predator, d) shoal size, e) value of the current forage patch, and f) internal or motivational state (e.g. hunger level). The absence of a threat leads to habituation through learning and the details of the object may be stored in the memory for a period of time. If the object provides intensely negative feedback, then fear will be invoked leading to evasion. Any object that provides strong negative feedback will also be stored in the memory of the prey for some period of time and require only infrequent reinforcement. If the negative feedback is moderately negative, then it is likely that the prey individual will continue to monitor the object at the expense of other activities.

If the cause of the disturbance is recognised (from past experience or basal cues) during the open cue assessment phase, recognition may lead directly to the determination of a level of threat (no threat- habituate, high threat- evasion, or moderate threat- monitor). During the monitoring loop the prey assesses the object using closed cue assessment. Closed cue assessment occurs on a much finer scale than open cue assessment and may enable prey individuals to identify specific predator species or individuals, and even the predator's motivational state.

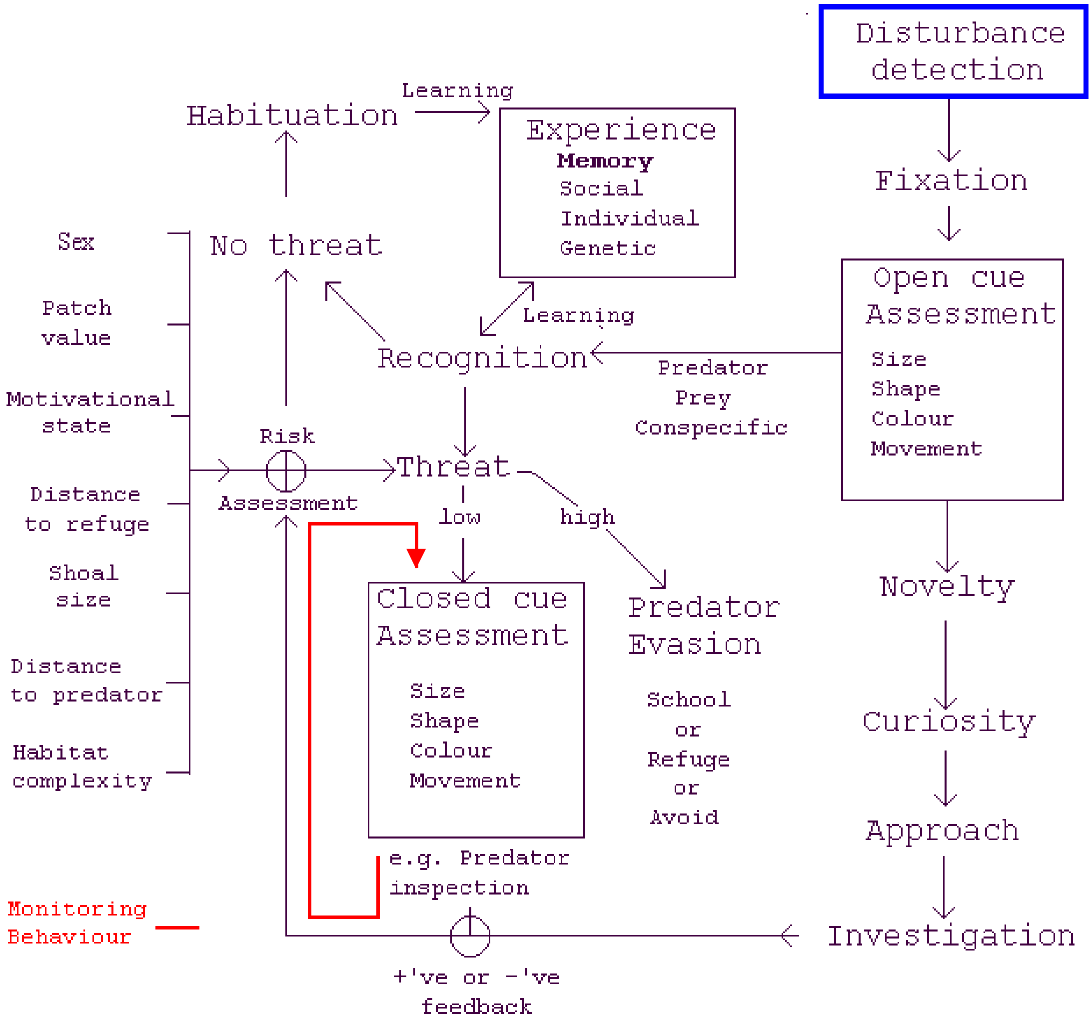

Figure 1.1. A theoretical diagram of the psychological pathways involved in predator recognition.

