9-2002

Do Female Rainbowfish (Melanotaenia spp.) Prefer to Shoal with Familiar Individuals under Predation Pressure?

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Recommended Citation

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ABSTRACT

Shoaling with familiar individuals may have many benefits including enhanced escape responses or increased foraging efficiency. This study describes the results of two complimentary experiments. The first utilised a simple binary choice experiment to determine if rainbowfish (Melanotaenia spp.) preferred to shoal with familiar individuals or with strangers. The second experiment used a "free range" situation where familiar and unfamiliar individuals were free to intermingle and were then exposed to a predator threat. Like many other small species of fish, rainbowfish were capable of identifying and distinguishing between individuals and choose to preferentially associate with familiar individuals as opposed to strangers. Contrary to expectations, however, rainbowfish did not significantly increase their preference for familiar individuals in the presence of a stationary predator model. Griffiths [J Fish Biol (1997) 51:489–495] conducted similar studies under seminatural conditions examining the shoaling preferences of European minnows and showed similar results. Both the current study and that of Griffiths were conducted using predator wary populations of fish. It is suggested that, in predator sympatric populations, the benefits of shoaling with familiar individuals are such that it always pays to stay close to familiar individuals even when the probability of predator attack is remote.

Introduction

When fish are separated from shoal mates and a predator appears, the most immediate response in many species is to rejoin a shoal and thereby find safety in numbers. Given a choice between a number of different shoals, the fish must make a decision about which shoal to join by taking a number of things into account. Fish may assess shoals based on species composition (Parrish 1989; Krause and Godin 1994), shoal size (Hagar and Helfman 1991), the size distribution of shoal members (Pitcher et al. 1985,

1986; Ranta et al. 1992; Pitcher and Parish 1993), fish colouration (McRobert and Bradner 1998), the level of parasitism (Krause and Godin 1996; Barber et al. 1998) or the reproductive status of members within each shoal (Van Havre and FitzGerald 1988). The preference to shoal with conspecifics may be overridden by size selectivity (Ranta et al. 1992; Krause and Godin 1994). Hence shoals of fish are not comprised of a random selection of individuals (Magurran et al. 1994; see Krause et al. 2000 for a review).

The decision to join a shoal may be determined by the situation in which the fish finds itself and its motivational state. Individuals may join and leave schools as their motivation changes (Seghers 1981). A balance may be struck between the perceived level of predator threat and hunger level (Morgan 1988). If the fish is threatened the decision may be made more quickly (Hagar and Helfman 1991).

It has been shown previously that guppies (*Peocilia reticulate*), bluegills (*Lepomis macrochirus*), paradise fish (*Macropodus opercularis*), sticklebacks (*Gasterosteus aculeatus*) and fathead minnows (*Pimephales promelas*) choose to shoal with familiar individuals (Brown and Colgan 1986; FitzGerald and Morrissette 1992; Miklosi et al. 1992; Magurran et al. 1994; Chivers et al. 1995; Griffiths and Magurran 1997a). Schools of fathead minnows comprising familiar fish show more effective anti-predator behaviours than schools comprising unfamiliar individuals (Chivers et al. 1995). On the other hand, pumpkinseed fish (*Lepomis gibbosus*) and juvenile rockbass (*Ambloplites rupestris*) do not spend more time with familiar conspecifics (Brown and Colgan 1986), possibly because these species are either solitary or territorial.

It is suspected that shoaling with familiar individuals enables the evolution of altruistic behaviour or reciprocity amongst unrelated individuals (Milinski et al 1990a, b; Roberts 1998). It seems likely that repeated interaction with the same group of individuals enables each member to recognise the other group members and possibly predict their behaviour in different contexts (e.g. feeding or predator inspection). Similarly recognising individuals enables guppies to mate with unfamiliar individuals, thus increasing their number of partners and encouraging out-breeding (Hughes et al. 1999; Kelly et al. 1999)

