Adaptive variation in antipredator behaviour in threespine stickleback

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A major aim in behavioural ecology is to understand how natural selection acts on behavioural variants. One way of unravelling the relationship between phenotype and selection is the comparative approach, in which behavioural variants are related to environmental features (Huntingford 1984; Krebs and Davies 1987). If a behavioural trait (for example, the removal of egg shells by parents after young gulls hatch) is regularly associated with a particular environmental factor (for example, risk of predation on chicks), it is likely that the former is an adaptation to the latter (Tinbergen et al. 1962). However, behavioural phenotypes are notoriously labile, so differences among populations may reflect flexible responses of the animals to environmental differences as well as evolved hereditary adaptations. Behavioural differences among populations can only be considered as the result of natural selection if a genetic basis for the behavioural differences can be demonstrated.

The comparative approach can be applied at the level of taxonomic units at the species level and above, or at the level of local populations within species. The latter is particularly valuable for testing adaptive hypotheses because the variance attributable to phylogenetic divergence (Harvey and Mace 1983; Ridley 1983; Lauder 1986) is limited. Regardless of whether interspecific or intraspecific comparisons are employed, it is important to show that the behavioural differences do not simply reflect common ancestry but are likely to be independent adaptations of the groups compared (Bell and Foster page 20 this volume). In this chapter we review the use of population comparisons to investigate the relationship between antipredator behaviour and local regimes of predation among populations of threespine stickleback, Gasterosteus aculeatus. The results suggest that different predation regimes can produce behavioural divergence. In some instances these may have a straightforward genetic basis, but in other cases their developmental origin is more complex, depending on interactions between innate behavioural predispositions and early social experience.

The chapter begins with a general overview of how threespine stickleback respond to predators, and then addresses the causes of variation in this
context. In particular we evaluate the causes of the extensive, seemingly adaptive, differentiation of antipredator behaviour among populations. Finally we describe the early ontogeny of antipredator behaviour and the proximate factors that affect its expression in adults.

ANTIPREDATOR BEHAVIOUR OF THE THREESPIKE STICKLEBACK

In spite of their protective armour, which includes the spines for which they are named, threespine stickleback fall prey to many kinds of piscivorous animals, among them mammals, birds, reptiles, fish, and insects (Reimchen Table 9.1 this volume). Although often effective (Hoogland et al. 1957), armour is a last line of defence, employed only after behavioural defences have failed.

Risk of predation can be reduced if potential prey either avoid encounters with predators or actively evade predators once encountered (the primary and secondary defences, respectively, of Edmunds 1974). Both kinds of defence are seen in stickleback. Fraser and Huntingford (1986) have shown that in the laboratory, stickleback (non-breeding adults) avoid feeding patches in which predatory fish (brown trout, Salmo trutta) are present. They also reduce the risk of detection by staying in or near aquatic vegetation or other forms of cover. For example, in the presence of a predator (brown trout), adult stickleback restrict their foraging to weed-beds (Ibrahim and Huntingford 1989a). In Crystal Lake, British Columbia, fry remain in or near vegetation until they reach 15 mm SL, a size at which they are no longer eaten by adult conspecifics (Foster et al. 1988). When predatory fish are rare or absent, stickleback avoid vegetation, and thus distance themselves from potential predation by dragonfly naiads that perch on vegetation (Foster et al. 1988; Fig. 10.1).

Once predators have been encountered, several evasive manoeuvres are possible. Threespine stickleback may form large schools (e.g. Wootton 1976; Bentzen and McPhail 1984; Foster et al. 1988), especially when feeding on plankton in open water. Small prey fish experience reduced individual risk of predation while schooling (e.g. Neill and Cullen 1974; Pitcher et al. 1983), as do individuals in smaller, less cohesive associations, such as those characteristic of stickleback on the breeding grounds (Neill and Cullen 1974; Pitcher et al. 1983). So stickleback may gain protection from group membership.

