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Predator recognition and anti-predator responses in the rainbowfish *Melanotaenia eachamensis*

Abstract Predator evasion behaviour patterns of three populations of rainbowfish (*Melanotaenia eachamensis*) were compared. The populations differed in the level of complexity of their natural habitats and the type and extent of predation. The predator recognition abilities of fish were assessed by exposing them to models differing in their degree of predator realism. The availability of vegetated cover and the location of the models with respect to cover were manipulated. Fish from Lake Tinaroo, a relatively open habitat containing numerous predators, showed strong changes in elective group size (EGS) in response to the different models but did not rely on cover as a place of refuge. In contrast, Dirran Creek fish originate from a small, fast-flowing, structurally complex stream lacking predatory fish species, and they showed little ability to distinguish between the different models and responded to threat by spending longer in vegetated areas. Members of the Lake Eacham captive stock increased their EGS in response to models representing low threat and with more threatening models increased the amount of time spent in vegetated regions of the arena. The contrasting reactions to predatory threat displayed by these populations highlights the need to use a number of different response indices when comparing the anti-predator responses of different fish populations. These data suggest that the level of habitat complexity as well as prior predator experience influence anti-predator responses of different fish populations.

Key words Rainbowfish · *Melantaenidae* · Predators · Recognition · Habitat complexity

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Introduction

In previous studies (e.g. Magurran and Girling 1986) it has been assumed that grouping tendencies vary with predation intensity, but few workers have considered how the structure of the natural habitat might shape the mode of response to predation. Depending on habitat structure, predator recognition and response in populations of fish differ between different geographical locations. Predator recognition is shaped by the predation history of a population, including individual experiences. Hence, it is not surprising to find differences in the recognition of, and response to, predators between local populations of a given species (Curio 1976; Magurran 1986; Magurran and Seghers 1990a, b). Typically it has been shown that predator-sympatric populations are better able to recognise and respond to predators than are predator-allopatric populations (Magurran 1986). However, we hypothesise that the modes of anti-predator response displayed by fish (e.g. schooling or hiding) are also highly dependent on the degree of habitat complexity in their natural habitats. Populations from habitats with high levels of complexity are more likely to rely on taking refuge or crypsis to avoid predation, whereas populations from largely open waters are more likely to rely on schooling (Everett and Ruiz 1993; Pitcher 1993). Schooling relies on the rapid transfer of information between individuals within a shoal, a process which breaks down in structurally complex habitats. Therefore, as habitat complexity increases, the effectiveness of schooling should decrease.

Rainbowfish (Family Melanotaenidae) are confined to Australia and New Guinea and number some 50 species. Rainbowfish are locally abundant in streams, lakes, dams and swamps where they are an important source of prey for larger fish species (Merrick and Schmida 1984). *Melanotaenia eachamensis* (the Lake Eacham rainbowfish) is a pelagic species that feeds during the day on aquatic and terrestrial insects. At

night they may float motionlessly near the surface or around coarse woody debris. Their life expectancy in the wild is unknown although in captivity they may live for up to 15 years and grow to 100 mm in length.

The Lake Eacham rainbowfish is listed as endangered and has a restricted range, possibly consisting of as few as three small isolated populations. Using the Lake Eacham rainbowfish as a model species, we tested the prediction that rainbowfish from areas of high predatory threat but low cover availability should respond to threat by increasing group size rather than by taking refuge in vegetation. We did this by measuring elective group size and cover use in fish from two wild populations with contrasting predator/habitat-complexity characteristics (high/low and low/high respectively). Further insight into the relative importance of these two parameters was obtained from a third population from a low predator/low complexity environment. In addition, to assess the reactions of fish to different levels of predatory threat we exposed them to several model fish predators differing in their degree of realism and examined the response of fish to contrasting model-habitat manipulations.

The specific hypotheses tested were therefore:

1. Group size and cover use vary between populations in relation to habitat complexity.
2. Group size and cover use are affected by the perceived level of predatory threat.