Rainbowfish are one of the most widespread and abundant freshwater fishes in Australia. They occupy virtually every freshwater ecosystem north of the Murray River on the Victorian-New South Wales border (Allen and Cross 1982). *Melanotaenia splendida* generally occupies regions of high predation on the North-East coast of Australia and its distribution is adjacent to and north of *M. duboulayi*, whose distribution is centred around Brisbane. They are, for all intents and purposes, very similar species occupying the same types of habitats and showing similar behavioural patterns. Rainbowfish are primarily pelagic and are opportunistic foragers, feeding mostly on terrestrial and aquatic insects and their larvae. Females typically spawn amongst aquatic plants and their eggs have two sticky web-like threads that prevent the eggs from being displaced by currents. Fry typically remain in this microhabitat (Pusey, personal communication) and it seems likely that emerging shoals of adults could show some degree of relatedness (Arnold 2000; Pusey et al. 2001). Little is known about dispersal, shoal site fidelity or even shoal fidelity in the wild. Nevertheless observations under water, video footage and snorkelling, suggest that females form the basis of shoals and males cruise from shoal to shoal in search of mating opportunities.

In light of such variation between species, I was interested to determine whether rainbowfish (*Melanotaeniidae* spp.) could recognise, and prefer to shoal with, familiar individuals. Furthermore, I wanted to determine if rainbowfish become more or less choosy when under threat of predation. Given the existing evidence, which suggests that shoaling with familiar individuals has predator avoidance benefits, it might be expected that the preference to shoal with familiar individuals will increase under threat from predation.

Materials and methods

Experiment 1: binary choice

Female rainbowfish (*M. duboulayi*) were collected using bait traps from two tributaries of the Mary River system 120 km north of Brisbane. Four traps were set within 5m of one another at each location and all the fish were captured within half an hour. Thirty fish were taken from each site. The sites were separated by approximately 50 km of stream. The fish were brought back to the laboratory and each population was isolated from the other in holding tanks for 2 months. The fish were fed once daily on flake food, pH was maintained at around 6.5–7, water temperature was 23 °C and the light regime was approximately 12 h light and dark. A glass tank (120 × 30 cm and 25 cm deep) was divided into three 40 cm compartments using two perspex partitions. The partitions had a number of holes drilled through them, allowing a flow of water to permeate through the tank. The middle compartment was further divided into three 13.3-cm (approximately equal to 2.5 body lengths) zones using a marker on the underside of the tank, one zone closest to each end compartment and a middle zone (Fig. 1). Most authors consider a fish to be part of a shoal if it is within 4 body lengths of other conspecifics (e.g. Magurran and Pitcher 1987). Therefore, fish occupying zones closest to the left or right side could only be considered as shoaling with the fish behind the closest partition. Shoaling is used here as an aggregation of individuals which are not necessarily orientated in the same direction (cf. schooling; see Pitcher 1983). The entire set-up was surrounded by a white cloth partition and illuminated by twin, fluorescent, 18 W light tubes suspended 1m above the tank. A video camera was placed overhead and all observations were made from video footage.
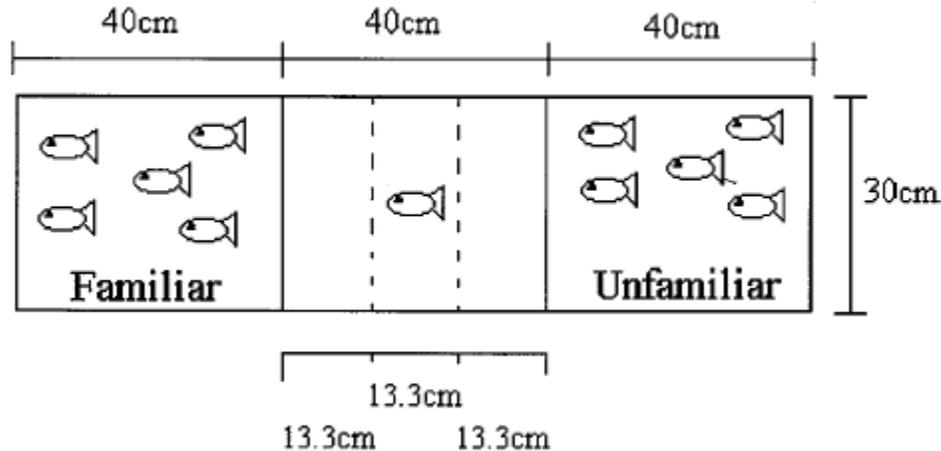