1.7 OUTLINE, AIMS AND OBJECTIVES

This project set out to investigate the behavioural ecology of predator avoidance behaviour using a genus of native Australian fish (rainbowfish; genus *Melanotaenia*, family *Melanotaeniidae*) as models. I set out to explore the various themes depicted in Figure 1 paying particular attention to predator evasion. The primary objective of this thesis was to discover how much variation exists in the anti-predator behaviour displayed by different populations and species of rainbowfish. I also wished to explore the roots of this variation by considering the major influences shaping the development of predator avoidance behaviour, namely the interaction between genetics, learning and the environment. An individual's behaviour cannot be considered without reference to its ecology, hence, the level of habitat complexity, predator density and the degree of habitat stability were also considered.

In order to avoid predators, prey must firstly be able to recognise them. One of the first objectives of this thesis was to take a closer look at one of the more important aspects of predator recognition, predator movement (Chapter 2). Chapter 3 examines the inheritance and plasticity of habitat selection and anti-predator responses in laboratory bred rainbowfish. Chapter 3 discusses how population differences in response may arise and if they may be altered through early life experience. In Chapter 4, I wanted to see if rainbowfish were capable of making associations between habitat types and predator presence and whether they used large-scale spatial cues or local, visual cues to do so. If in fact rainbowfish are capable of doing this, then it follows that being familiar with an area may also confer anti-predator benefits. Chapter 5 investigates the effect of environmental familiarity on the behaviour of rainbowfish.

Apart from between population variation in escape responses, we might also expect to find variation within a population due to demography. Male and female rainbowfish appear to have different costs and benefits associated with particular activities (especially when under predation pressure). In Chapter 6, I wanted to compare and contrast anti-predator responses of male and female rainbowfish.

Since most of the studies in this thesis were conducted in the laboratory, I wanted to compare some of the expectations arising from these studies to what happens in the wild (Chapter 7).

The final three chapters focus on some of the benefits of living in groups. Chapter 8 considers the importance of shoal-mate familiarity in group formation and anti-predator responses. I was especially interested in looking at the importance of social learning and some of the benefits of group association in predator avoidance (Chapters 9 & 10). Social learning might be one mechanism by which population differences are maintained over successive generations (i.e. cultural traditions).

The Appendix addresses logistical and theoretical questions such as: how do groups form, how do we define a group, and how do we measure changes in group structure?

1.7.1 The specific hypotheses tested:

1) Does predator activity invoke different responses from predator naïve and predator wary rainbowfish (Chapter 2)?
2) Can predator naïve fish acquire appropriate anti-predator responses through learning (Chapter 2 and 5)?
3) Is habitat selection in rainbowfish genetically predetermined or is it influenced by past experience (Chapter 3)?
4) Are prey able to associate predators with particular micro-habitats or locations (Chapter 4)?
5) Does familiarity with the environment enhance escape efficiency (Chapter 5)?
6) Do males and females differ in anti-predator responses (Chapter 6)?
7) Do field observations contrast with those obtained in the laboratory (Chapter 7)?
8) Do rainbowfish recognise and preferentially shoal with familiar individuals (Chapter8)?
9) Does preference for familiar individuals increase in the presence of a predator (Chapter 8)?
10) Does increased shoal size improve predator avoidance (Chapter 9)?
11) Is social learning important in the acquisition of anti-predator behaviour (Chapter 10)?