Methods

Rainbowfish were collected from Lake Tinaroo (17°15′S 145°30′E), a large open lake almost completely devoid of refuge opportunities. The Tinaroo population lives sympatrically with numerous predatory fish species, including mouth almighty (*Glossamia aprion*) and barramundi (*Lates calcifer*). A second population was obtained from a small headwater stream, Dirran Creek (17°28′S 145°33′E), which is dominated by complex structures such as submerged and emergent aquatic vegetation, intrusive terrestrial vegetation (grass, tree roots, overhanging branches) and a bouldery substrate. Dirran Creek lacks large fish predators. A third captive population of Lake Eacham rainbowfish was obtained from James Cook University. This population has been held in captivity for 15 years since the extinction of *M. eachamensis* from Lake Eacham (17°19′S, 145°38′E). The captive population has had little experience of predators, except for crayfish, during its period in captivity. Prior to this Lake Eacham was devoid of piscivorous fish species until their introduction heralded the extinction of rainbowfish in the lake. No *M. eachamensis* populations in high predation/high habitat complexity environments have yet been found. Fish from the three populations vary little in general morphology. The standard length of the Dirran Creek fish tended to be smaller by a few centimeters than either the Tinaroo or Lake Eacham fish, which average around 7 cm standard length.

Approximately 60 fish were captured at Dirran Creek and 50 at Lake Tinaroo by electro-fishing. A stock of 40 Lake Eacham rainbowfish was obtained from James Cook University. All fish were placed in plastic bags, put in polystyrene containers and airfreighted to the University of Queensland.

From numerous pilot studies it became evident that the number of fish in the test groups and the sex ratio of the groups greatly influenced behaviour. As a result group sizes were set at seven fish,

with the same sex ratio in each group (3 females and 4 males). After removing several fish for breeding and allowing for sex ratio limitations, five groups of seven fish were created for the Dirran Creek fish, four groups of seven for the Tinaroo fish, and two groups for the Eacham fish. All groups were separated and placed in isolated storage tanks.

The storage tanks measured $40 \times 20 \times 20$ cm. The water in all tanks had a hardness of 70–100 ppm and the temperature was kept constant at 22 °C. The pH was maintained at around 6.8. All the tanks had a homogenous layer of fine, brown river gravel covering their base. Lighting consisted of natural light (not direct sunlight) and artificial fluorescent lighting. All fish were fed on standard tropical fish flake flood augmented with brine shrimp. They were fed once a day for 5 min or until satiation occurred (whichever occurred first).

The experimental tank consisted of a large, glass fish tank measuring 110×110 and 35 cm high. It was divided into quadrants using gravel to mark out each quadrant. Each quadrant was assigned a letter (A, B, C or D). The water depth was kept constant at 25 cm and the water condition was similar to that of the housing tanks. Lighting was provided by overhead fluorescent globes. A white polystyrene sheet was placed under the tank. The arena was surrounded by two walls, an erected barrier and a curtain. Observations took place through a small hole cut in the curtain which hung 30 cm from the edge of the tank.

In order to quantify shoaling behaviour a measure of shoal cohesion was required. Pitcher (1993) defined elective group size (EGS) as the number of fish in any social group within 4 body lengths of one other which are considered to be behaving together. EGS is distinguished from an artificial group size deliberately created by the experimenter. EGS scores are readily repeatable by different observers (Magurran and Seghers 1990b); however only one observer recorded EGS in this experiment.

Fish are known to respond to threat by either forming tighter schools, or fleeing and finding refuge in complex structures (Seghers 1973; Magurran 1990; Pitcher 1993). We used changes in EGS and the relative time spent in cover as indices of response to a range of model objects.

The objects were placed in the arena prior to the introduction of the fish. Each model was suspended 2 cm above the bottom of the tank by a string attached to an overhead anchor. The following "predator" models were used: (i) a white cylinder 15 cm long and 6 cm diameter; (ii) a white plaster mould of a mouth almighty 15 cm long; (iii) a plaster mould of a mouth almighty realistically painted by an artist and; (iv) a realistically painted mouth almighty model attached to an electronically controlled pulley system designed to simulate predatory stalking movements. The stalk was in a triangular path through a nominated quadrant.

Treatments (see Fig. 1)

Three treatments were conducted:

1. Bare tank with models in one quadrant (Bare)
2. Arena containing artificial submerged aquatic vegetation (SAV) in 1.5 quadrants and the models in a third quadrant (Grass)
3. Arena the same as in 2, but with the models in the fully vegetated quadrant (Ingrass)

The SAV was constructed from strips of green garbage bags tied to a grey plastic mesh and weighted with fishing sinkers. The strips were approximately 0.8 cm wide and were long enough to reach the surface of the water. The appropriate level of habitat complexity (i.e. strand density of SAV) for treatments Grass and Ingrass was determined from pilot studies and set at approximately $50/m^2$. The density had to be low enough to allow the fish to be seen by the observer, but dense enough to provide adequate refuge.