Fig. 1. Diagram of the layout of the experimental tank in experiment 1 (top view)

Only females were used in the experiment because they are considered to form the core of shoals in rainbowfish whereas males tend to be more solitary and aggressive. Five females from each of the two locations were matched for size and placed in each of the end compartments. The end that the fish were placed was randomised between trials to eliminate any right-left bias. The same shoal of fish was used throughout the experiment. A chooser female was picked randomly from one of the holding tanks and introduced to the middle third of the centre compartment in a clear plastic bottle. After 15 min the bottle was lifted away by a remote pulley device and the chooser was allowed to roam freely throughout the

centre compartment. The chooser female had to move from the centre zone and visit both zones closest to the side compartments and then return to the centre zone in order to pass the stringent criterion before recording began. This criterion ensured that the test fish had sampled both stimulus shoals prior to the onset of recording. Moreover, the criterion eliminated fish that showed a pronounced fright response (a rapid dash to one corner and freezing for the remainder of the trial) when the bottle was raised. Fish that showed such fright responses had clearly not sampled the stimulus shoals and, therefore, could not have chosen between them. The maximum length of each trial was 30 min. The amount of time (in seconds) spent in either of the thirds closest to the side compartments (stimulus shoal zones) was recorded and then transformed to a percentage score (the time spent in either stimulus shoal zone after the chooser female had satisfied the choice criterion divided by the total time spent in the both stimulus shoal zones). The percentage score enabled a comparison between females, as some satisfied the criterion more quickly than others. After testing, the standard length of each chooser was measured. The average standard length of the test females was 5.8 cm (±0.25 cm SE). No females were tested more than once and none of the chooser females was ever used as part of a shoal.

Of the 16 females tested only 9 passed the choice criterion for recording. Of these, 2 fish were from one site and 7 from the other. Owing to the low replicate size from one of the populations the data from the two sites were pooled. The percentage data were arc-sin transformed and checked for normality. A two-tailed paired t-test was then conducted. A regression analysis was performed on the fish length data to highlight any possible effects size may have had on shoal choice.

Experiment 2: free range

Rainbowfish (*M. splendida splendida*) were captured using bait traps in the North Johnstone River (50 km south-west of Cairns) and air freighted to Brisbane. Once in the laboratory, the females were separated out and divided into three groups that were kept in isolation from one another. One group contained 14 individuals (familiar fish) and the other two groups contained 7 fish each (unfamiliar fish). The familiar fish were marked using a fluorescent polymer (Frederick 1997). Marking did not have any noticeable effect on shoaling behaviour. Each group was housed separately under identical conditions as outlined in experiment 1.

After a 1-month separation, two familiar fish and two unfamiliar fish (one from each tank of seven fish) were selected at random and placed into a test tank. The test tank measured 90 × 35 cm and the water depth was maintained at 25 cm. A video camera and light were mounted overhead as with experiment 1. Following a 15 min settling period the locations of all four fish were recorded every 30 s for 15 min. Values for depth could not be obtained using a single overhead camera and it was assumed that differences in depth were negligible given the tendency of fish to occupy the centre of the water column. After 15 min a realistic predator model of a mouth almighty (*Glossamia aprion*) (standard length 20 cm, see Brown and Warburton 1997 for details) was gently lowered into the tank via a remote pulley system. Mouth almighty is a widespread and common predator of rainbowfish in the North Johnstone River. The location of the rainbowfish was then monitored for a further 15 min. The mean number of times that a familiar or unfamiliar fish was the nearest neighbour of the familiar fish was calculated from video footage. These data were then used to calculate the mean proportion of time the familiar fish spent as the nearest neighbour of each of the other fish. Nearest neighbor distances provide us with an estimate of which individuals the fish prefer to be closest to. The protocol was replicated seven times. The data were arc-sin transformed and the differences in preference between control and predator periods were examined using a repeated measures ANOVA. Preference for shoaling with familiar individuals was analysed by comparison to the expected result using a repeated measures ANOVA. It was expected that if familiar fish chose their nearest neighbour at random, they would spend 33% of their time with a familiar individual.