Effective evasive manoeuvres are also performed by solitary stickleback. On detecting a potential predator such as a pike, Esox lucius, the immediate response of a stickleback is to stop what it is doing, raise its spines, and fixate on the predator (Hoogland et al. 1957, Benzie 1965). Often, it will then move closer (Huntingford 1976a). This is predator inspection (a term coined by Pitcher et al. 1986 with reference to minnows, Phoxinus
Fig. 10.1 Use of open water, as opposed to vegetation, by (a) medium-sized stickleback fry (11–15 mm SL) and (b) larger fry (21–25 mm) in pools with no predators (control), with potentially cannibalistic adult stickleback, and with dragonfly naiads. Dots represent means from replicates and lines represent group means. Lines below the horizontal axis connect treatments that do not differ significantly (after Foster et al. 1988).

*phoxinus*, during which the stickleback, seemingly acquires the information necessary for assessing predator identity and implicit level of risk, as they are known to do (Foster and Ploch 1990).

If the potential predator is deemed to pose a risk, the stickleback responds with one of a variety of evasive manoeuvres (slow retreat, unpredictable jumps, or rapid swimming to cover). Although there is no detailed
information on this point, choice of response probably depends on some combinations of the species (Foster and Ploch 1990), hunting style (Hoogland et al. 1957), size (Foster and Ploch 1990) and proximity of the predator, its speed of attack, and the availability of cover (Hoogland et al. 1957; Benzie 1965). If cornered, the stickleback locks its spines in a raised position, and the manipulation required to swallow a stickleback that has its spines locked in this way affords it a chance to escape (Hoogland et al. 1957; Reimchen 1983, page 269 this volume). Stickleback that do escape at any point in the encounter may remain frozen or hidden for a period before resuming normal activities.

**VARIATION IN ANTIPREDATOR BEHAVIOUR**

Although all threespine stickleback have the capacity to perform these antipredator responses, the intensity and nature of the responses are extremely variable, even when the fish are exposed to the same kind of predator under standardized conditions (Fig. 10.2). Why do some individuals fail to show any response to a direct attack, others give a weak response followed by rapid resumption of normal behaviour, while still others respond vigorously and remain frozen in cover for many minutes? Some of the variability comes about because the same individual fish responds differently from one occasion to the next when presented with an identical predatory

![Graph](image-url)

**Fig. 10.2** Variability in antipredator responses of non-breeding, adult threespine stickleback. Recovery time is the interval between response to a simulated attack by an avian predator and recovery of normal activity in 5 min tests on 164 different non-breeding adult threespine stickleback (J.E. Tierney, F.A. Huntingford, and D.W.T. Crompton unpubl. data).
stimulus. In contrast to such within-individual effects, another source of variability is the existence of permanent between-individual differences in behavioural phenotype.

**Within-individual variation**

Effects of parasites

Some spectacular changes in the antipredator behaviour of individual stickleback are caused by parasitic infection. There is a large and expanding literature showing that the larval stages of many parasite species effect changes that render their intermediate hosts more vulnerable to predation by the definitive host; such changes potentially increase the parasites' chances of successfully completing their life cycle (see reviews by Milinski 1990; Moore and Gotelli 1990). Sometimes the changes are morphological, but often the parasite interferes with the antipredator responses of the intermediate host.

In threespine stickleback, changes of this kind occur as a result of

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**Fig. 10.3** Effects of parasites on one aspect of the antipredator responses of threespine stickleback. Median duration is the median interval for individuals between first response to a simulated attack by an avian predator and resumption of normal activity (recovery time) in non-breeding adult threespine stickleback. Recovery time is shown in relation to infection with the cestode *Schistocephalus solidus*. Uninfective worms are those weighing less than 50 mg; above this weight, the worms are fully capable of establishment in the definitive host, but below this weight establishment is effectively impossible. The three groups are statistically distinct at \( P < 0.001 \) (\( H = 13.62, N = 51 \)) using a non-parametric ANOVA (Tierney et al. in press).
infection by the tapeworm (Cestoda) *Schistocephalus solidus* (Giles 1983b; see Milinski 1990 for review). During the early stages of infection, before the parasite is sufficiently mature to become established in its definitive host (a bird), various aspects of the responses of infected stickleback to simulated avian attack (including freezing and suppression of normal activity) are enhanced (Fig. 10.3; Tierney et al. in press). Although the following consequences remain to be documented, such a behavioural shift probably reduces the chances that the fish will be captured by a predator, and thus promotes the survival of the parasite.