Each group of fish was randomly assigned a shoal number and the treatment order for each shoal was determined by reference to an incomplete latin square arrangement.
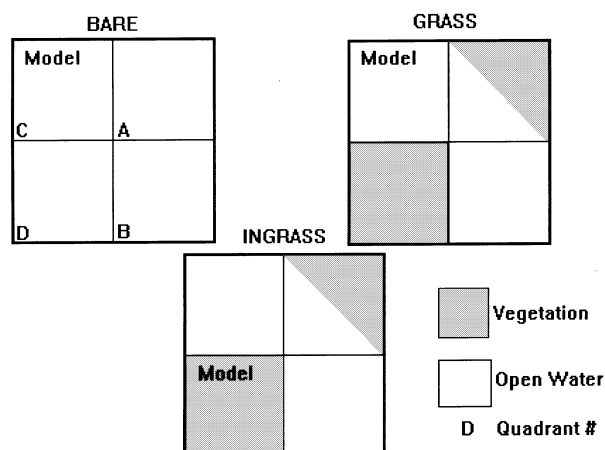
Fig. 1 The layout of the experimental tank for each of the three treatments

Trials

Each treatment comprised seven trials, namely two adjustment (acclimation) trials, a trial with no model, then one trial with each of the four models. Following the two adjustment trials, the trial order for each group of fish and for each treatment was randomised to eliminate any effect of trial order, learning or habituation. The entire experimental protocol was designed in three blocks of seven trials separated by 2 test-free days designed to reduce stress in the fish associated with repeated trials. The order of groups to be tested was randomised and each group was assigned a test time. All groups were tested at the same time each day, tests being separated by 24 h.

For each trial the fish were fed 35 min beforehand and moved into the test arena. They were allowed to settle for 10 min before data recording commenced. Every 30 s for 25 min the size and the position of each shoal was recorded. At the end of each trial the mean EGS and mean percentage time spent in each quadrant was calculated.

Tests to determine normality in the data revealed that three outliers were skewing the data set. Two of the outliers resulted from a test when a fish from Tinaroo group 2 leapt out of the bucket while being transferred from the holding tank to the experimental arena. The fish landed heavily on the floor and showed signs of stress when placed back in the water. The results from this, and the following trial, showed extraordinarily high EGSs. The third outlier occurred again when Tinaroo group 2 was in the test arena. During the trial the erected barrier fell and landed heavily against the tank causing the fish to be startled for most of the trial.

After the removal of the three outliers, skewness and kurtosis tests indicated that the data were distributed normally. We conducted a general linear model analysis on both the location and EGS data. A multifactorial, repeated measures ANOVA with interactions was conducted using treatment, trial, population and group number as variables.

A trend analysis between EGS and successive trial-days was conducted to determine the effects of habituation displayed by each population. All statistics were performed using the SAS system.

Results

Elective group size

The ANOVA for mean EGS over the entire experiment revealed no significant difference in EGS between the populations (Table 1). However, the result was marginal ($P = 0.074$) and power analysis (Cohen 1988; Faul and Erdfelder 1992) indicated that a power of 0.7 would have been achieved in a one-way ANOVA of EGS if the number of groups of captive Eacham fish was raised from two to five, to match the level of replication for the other populations. Since the Dirran Creek and the Lake Eacham populations showed the greatest divergence in mean EGS (1.953 and 2.368 respectively) and the lowest standard deviation (0.248 and 0.247 respectively), it is likely that non-significance was strongly influenced by low replication among the Eacham fish. The Tinaroo population had a mean EGS of 2.349 and a standard deviation of 0.258.

There was no significant treatment effect, indicating that the presence or absence of SAV made no difference to mean EGS. However, a highly significant effect of model realism was evident: multiple range comparisons revealed significantly higher EGSs with the moving realistic model than other model treatments (Fig. 2). Compared to the other two populations, the Dirran Creek fish showed poorer ability to distinguish the stationary realistic models and the cylinder. However, the overall population-model interaction was not significant (Table 1).

A significant group × treatment interaction indicated that the responses of the experimental groups varied depending on the presence or absence of SAV or the location of the model. Significant group differences were probably due to consistent individual variation.

In all groups habituation was evidenced by a significant decrease in EGS over repeated exposures to models in the test tank during the experimental time period (i.e. 25 days). The Dirran Creek population maintained the decrease in EGS over the first 16 days. In contrast the remaining two populations showed a decrease over only the first 7 days (Fig. 3).