Results

Experiment 1: binary choice

As indicated in the Materials and methods section, 9 out of the 16 fish tested satisfied the choice criterion. Many of the fish that failed the criterion simply moved to one end of the tank and stayed there for the remainder of the trial. Those fish that did satisfy the criterion spent, on average, 69% of their time in the zone closest to fish from the same location (Fig. 2), representing a significant preference for familiar fish ($t = 2.448$, $df = 8$, $P = 0.02$) and a significant deviation from a random distribution ($df = 1$, $F = 6.814$, $P = 0.019$). There was no correlation between fish size and the amount of time spent close to the familiar fish ($R^2 = 0.031$, $n = 9$, $P = 0.649$).
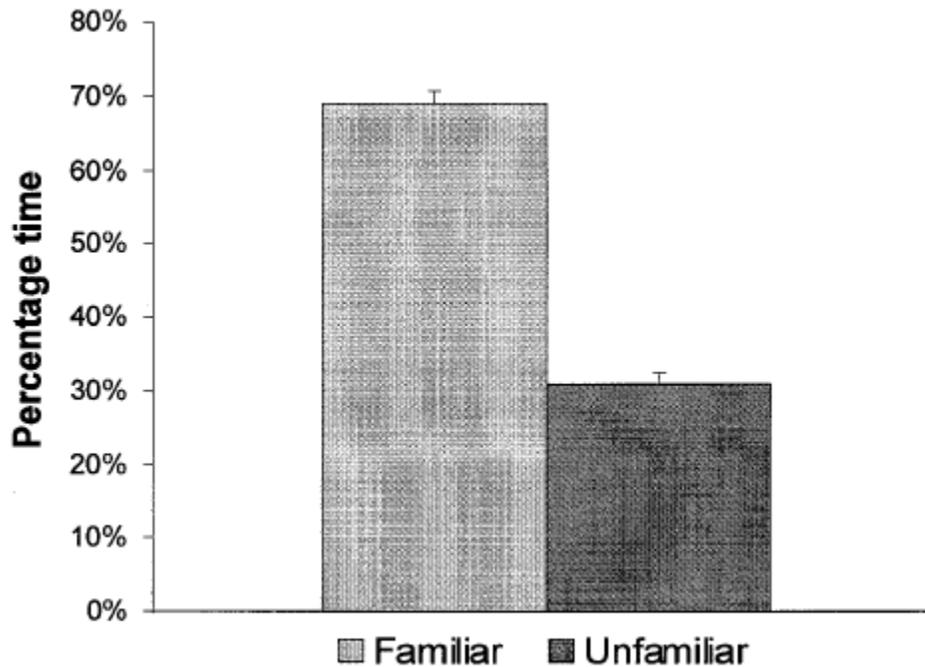

Fig. 2. Experiment 1. The mean percentage of time (±SE) the choosing individual spent in the zones closest to the familiar and unfamiliar shoals. The choosing females spent significantly more time in the zone closest to the shoal containing familiar individuals

Experiment 2: free range

During the predator-free period the all of the fish spent the majority of the time within 5–6 body lengths of one another. They rarely spent time on their own and together they acted as a loose shoal. When the predator was introduced the fish formed a relatively tight school and initially spent a large proportion of their time at the end of the tank furthermost from the model. After some time they began to approach the model, typically as a single school. The behavior observed was typical of that shown by most predator-experienced rainbowfish towards predator models (see Brown and Warburton 1997, 1999). Although the general behaviour of the fish changed, there was no significant difference between the control and predator periods in the proportion of time familiar fish spent closest to one another ($F = 0.056$, $n = 7$, $df = 1$, $P = 0.944$). Data for the two periods were then compared to the expected result to test for a significant