Once the tapeworm is infective to the definitive host, the behaviour of the stickleback changes so that an attack elicits no more than a weak and short-lived response (Fig. 10.3; Tierney et al. in press). Once again the effect remains to be documented, but in nature this change in behaviour may have the effect of promoting transmission of the tapeworm from the intermediate host to the definitive host. These behavioural changes may be by-products of infection, perhaps caused by enhanced food and oxygen requirements in heavily infected fish (Giles 1987a,b), but may also be the result of a direct change in responsiveness to danger (Milinski 1990). So some of the variability in antipredator behaviour documented in Fig. 10.2 may depend on the acquisition of a parasitic infection and on the developmental stage of the parasite.

Reversible responses to altered environmental conditions

Other intra-individual differences are the result of flexible responses to changes in the balance of advantages and disadvantages of performing antipredator behaviour. Although the advantages of avoiding being eaten are self-evident, the benefits of showing a particular response may vary with circumstances. For example, adult sticklebacks in mixed shoals of *G. aculeatus* and *G. wheatlandi* gain protection from predation, so that individuals within the shoal are less vulnerable, especially if the group is large. Fitzgerald and van Havre (1985) have shown that in such shoals the rate of recovery from disturbance is negatively correlated with group size, suggesting that the fish adjust their behaviour to the protective effect of group membership.

Antipredator responses can also have disadvantageous consequences that may reduce fitness, such as interference with other important activities like feeding or reproducing. For brevity, such disadvantageous consequences are referred to here as the costs of antipredator responses. These costs, and with them the risk that animals are willing to accept in order to perform other essential activities, can change as a result of alterations in internal state and external conditions (e.g. Carlisle 1982; Lima and Dill 1990).

For example, hungry threespine stickleback (non-breeding adults) are willing to accept greater risks of predation in order to feed than are recently
fed individuals (Fraser and Huntingford 1986). The reproductive condition of males also influences their antipredator behaviour. In laboratory aquaria, non-territorial male sticklebacks flee more readily from a hunting pike (a predator at the site from which they were collected) than do those with territories but no young, which in turn flee more readily than those with young (Huntingford 1976b). Similarly, in the field, when confronted with a tethered trout, territorial males with young in their nests are slower to take flight, and hide for shorter periods, than do those without young (Kynard 1978a; see also FitzGerald and van Havre 1985). In some lakes in British Columbia, Canada, territorial males confronted with a large prickly sculpin, Cottus asper, hid for shorter periods and accepted greater risk in attacking the sculpin when they had young in the nest, especially if the young were numerous and/or well developed (i.e. of greater reproductive value; Pressley 1981; but see Foster and Ploch 1990).

Pike, trout, and sculpin are predators of adult stickleback, so that in this case, fleeing probably increases the chance of survival of the individual concerned. As sculpin also feed on young stickleback in the nest, one direct cost of flight by breeding males is potential loss of their brood (Pressley 1981; Foster and Ploch 1990). An additional, indirect cost to breeding males of responding to a predator is interrupted paternal care. When required to defend their territories against other males in the presence of a predator (brown trout), male stickleback with a brood of eggs maintain higher levels of attack towards the intruding conspecific than do those with an empty nest. The highest rates of attack were elicited when males were defending broods acquired early in the season. At the site used in this study, fish from late-hatched broods often fail to breed in the following summer, and few fish survive for more than 14 months; early-hatched broods are therefore more valuable than those acquired later. The parental males themselves die shortly after breeding, and thus the prediction is that they would invest heavily in later broods, as these represent their last opportunity for breeding. A low level of investment in late-hatched broods (which has also been reported both in the laboratory and in the field by Kynard 1978b) is therefore paradoxical, and may represent a relictual behaviour from the perennial condition (Ukegbe and Huntingford 1988). In any event, breeding male stickleback adapt their antipredator responses to the costs of keeping safe, adjusting accepted risk in relation to the presence and value of their brood. This adjustment presumably comes about because the mechanisms that govern the response to a predator are susceptible to internal cues (such as hormonal state) and external cues (such as the presence of young in the nest) that track the reproductive status of the father and the value of the brood.
Between-individual variation

Gender effects
In contrast to parasite-induced behavioural shifts and flexible responses to the changing costs of self-preservation, other differences in antipredator responses reflect permanent differences among individual stickleback. For example, especially during the breeding season, male stickleback show weaker responses than females, both during encounters with a pike and following a simulated attack by a model bird (Giles and Huntingford 1984). The reasons for these gender differences are obscure. In causal terms, they may be the result of shared physiological controls for aggression and predator avoidance in males (Bakker page 349 this volume). In functional terms, the value of ensuring protection to the brood may outweigh the cost of an enhanced predation risk.