Table 1 The results of the multifactorial ANOVA using a general linear models procedure (SAS) on the dependent variable mean elective group size (EGS). Note the significant group, model realism and day(habituation) effects (*Grp* group, *Pop* population, *Trt* treatment)

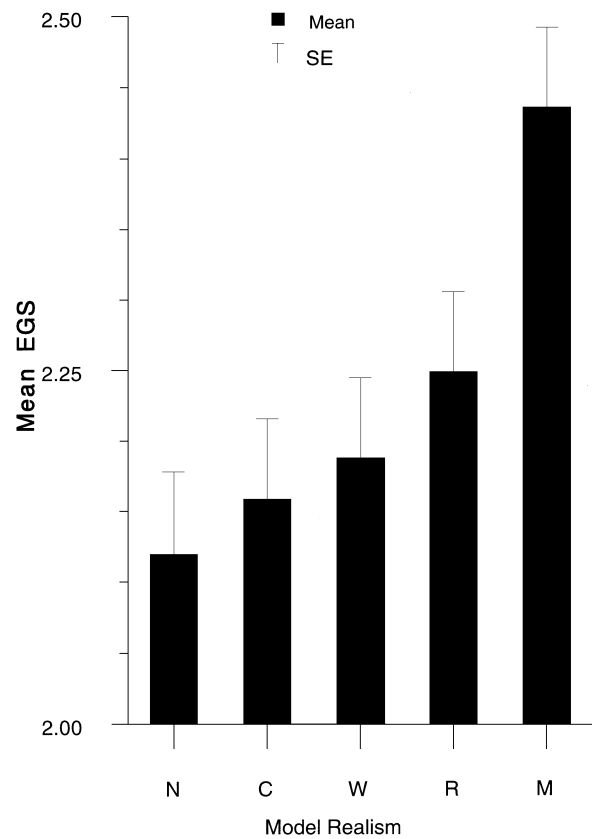| Source	df	F	P
Grp (Pop)	8	10.00	< 0.001
Grp × Trt (Pop)	16	3.86	< 0.001
Model	4	4.69	0.002
Pop × Model	8	0.55	0.81
Trt × Model	8	1.86	0.076
Pop × Trt × Model	16	1.43	0.14
Day	1	6.96	0.01
Tests of Hypotheses using the type I MS for Grp (Pop) as an error term			
Pop	2	3.367	0.074
Tests of Hypotheses using the Type I MS for Grp × Trt (Pop) as an error term			
Trt	2	0.38	0.68
Pop × Trt	4	0.94	0.46

Fig. 2 The effect of increasing model realism of elective group size (combined data for all populations; *N* no model, *C* white cylinder, *W* white predator model, *R* realistically painted predator model, *M* moving realistically painted predator model)

Fig. 3 Changes in elective group size resulting from habituation over the 25-day experiment

Use of cover

A significant population effect revealed that fish from different locations utilised the available cover to varying degrees (Table 2). Dirran Creek fish, from a relatively complex environment, spent 49.2% of their time in cover while Eacham fish spent 37.3% and Tinaroo fish 18.5%. A fish moving in a random fashion would be expected to spend 37.5% of its time in cover in line with the relative area of SAV (Fig. 4). Multiple range testing revealed that the differences between all three populations were significant ($P < 0.0297$).

Differences between the three treatments (Bare, Grass, Ingrass) did not significantly affect the overall use of cover (Table 2). However, a further ANOVA (with the same model structure as in Table 2) revealed that treatment did affect the time spent in the non-vegetated quadrant C, the open habitat Tinaroo fish spending more time in clear areas when cover was introduced (Population × Treatment interaction: $F = 4.049$; $P = 0.018$; $df = 4$). In contrast, the Dirran Creek and captive Eacham fish prefer cover areas, even when the predator models were present in the same vegetated quadrants (Fig. 5).
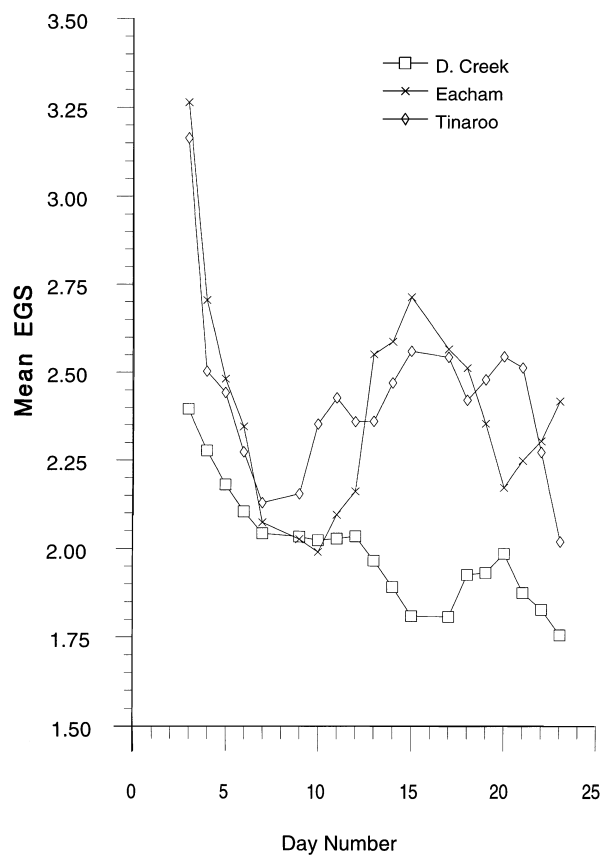
Combined response