preference for familiar individuals. Familiar fish spent 48% of their time closest to one another, which differs significantly from the expected value of 33% ($F = 5.611$, $df = 1$, $P = 0.036$) (Fig. 3).
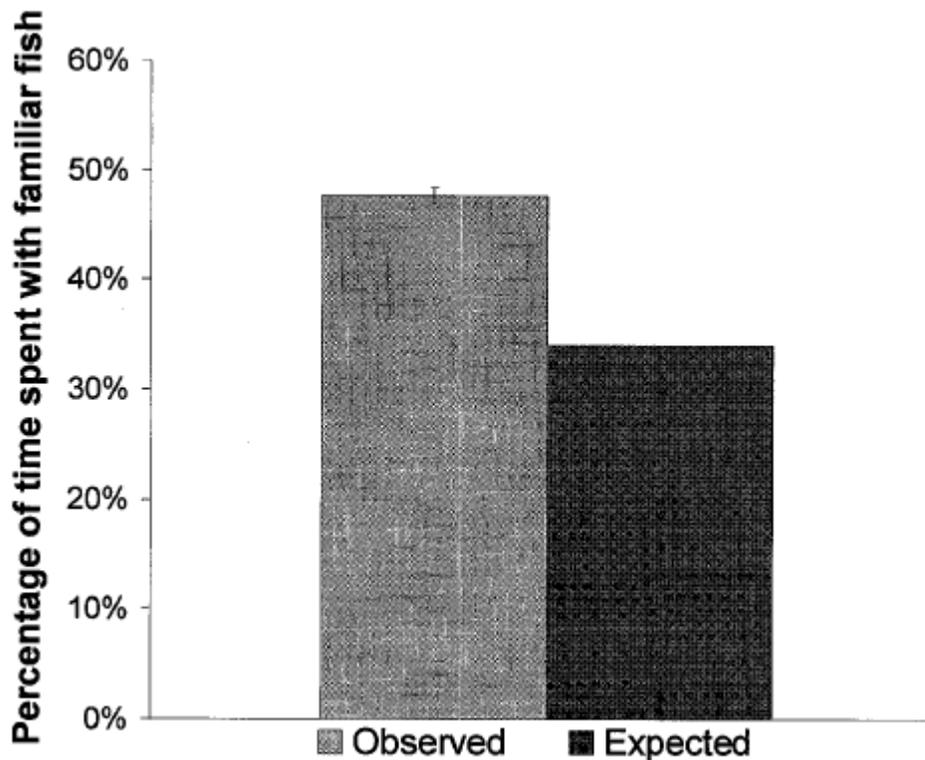

Fig. 3. Experiment 2. The mean percentage of counts (±SE) when familiar fish were nearest neighbours. Counts are lumped for the control and predator present periods. Familiar individuals were the nearest neighbours significantly more often than expected by chance

Discussion

It is clear from this study that rainbowfish, like other similar sized fishes from America and Europe, show strong preferences for shoaling with familiar individuals. However, this preference did not increase under the threat of predation as predicted. Data for the exact distances between individuals would perhaps provide a clearer picture of how close the fish were to one another. It may be that the distance between the familiar fish decreased when the predator was introduced. Further analyses are required to determine if this was the case. Nevertheless this does not alter the fact that the preference for remaining closest to familiar individuals did not change with the introduction of the model predator. Individual recognition has been demonstrated in a number of studies conducted on fish (Myerburg and Riggio 1985; Brown and Colgan 1986; Van Havre and FitzGerald 1988; Miklosi et al. 1992; Brown and Smith 1994) and could potentially allow a fish to associate certain individuals with certain tasks based on prior experience. Shoals of fish often disband at night and reform at dawn (e.g. Helfman 1981) and schools are often made up of the same individuals day after day (McFarland and Hillis 1982; Helfman 1984). Familiarity with shoal mates may be one of the benefits of repeatedly shoaling with the same individuals (see Chivers et al. 1995).

The fish used in experiment 2 were from predator sympatric environments and, contrary to expectations, their preference for familiar individuals did not increase with the introduction of a predator. Similarly, Griffiths (1997) found no difference in the amount of time European minnows spent shoaling with familiar individuals under increased threat from a predator model in a semi-natural flume. Helfman (1984) suggests that populations that suffer from high predation pressure are more likely to show higher levels of school fidelity. When faced with a predator, knowing how shoal mates are likely to react has obvious benefits. For example, fish prefer to inspect predators in the company of individuals who are known to be less likely to defect during an inspection visit (Milinski et al. 1990a, b; Dugatkin and Alfieri 1991). It could be that the rainbowfish tested in experiment 2 and the population of minnows tested by Griffiths (1997) showed risk hypersensitivity (Helfman and Winkelman 1997), that is, they remain in relatively close contact with familiar individuals at all times, irrespective of the level of risk. This latter hypothesis is not unexpected given the high level of predation pressure faced by the populations of fish tested so far. In future it would be interesting to compare populations originating from areas with differing levels of predation pressure. Indeed, this was the original aim of the first experiment, however, most of the predator naïve fish failed to pass the stringent choice criterion. While Chivers et al. (1995) clearly demonstrated that schools comprising familiar fish show more effective antipredator behaviours than schools comprising unfamiliar individuals, the data from the current study suggest there may be benefits for shoaling with familiar individuals other than those associated with predator avoidance such as improved foraging efficiency.