Population effects
In a number of species, antipredator behaviour has been shown to covary with predation risk, for example in ground squirrels (Owings and Coss 1977; Towers and Coss 1990), in prairie dogs (Loughry 1988, 1989), in garter snakes (Arnold and Bennett 1984; Herzog and Schwartz 1990), in salamanders (Brodie et al. 1984; Dowdey and Brodie 1989), and in spiders (Riechert and Hedrick 1990). Such relationships have been particularly well studied in small freshwater fishes, which are vulnerable to a range of predators and which often exist in many localized populations exposed to varying predation regimes. For example, guppies, Poecilia reticulata, from sites where predatory fish are abundant show well-developed antipredator responses, including strong schooling (which provides protection against predatory fish), compared with guppies from sites at which predatory fish are rare or absent (Seghers 1974; Magurran and Seghers 1990; Reznick et al. 1990). Guppies that coexist with an invertebrate predator, the freshwater prawn,Macrobrachium crenulatum, are particularly responsive to this predator (Magurran and Seghers 1990). Similarly, various protective responses (including schooling and predator inspection) are well developed in minnows, Phoxinus phoxinus, from a site where pike are abundant compared with those from a site where pike are absent (Magurran 1986, Magurran and Pitcher 1987).

The predation regimes to which threespine stickleback populations are exposed also vary, and this appears to have influenced the evolution of a number of morphological traits (Reimchen Chapter 9 this volume). Is there any evidence that their antipredator behaviour has also diversified? Foster (1988, 1990) found that in populations of threespine stickleback in which cannibalism by groups is common, breeding males perform diversionary displays that distract the attention of potential cannibals from their nest; this behaviour is not shown by males from sites where such
cannibalism does not occur.

The antipredator responses of sticklebacks do not always reflect extant predation regimes. Pressley (1981) demonstrated that male stickleback in Trout Lake, British Columbia, Canada, would inspect and attack a preserved prickly sculpin and adjusted their response to brood value, just as did stickleback sympatric with the sculpin, even though it was absent from Trout Lake. In contrast, in Crystal Lake, British Columbia, male stickleback approached a preserved sculpin directly and rapidly, without adjusting their response to the value of the brood. Absence of any adjustment of protective responses in relation to the status of a brood is probably a derived character, as prickly sculpin are native to shallow marine waters where the ancestral marine form is found (Foster and Ploch 1990). These examples suggest that in stickleback, as in guppies and minnows, population differences in antipredator behaviour may reflect local predation risk. This possibility has been studied most intensively in sticklebacks from a number of sites in the United Kingdom; and the rest of this chapter focuses on these studies.

**VARIATION IN ANTIPREDATOR BEHAVIOUR AMONG UNITED KINGDOM POPULATIONS**

**Boldness and risk of predation**

In an initial survey of 13 populations of freshwater stickleback (Huntingford 1982), sites were classified on the basis of gill netting and stomach content analysis of potential predators into sites with abundant piscivorous fishes

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**Table 10.1** The behaviour patterns with significant loadings on the ‘boldness’ factor identified by multivariate analysis in Huntingford (1982) and shown in Fig. 10.4. This comprised a principal components analysis followed by varimax rotation, using a total of 17 behavioural variables and 145 subjects. Initial analyses were run on the separate populations to confirm that the relationships between variables were consistent before combining data for a single analysis. The boldness factor accounted for 35 per cent of the total variance in the data.

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<tr>
<th>Behaviour patterns with:</th>
<th>Negative loadings</th>
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<tr>
<td>Positive loadings</td>
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<tr>
<td>Time pectoral sculling(^a)</td>
<td>Time hiding in weed</td>
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<td>Time feeding</td>
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<td>Time facing/approaching(^b)</td>
<td>Time continuous swimming(^a)</td>
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<td>Time to resume pectoral sculling</td>
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\(^a\) Pectoral sculling is the mode of swimming typical of undisturbed threespine stickleback, whereas disturbed gickleback typically swim continuously.