Figures 6 and 7 display the combined response of all three populations for the Grass and Ingrass treatments respectively. The Tinaroo fish clearly respond to a threat in the EGS plane whereas the other populations respond more equally in the two planes. It can be seen that the

Table 2 The results of the multifactorial ANOVA using a general linear models procedure (SAS) on the dependent variable % time spent in cover. Note the significant group and population effects

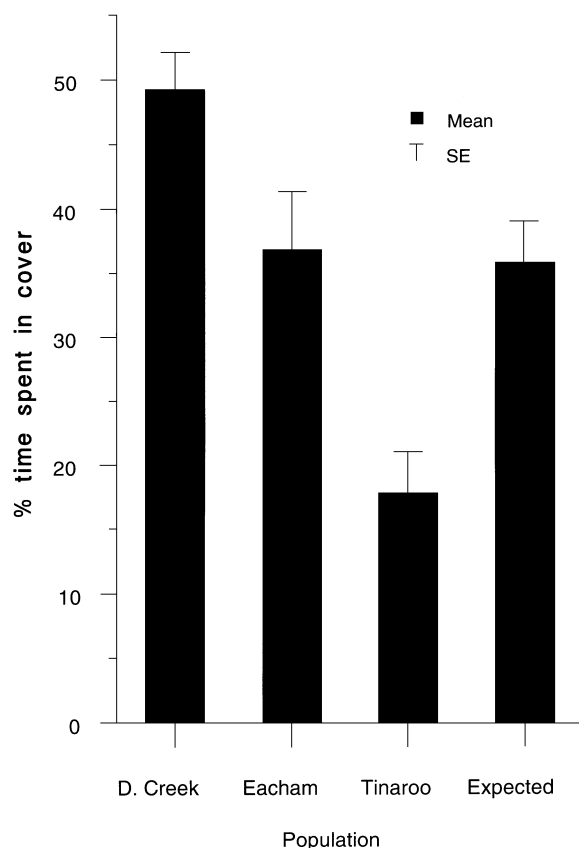| Source	df	F	P
Grp (Pop)	8	6.13	<0.001
Grp × Trt (Pop)	8	8.23	<0.001
Model	4	0.50	0.74
Pop × Model	8	0.73	0.67
Trt × Model	4	0.38	0.82
Pop × Trt × Model	8	0.92	0.50
Tests of Hypotheses using the type I MS for Grp (Pop) as an error term			
Pop	2	34.61	0.001
Tests of Hypotheses using the Type I MS for Grp × Trt(Pop) as an error term			
Trt	1	0.47	0.51
Pop × Trt	2	0.23	0.80