Could familiarity provide a mechanism for kin recognition? FitzGerald and Morrissette (1992) found that stickleback fry chose to shoal with kin rather than non-kin when confronted by a predator (but see Peuhkuri and Seppa 1998). However, FitzGerald and Morrissette (1992) could not rule out the possibility that fry had learned to recognize one another early in development through olfactory cues (see also Warburton and Lees 1996 for guppies). In many cases it may be possible to dispense with the notion that kin recognition involves some kind of unique recognition system, since it is likely that familiarity could just as easily be invoked (Griffiths and Magurran 1999). Familiarity may provide the most parsimonious model to explain observations of non-random associations forming within shoals (Magurran et al. 1994). Nevertheless, a recent study by Arnold (2000) found that lake Eacham rainbowfish (*M. eachamensis*) could recognise unfamiliar full siblings and even half siblings. However, in the absence of visual cues the preference to shoal with related individuals broke down. This is unusual since previous studies, primarily involving salmonids, have suggested that kin recognition is probably mediated through pheromones (or other chemicals in the urine) that may be indicative of genotype (for example MHC; Olsen et al. 1998).

Female rainbowfish resemble one another very closely. Since only females were used during these experiments, the data from this study and that of Arnold (2000) suggest that rainbowfish must rely on very subtle behavioural or morphological cues to discriminate between individuals. Visual cues are also be used by female guppies, which appear to be equally similar to one another, to recognise individuals (Dugatkin and Alfieri 1991; Warburton and Lees 1996). Such visual cues are also likely to be involved in the development of dominance hierarchies (Barnard and Burk 1979) and the recognition of predators (Brown and Warburton 1997). However, we cannot rule out the importance of chemical recognition particularly in environments where water clarity is poor (see Olsen et al. 1998).

The study of familiarity is relatively new and a number of opportunities present themselves for further study. It is unknown, for example, how long it takes for familiarity to build up between individuals in a group of rainbowfish or how long it is maintained, particularly in the wild. Griffiths and Magurran (1997b) found that familiarity takes around 12 days to establish in guppies. This figure, however, is likely to vary between species and may be population and context dependent, although 12–14 days seems consistent with the data obtained from fathead minnows (Brown and Smith 1994). In the second experiment

described herein the fish were all collected from the one site and the unfamiliar fish were isolated for 1 month. Evidently this amount of time is sufficient for familiarity to break down. It is assumed that rainbowfish, like many other similar sized fish, remain within a single pool for the majority of their lifetimes. Within that pool several large schools of fish can be found at any point in time, but individuals may move between groups. A level of familiarity may be maintained between many individuals within a large pool if fish are constantly receiving punctuated reinforcement as they move between shoals and interact with different individuals. However, there must be limits to a fish's ability to recognise other conspecifics. At what point does familiarity break down as group size increases? Griffiths and Magurran (1997a) found that the tendency for female guppies to school with familiar fish decreases as group size increases. It may well be that the optimal number of individuals essential for familiarity to occur may play a role in determining the size of shoals observed in the wild.

It would be interesting to investigate how animals in dynamic environments use familiarity. Do animals associate with certain individuals for certain tasks? Fish are capable of associating individuals with the probability that they will continue to aid in the inspection of a predator rather than defecting and lagging behind (Milinski et al. 1990a, b; Dugatkin and Alfieri 1991). Furthermore, hungry fish can recognise and preferentially associate with poor foragers, thus providing a foraging benefit to fish that associate with familiar conspecifics (Van Havre and FitzGerald 1988; Metcalf and Thomson 1995). I would predict, therefore, that familiarity provides a mechanism that allows the dynamic selection of shoaling partners, enabling fish to shoal with different individuals as their internal state and external circumstances dictate.

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