\(^b\) Predator inspection loads positively on the boldness factor because only the boldest fish showed any predator inspection towards the live, actively hunting pike.
of any species known to eat stickleback (high-risk sites) and those at which such fishes were rare or absent (low-risk sites). Non-breeding adult stickleback were collected from each site and maintained in the laboratory for at least one month, during which time they were fed the same rations. Their responses to a predatory fish were screened in a standard laboratory test, during which they were given 10 min exposure to a pike that was motivated to stalk but not to strike.

For the purpose of this initial survey, the behaviour of each fish was measured by a single compound score (derived from a principal components analysis) that summarized its 'boldness' during the encounter with the pike (Huntingford 1976a; Table 10.1). The results are unambiguous; wild-caught stickleback from high-risk sites were markedly less bold (i.e. they had better-developed antipredator responses) than those from low-risk sites (Fig. 10.4). Subsequent studies on other populations have confirmed this general conclusion and have also shown that stickleback respond differently to predatory birds in relation to local risk of avian predation (Giles and Huntingford 1984).

**Behavioural differences between a high-risk and a low-risk site**

To characterize more precisely the differences between threespine stickleback from high-risk and low-risk sites, more detailed behavioural studies

![Graph showing differences in multivariate boldness score between high and low predation risk sites.](image)

**Fig. 10.4** Site-specific levels of antipredator responses in non-breeding adult stickleback. Mean values (±1 SE) of a multivariate boldness score (see Table 10.1) are shown for stickleback from 13 sites in the UK (N ≥ 10 fish per site) in which piscivorous fish are abundant (shaded bars) or rare (hatched bars). The population means for low-risk sites fell above the overall mean significantly more often than did those for high-risk sites (P < 0.001, Fisher's exact test; after Huntingford 1982).
were conducted on two populations whose antipredator behaviour had been shown to differ markedly in the previous surveys. One of these, the River Endrick, is part of the Loch Lomond drainage system and contains a variety of predatory fish that are known to prey on stickleback at this site. In addition, piscivorous birds, especially heron, are abundant and are known to take stickleback from this river (Giles and Huntingford 1984). This site was therefore designated a high-risk site. The other site, Inverleith Pond, Edinburgh, is a small pond that has been in existence for several hundred years at least. The pond contains no fish other than stickleback. In the course of extensive sampling, no invertebrate predators of stickleback have been found, and piscivorous birds are rare (although black-headed gulls sometimes roost on the pond). This site was therefore designated a low-risk site.

Differences between wild-caught adults

Rather than using compound scores for comparison of these two populations, each aspect of the stickleback’s reaction to predators was analysed separately. Wild-caught, non-breeding adult stickleback from the two sites were individually videotaped for an 8 min period during which they were exposed to a realistic fibreglass model of a brown trout (Tulley 1985). The model was moved according to a pre-arranged routine that included a

![Graph]

**Fig. 10.5** The frequency of predator inspection by pairs of stickleback from a site without predatory fish (low risk) and from another site in which predatory fish are abundant (high risk) when confronted with a model trout \((N = 30\) pairs for the low-risk site and 50 for the high-risk site, \(G = 19.40, P < 0.001;\) Barrie and Huntingford, unpubl. data).
period when the trout was hidden in the weeds, a period when it moved out of the weeds and remained stationary in open water, and a period when it charged the stickleback at a fixed speed. In a separate study, inspection responses to the model by pairs of fish from the two study sites were recorded (Barrie and Huntingford unpubl. data).

Stickleback from the high-risk site inspected the predator far more often than did those from the low-risk site (Fig. 10.5), and responded by keeping still or freezing rather than by jumping (a less effective response), both to the first movement of the trout (Fig. 10.6(a)) and as an initial response to a direct attack (Fig. 10.6(b)). They subsequently made faster escape responses (median speed = 45 cm s$^{-1}$ compared with 31 cm s$^{-1}$; Mann–Whitney $U = 7$, $N_1 = 7$, $N_2 = 8$, $P < 0.05$). In addition, when escaping, the stickleback from the high-risk site were significantly more likely to move at right angles to the line of attack than were those from the low-risk site (which tended to swim towards the approaching predator) and took longer to resume normal activity following an attack (Huntingford and Wright unpubl. data).