Fig. 4 The percentage time spent in cover (i.e., quadrants containing artificial submerged aquatic vegetation) throughout the experiment. The *expected* column represents the time a randomly moving fish would have spent in cover
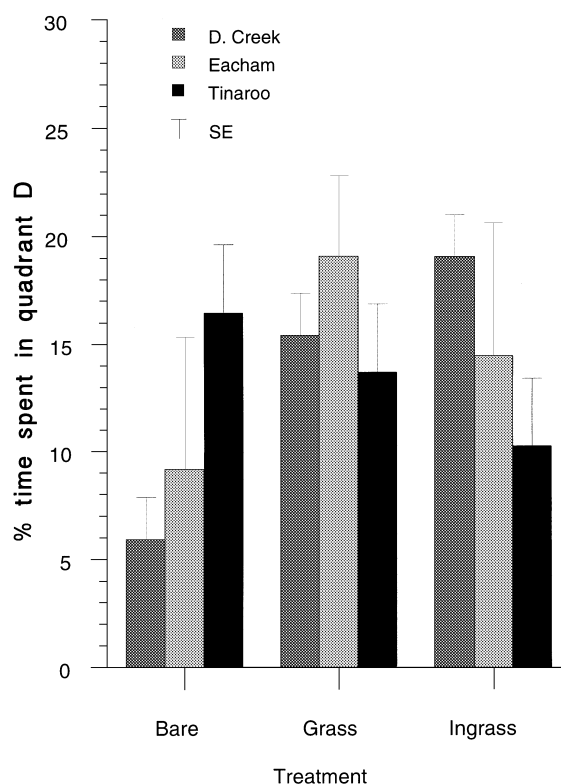

Fig. 5 The percentage time spent in quadrant D for the treatments Bare, Grass and Ingrass. Artificial vegetation was added to this quadrant for the Grass and Ingrass treatments. Predator models were present in the Ingrass treatment

Dirran Creek fish response differs from the Eacham fish by maintaining lower EGS's and spending greater amounts of time in cover. Both the Tinaroo and Eacham responses were amplified when the model was moved into cover.

Discussion

Anti-predator responses: the importance of habitat complexity

We hypothesised that the manner in which fish from the different populations respond to threat may differ primarily because of different levels of structural complexity in their natural habitats. The results support this prediction, but while there was significant between-population variation in cover use, there was only weak variation in group size. The contrast between these two models of response suggests that habitat variation is the dominant factor shaping population-specific strategies of predator evasion. Parrish (1992) emphasised that in small-scale systems (e.g. headwater streams) schooling prey have the option to break ranks and rely on shelter

for refuge, but this option is not available in more "open" habitats. Pitcher (1993) added that in open water, fish are more commonly found in larger shoals because they lack refuge opportunities. These hypotheses are supported by the data from this study. The general response to threat displayed by the Tinaroo fish was to head for open water and form larger schools. Even when these fish were given the choice of utilising complex structure to hide in, they still actively avoided the structure and relied on schooling. The Lake Tinaroo habitat is a vast open water body which provides few physical structures for refuge. Some of the small bays have a little grass and the occasional water lily in the water, but the amount of physical structure is unlikely to facilitate predator avoidance.

In contrast to the Tinaroo population, the Dirran Creek fish responded to increasing threat by increasing their EGS slightly and increasing the amount of time spent in cover. Dirran Creek is a narrow, highly structured complex habitat. Even when the structure contained the threat during our experiments, the Dirran Creek fish did not move out of the structure nor did they rely on schooling to avoid the threat. Thus when making comparisons of anti-predator response between populations, the use of EGS as a response to threat may be misleading since schooling represents just one mode of response to threat displayed by fish populations. Fur-
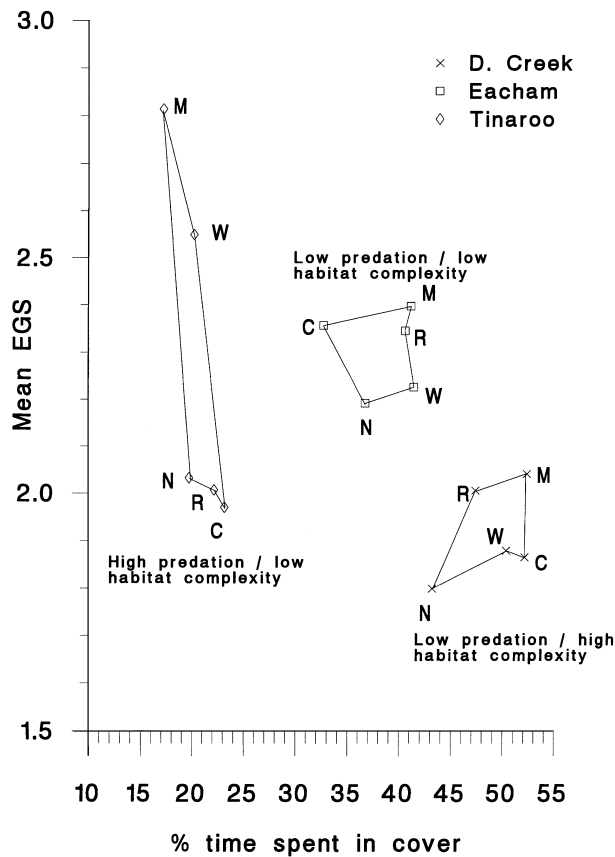
Fig. 6 The combined response (elective group size and cover use) for each population during the Grass treatment. Model symbols as in Fig. 2

Fig. 7 The combined response (elective group size and cover use) for each population during the Ingrass treatment. Model symbols as in Fig. 2

thermore schooling is not likely to be the primary response displayed by fish populations in small complex systems such as headwater streams.