1.8 THE STUDY ANIMALS

The family Melanotaeniidae (commonly known as rainbowfish) is one of the most important families of freshwater fishes in Australia. The family's distribution is exceptionally broad, ranging from the tributaries of the Murray-Darling system in Victoria, northwards up the east coast to Cape York, and west to the north-west coast of the Kimberly district (see Allen and Cross 1982). The southern limits of the distribution are almost certainly controlled by winter minimum water temperatures. Rainbowfish occupy virtually every type of freshwater ecosystem, from wallum swamps to fast flowing rainforest streams and the billabongs and water holes of the arid channel country. Within this range the variation in predator pressure is vast. The diet of rainbowfish consists mostly of terrestrial and aquatic insects, but filamentous algae are also frequently ingested. Strong sexual dimorphism is present in the species with males typically being larger and brighter in colouration. The behaviour between the sexes also appears to vary with females forming the basis of many aggregations while males cruise in search of mating opportunities.

Members of the genus *Melanotaenia* vary in size from the pygmy rainbowfish (*M. pygmaea*) which reaches a maximum standard length of a little over 50 mm, to members of the *M. splendida* complex, which commonly exceed 150 mm. Variation in morphology within the genus is highly conserved, with species differing from one another though small variations in colour, morphology and meristics. At the same time, body form within species is relatively plastic and appears to be dependent upon streamflow and correlated habitat characteristics (unpublished data), which can make identification in the field difficult (Zhu et al 1998).

The investigations undertaken in this thesis utilised four members of the *Melanotaenia* genus, namely *M. duboulayi*, *M. splendida splendida*, *M. eachamensis* and an undescribed species known as Utchee type. All four species are found on the east coast of Australia. *M. duboulayi* inhabits the coastal drainages of the east coast of Northern New South Wales from the Macleay River region to the Burnett River in southern Queensland. *M. s. splendida* occupies the east coast drainages of Queensland from the Burnett River region in the south, to the tip of Cape York (Allen and Cross 1982). The exact species boundaries are unknown and it may be that these two species live sympatrically in some locations. *M. eachamensis* was once thought to be confined to a crater lake (Lake Eacham) on the Atherton Tablelands, south-west of Cairns. In the mid 1980's it disappeared from Lake Eacham and was thought to be extinct in the wild (Barlow *et al*. 1987). Recent survey work has located the species in several headwater tributaries of the North and South Johnstone Rivers and a couple of crater lakes on the Atherton Tablelands (Zhu *et al.* 1998). The Utchee type rainbow occupies a similar region to that of *M. eachamensis*, but also inhabits a few lowland tributaries and regions of the main channel in the Johnstone River (McGuigan and Jones unpublished data). The Utchee type and *M. eachamensis* are thought to be the original inhabitants of the area and *M. s. splendida* may have invaded relatively recently. The species boundaries of all three species are not well defined and recent evidence suggests that at least some populations have hybridised in the streams of the Cairns-Atherton region (F. Jones unpublished data). DNA analysis suggests that Utchee, *M. eachamensis*, *M. duboulayi* and *M. australis* (Western Australia) are all closely related, providing support for the hypothesis that *M. spendida* has invaded recently (Zhu *et al.* 1998, McGuigan and Hurwood pers. comm.).

The four species all vary in the habitats they occupy. *M.eachamensis* only occupies upland water bodies that are devoid of predators. *M.eachamensis* can be found in isolated crater lakes and small, fast flowing rainforest streams and rivers. The Utchee fish occupy a similar habitat to that of *eachamensis* except that they also occupy the main river channel and live sympatrically with a number of piscivorous fish species. *M. s. splendida* primarily occupies the lowland reaches occupying water bodies that contain voracious predators including barramundi (*Lates calcarifer*), jungle perch (*Kuhlia rupestris*), sooty grunters (*Hephaestus fuliginosus*), mouth almighty (*Glossamia aprion*) and spangled perch (*Leiopotherpon unicolor*). *M. duboulayi* also occupies a wide range of habitats and can be found living both with a variety of predators in lowland lakes, rivers and streams, and in the absence of predators in headwater creeks (Pers. obs.).

This group of animals presents the perfect opportunity to investigate variations in behavioural responses observed in different populations. In particular, the variation in predation pressure and habitat complexity experienced by the rainbowfish species mentioned above, enable a comprehensive study of how these two factors interact to shape anti-predator responses.

References

Back to contents