In brief, therefore, as compared with stickleback from a low-risk site, those that are naturally at risk of predation by piscivorous fish stand out as showing greater vigilance, more effective responses to direct attack,

![Diagram](image)

**Fig. 10.6** The responses of stickleback from a site without predatory fish (low risk) and from another site in which predatory fish are abundant (high risk) (a) to the first movement of a model trout and (b) to a direct attack. Freezing is distinguished from still by complete cessation of respiratory movements. (a) $G = 10.83$, $N = 20$ for both sites, $P < 0.01$; (b) $G = 39.34$, $N = 20$ for both sites, $P < 0.001$ (Huntingford and Wright unpubl. data).
and a longer period of behavioural suppression following such an attack. Conversely, fish from low-risk sites give higher priority to other important requirements such as foraging. These behavioural traits are likely to promote survival in the habitat in which each population lives.

Ontogeny and plasticity of site-specific antipredator responses
Because stickleback can modify their behaviour after an encounter with a hunting pike, showing enhanced vigilance and stronger escape responses (Benzie 1965), the differences in antipredator responses between wild-caught fish from high-risk and low-risk sites could be the result of differential exposure to unsuccessful attacks prior to capture. On the other hand, they may represent inherited behavioural differences that develop regardless of experience. In guppies (Seghers 1974; Breden et al. 1987) and in minnows (Magurran 1990), the site-specific levels of response persist in fish raised in the laboratory without any encounters with predatory fish. Such results indicate that the behavioural differences are inherited traits.

To determine whether the differences in antipredator behaviour of threespine stickleback are also inherited, we compared the responses of laboratory-reared individuals from Inverleith Pond (low risk) and from a tributary of the River Endrick (high risk) to a simulated attack by a predatory bird. Little response to the model bird was elicited from small

Fig. 10.7 Responses of predator-naive stickleback of two sizes from a high-risk and a low-risk site to exposure to a model avian predator. Bars depict median value of a multivariate 'boldness' score (Table 10.1) in laboratory-reared stickleback from a high-risk and a low-risk site at standard lengths of about 10 mm and 30 mm. The 30 mm fish from the high-risk site (a tributary of the River Endrick, see text) have lower scores than do the other three groups (after Tulley and Huntingford 1987a).
individuals (about 10 mm in length) from either population (Fig. 10.7). However, strong and potentially effective predator avoidance developed in the offspring of fish from the high-risk site by the time they were 30 mm long (large enough to be eaten by a heron, *Ardea cinerea*, for example, Giles 1984b), even though they had never experienced an attack. In contrast, the offspring of stickleback from the low-risk site remained unresponsive as adults (Fig. 10.7; Tulley and Huntingford 1987a).

Similarly, when laboratory-bred stickleback were exposed to a model of a predatory fish, they showed the pattern of antipredator behaviour typical of their site of origin. Fish from the River Endrick (a high-risk site) that were reared by their fathers and exposed to a model piscivorous fish at an age of 8 w tended to be more vigilant, showing more pronounced responses to the first movement of a distant predator than did similarly reared fish from the low-risk, Inverleith Pond population (Fig. 10.8(a)). In addition, in response to a direct attack, high-risk fish were more likely

**Fig. 10.8** The responses of laboratory-reared stickleback from the high-risk and low-risk populations elicited by the first movement of a model piscivorous fish: (a) normally reared, (b) orphans. Normally reared, high-risk fish are more likely to freeze ($\chi^2 = 7.10$, d.f. = 1, $P < 0.01$) than to jump or to do nothing (the last two being combined to avoid small expected values; $\chi^2 = 7.92$, d.f. = 1, $P < 0.01$) in response to the first movement of the model than are all other categories of fish. No other comparisons were significant. (Overall: $\chi^2 = 20.27$, d.f. = 3, $N = 110$, $P < 0.001$; Huntingford and Wright unpubl. data).
to escape at right angles to the line of attack than to move directly towards or away from the predator (Fig. 10.9(a)). Following an attack, the fish from the high-risk site underwent a longer period of behavioural suppression than did low-risk fish (median = 50 s compared with 8 s; Kruskal–Wallis ANOVA, \( H = 11.54, N = 13, 31, P < 0.001 \); Huntingford and Wright unpubl. data). These results suggest that the characteristic features of stickleback from high-risk and low-risk sites are inherited traits that develop in the absence of differential experience of attack by predators.