The captive bred Lake Eacham fish responded to realistic predator by utilising complex structures while maintaining high EGS. Unlike the Tinaroo population, the Lake Eacham fish did not actively avoid complex patches. It seems that the Lake Eacham rainbowfish, in its natural habitat, may have relied on structure (e.g. coarse woody debris and submerged aquatic vegetation), as well as schooling, as an integral part of its anti-predator response. It appears that schooling and the use of complex structures are not necessarily exclusive anti-predator alternatives.

Predator recognition: identifying threat

Our second prediction, that the strength of anti-predator response should be related to the level of perceived threat (i.e., model realism), was also supported. However, this relationship was true for only one of the two response variables, namely group size. In this respect, the effect of model realism contrasted with the effect of population, where cover use but not group size varied significantly. This apparent complementarity may indi-
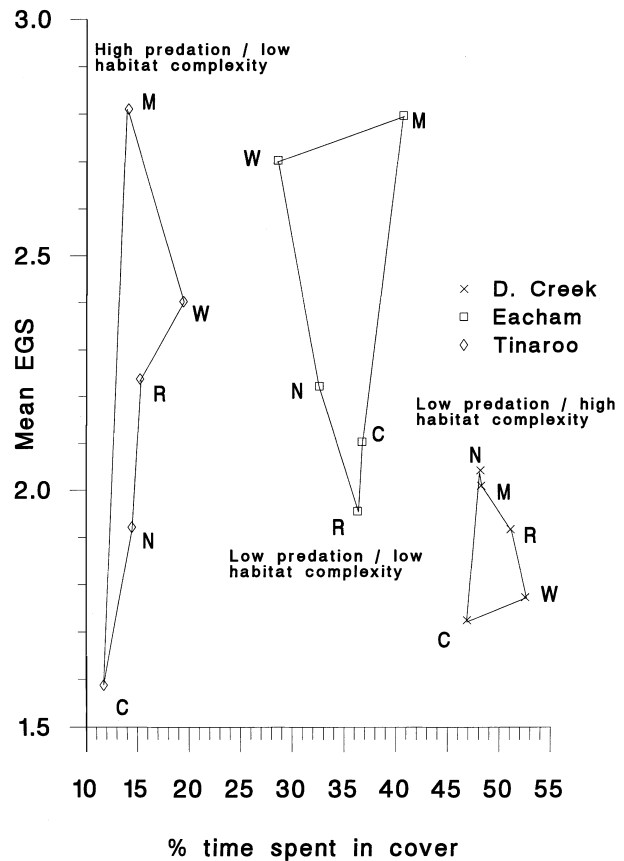
cate that rainbowfish have evolved habitat-specific behavioural strategies which match predator avoidance and resource use to cover availability, while also retaining a generalised ability to make short-term adjustments to group size depending on the level of immediate threat. This interpretation is supported by the fact that these immediate threat-related adjustments to group size did not vary significantly across the three populations.

There appear to be a number of generalised cues which fish universally associate with threat and more subtle cues which may be associated with specific threats, such as particular predator species (Karplus et al. 1982; Guthrie 1983). It is likely that the responses to more general cues are inherited, while species specific cues are learnt through individual experience (Edge et al. 1993; FitzGibbon 1994).

Subtle cues involving particular predator species are likely to be population-specific. Compared with minnows from predator-allopatric populations, predator-sympatric populations of minnows showed a relatively early response to a cylinder, inspected plain models of pike more frequently and skittered most to a realistically marked and shaped pike model (Magurran and Girling 1986). Significant population-specific differenced in responses to models could not be demonstrated in this

study, but it may be relevant that the Dirran Creek fish, from a habitat lacking predatory fish, showed little difference in response to the stationary realistic models and the cylinder.