However, things are not so simple. In the same experiment, other broods of stickleback from these two populations were reared in the laboratory as orphans, without a period of paternal care, and at 8 wk were also subjected to a simulated encounter with a predatory fish. High-risk fish now showed poorly developed protective responses similar to those of their low-risk counterparts. The pattern of response to the first movement of the model predator is the same for high- and low-risk orphans (Fig. 10.8(b)), as is the distribution of escape directions (Fig. 10.9(b)), and so is the

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**Fig. 10.9** The direction of escape responses of laboratory-reared stickleback from low-risk and high-risk populations when ‘attacked’ by a model piscivorous fish: (a) normally reared, (b) orphans. Normally reared, high-risk fish are more likely to escape to the side, as opposed to towards or directly away from the line of attack (the last two being combined to avoid small expected values; \( \chi^2 = 3.46, \text{ d.f.} = 1, 0.1 > P > 0.05 \)), than are all other categories of fish. No other comparisons were significant. (Overall: \( \chi^2 = 8.77, \text{ d.f.} = 3, N = 54, P < 0.01 \); Huntingford and Wright unpubl. data).
period of behavioural suppression following an attack (recovery times for high-risk and low-risk orphans are 10 s and 4.5 s respectively; Kruskal-Wallis ANOVA, $H = 1.52$, $N = 26$, 12, $P > 0.22$). Similar results were found for stickleback tested with a model piscivorous fish at an age of 4 months (Huntingford and Wright, unpubl. data; see also Tulley and Huntingford 1987b).

The explanation for this seemingly bizarre result lies in the nature of the interaction between stickleback fathers and their fry. When young stickleback have absorbed the yolk sac and start to disperse from the nest, their fathers swim after them, gather them up in their mouths, and return them to the nest (Rowland page 338 this volume). If the fry attempt to escape, as they often do, the fathers swim quickly after them and retrieve them. In these cases, young stickleback experience an encounter with a rapidly accelerating larger fish bent on snapping them up. Evidently, this sufficiently resembles an actual encounter with a predatory fish that the young learn to avoid attacks by larger fish more efficiently in consequence (a possibility originally suggested by Benzie 1965). Interactions between guppies and cannibalistic conspecifics enhance the predator avoidance abilities of experienced survivors (Goodey and Liley 1986), and there is little reason to expect that retrieval interactions between paternal stickleback and their young should not have the same effect.

Thus, interactions with their father promote the development of effective predator avoidance in stickleback from high-risk populations, but they do not have the same effect on low-risk fish. The duration of the paternal phase and the amount of time devoted to seeking straying fry was similar in the two populations, both in the laboratory and in the field (Huntingford and Wright unpubl. data). At a temperature of 15–16°C, the fry remained in or near the nest for 2–3 d after hatching, until absorption of the yolk sac was complete. After this time, they gradually dispersed from the nest area (on foraging trips), and started to experience retrieval attempts by the father. From 3 d to 6 d after the brood had hatched, in the laboratory, males of both populations spent approximately 40 per cent of their time searching for and retrieving fry; they then began to build a new nest and subsequently ignored their now-independent young.

Although there were no differences between the two sites in the duration of the father–fry relationship, there were differences in its nature. In particular, both retrieval by fathers and escape by fry were faster in fish from the high-risk population (Fig. 10.10). Retrieval and fry escape speeds were significantly correlated for both categories of fish, but fry from the high-risk site (unlike their low-risk counterparts) were potentially able to outswim their fathers. From hatching, high-risk fry reacted more strongly to their fathers’ approaches than did low-risk fry, which consistently ignored their fathers when they swam near by (Fig. 10.11) and jumped up towards them as they approached. It is not yet clear whether this difference in
Fig. 10.10  Speed of retrieval attempts by paternal stickleback in relation to the escape speed of their fry in fish from a high-risk site (open circles) and a low-risk site (filled circles). Father and fry speeds are correlated in both populations (Spearman rank-order correlations, high-risk site $r_s = 0.73$, $P < 0.01$, $N = 18$; low-risk site $r_s = 0.86$, $P < 0.01$, $N = 20$). Speeds are significantly greater for high-risk fish than for low-risk fish, both for fathers (medians $= 11.9\text{ cm s}^{-1}$ and $3.9\text{ cm s}^{-1}$ respectively; Mann–Whitney $U = 43$, $P < 0.001$) and for fry (medians $= 17.7\text{ cm s}^{-1}$ and $3.6\text{ cm s}^{-1}$ respectively; Mann–Whitney $U = 9$, $P < 0.001$). High-risk fry have significantly higher speeds than do their fathers (Wilcoxon $T = 1.5$, $P < 0.001$), but this is not the case for low-risk fry (Wilcoxon $T = 65$, $P > 0.1$; Huntingford and Wright unpubl. data).