The general reaction to increasing predator realism displayed by rainbowfish in this study showed a significant change in behaviour in reaction to the moving realistically painted predator when compared to the other stationary models. Other authors have found that live predators provide better threat stimuli than moving models, which in turn are more threatening than stationary objects (Godin and Crossman 1994). Pitcher et al. (1986) stated that a moving object poses a greater threat than a stationary one because a predator in motion in more likely to attack. Movement and size seem to be generalised cues to which many species respond.

Although the Eacham population had been captive for some 15 years, Eacham fish showed a strong anti-predator response, particularly when the models were partly obscured from view. One explanation for this observation is that lack of parental care and the possible effects of cannibalism could have favoured the acquisition of innate anti-predator responses and may also provide the fry with "predator training" (Tulley and Huntingford 1987; Benzie 1965, cited in Dill 1974; Goodey and Liley 1986). The captive stock used in these experiments were derived from relatively small artificial enclosures containing a large number of fish. In such an environment young fry are subject to intense predation from larger individuals. Other species of fish have shown similar "enhanced" predator reactions when predators are obscured from view (Eklov and Persson 1996). It is suggested that when a predator is not in plain view, discovering the motives of the predator is far more difficult for the prey. Therefore, increases in inspection behaviour and flight responses are observed.

In the present experiments, it is likely that fish assessed threat intensity both in terms of the realism of predator models and in terms of the location of the models with respect to cover. The location of the simulated predator relative to cover did not influence the overall cover use. However, further analysis revealed that the model/cover treatment did effect the time spent in the open quadrant (C). Thus, evidence for subtle interactions between the effects of predator threat and habitat structure emerges when different indices are compared.

Habitat complexity and the co-existence of predators and prey

The behaviours of the Dirran Creek and Eacham fish provided support for the hypothesis that the presence of complex patches enhances the coexistence of predators and prey within patches (Murdoch and Oaten 1975; Fraser and Cerri 1982; Sih 1987). When SAV was added, fish from both these populations increased the amount of time spent in the main vegetated quadrant, even when the models were placed into the same quadrant. So complex structures containing predators were still more attractive than bare regions.

Although the Dirran Creek fish did break up into small groups or singletons, they still preferred to remain in cover even when they were in close proximity to danger. That is to say, they perceived that the costs associated with leaving the complex habitat and entering open water outweighed those associated with the close proximity to the predator. Fraser and Cerri (1982) found that prey minnows were less likely to leave a patch with predators present, if that patch was structurally complex (see also Fraser and Sise 1980; Sogard and Bori 1993). However, the Dirran creek fish had an alternative complex patch to go into which did not contain a model. Why then, did the fish choose to enter the patch closest to the models? The most plausible explanation is that it enabled them to get up-to-date information about the predator's whereabouts and "intentions" (Magurran and Seghers 1994). In order to inspect the model the fish frequently darted from the small "safe" patch on the far side of the tank into the patch containing the model. Once in the patch with the model, they spent a short while fixating on the model then returned to the safe patch. When some of the less realistic models were present in the arena the fish not only approached the model but also probed it. Some fish appeared to test the response of the model by approaching side-on (attack cone avoidance; Magurran and Seghers 1990b) and darting across the front of the model. They quickly turned to see if the object had responded. If no response or fright occurred then the fish would either start to ignore the object (i.e. habituate) or even take refuge under it.

Habituation

Different rates of habituation between populations have been linked to differences in the levels of predation pressure. Magurran and Girling (1986) believed that in the presence of high or fluctuating predation pressure, habituation following the first encounter would be disastrous since a predator may not be hungry on the first encounter and there is no guarantee that its motivational state will be similar on the next encounter.

Predator-sympatric populations have been shown not to habituate on the first few encounters, whereas predator allopatric populations show rapid habituation (up to 30%) following their first encounter (Huntingford and Coulter 1989). Predator-sympatric populations are better able to determine different levels of threat by reference to predator cues and alter their behaviour appropriately (Helfman 1989; Fraser and Huntingford 1986; Cerri 1983). These findings would suggest that the Dirran Creek fish should habituate more readily than those from Lake Tinaroo, a result which was observed in the pattern of declining EGS over the 25-day experiment.

Habituation rates may also reflect fluctuation or instability in the environment. Dirran Creek is a more variable environment than either Lake Tinaroo or Lake Eacham. Variations in flow rates depend on rainfall and all manner of debris, including novel objects, must frequently get washed downstream, so that Dirran Creek fish must be able to adjust relatively rapidly to changing circumstances. Because the Tinaroo and Eacham fish originate from large, structurally stable environments, they have less need for habituation to changing environmental conditions.

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