Fig. 10.11  Responses of stickleback fry from the high-risk (HR) and low-risk (LR) sites to close approaches by their father on hatching (yolk sac) and on the first day of the retrieval period (day 3). Comparison at the level of broods shows that high-risk fry are significantly more likely than low-risk fry to respond to their father (by either giving a startle response or remaining still) as opposed to showing no response (Mann–Whitney $U = 9$, $N_1 = 7$, $N_2 = 9$, $P < 0.05$; Huntingford and Wright unpubl. data).
responsiveness is a cause or an effect of the faster retrieval attempts.

Either way, in response to these faster chases, during the course of the paternal period the high-risk fry (but not their low-risk counterparts) became more vigilant and more effective at escaping from their fathers; their initial simple escape responses were amplified into a full spectrum of effective responses to a potentially dangerous larger fish. In nature, this early effect of paternal care may well make the difference between

(a) **LOW RISK**

![Graph showing fish remaining over days for low risk](image)

(b) **HIGH RISK**

![Graph showing fish remaining over days for high risk](image)

**Fig. 10.12** The number of predator-naive stickleback from the two study sites that had failed to reach the criterion for learning to avoid a previously favoured but now-dangerous feeding patch on successive days of avoidance training. High-risk fish took significantly fewer days than low-risk fish to reach the criterion (median = 6 and 8 days respectively; Mann–Whitney $U = 11$, $N_1 = 8$, $N_2 = 8$, $P < 0.05$; after Huntingford and Wright, in press).
life and death when the young stickleback first encounter a real predator.

It is possible that the different intensity of paternal care experienced by young stickleback from the two study sites could interact with a predisposition in fish from the high-risk site to modify their behaviour in the light of adverse experience. Laboratory-reared, predator-naive stickleback from the two study sites (aged 6–9 months and measuring 30–35 mm SL) were subjected to an avoidance conditioning regime. The fish were trained to feed in two equally profitable feeding compartments; they learned this quickly, but in every case developed a strong preference for one of the compartments. During the avoidance conditioning procedure, the fish were given one session per day in which each entry into this favoured compartment was followed by a single simulated attack from a model predator (a dark looming object approaching rapidly from above). When not participating in training sessions, the subjects were confined in a separate compartment that contained no food. The criterion for learning this task was failure to enter the previously favoured but now-dangerous compartment on three successive days (see Huntingford and Wright 1989 for details).

With two exceptions, all the fish reached this criterion within 15 d. However, stickleback from the high-risk site were markedly quicker at learning to avoid the dangerous patch (Fig. 10.12; Huntingford and Wright in press b). Laboratory-reared minnows from a high-risk site that had been given a single exposure to pike subsequently showed stronger responses than did naive fish from the same site; no such experience-induced adjustment was found in fish from a low-risk site, suggesting that these fish also have an inherited difference in readiness to adapt their behaviour in the light of adverse experience (Magurran 1990).

CONCLUSIONS

The antipredator behaviour of threespine stickleback is very variable, and some of this variability can be ascribed to intra-individual changes in state. In particular, how a stickleback behaves in any given encounter with a predator is influenced by the likely adverse and beneficial consequences of the possible responses. Long-term, interindividual differences also contribute to the observed variability in antipredator behaviour in threespine stickleback, and some of these differences can be related to local environmental conditions, and in particular to the predation risk prevailing at different sites.

These site-specific levels of antipredator behaviour appear to have a rather complex developmental origin. Comparison of a pair of sites with markedly different predation regimes has shown that, as a result of a difference in the vigour with which paternal stickleback retrieve their fry, young from the high-risk site have more opportunity than do their low-risk counterparts to learn effective techniques for avoiding larger fish. They
make good use of this opportunity, having a predisposition to modify their behaviour in the light of adverse experience. In consequence, a small initial divergence in behaviour (more vigorous response to the father's approach in young stickleback from the high-risk site) is amplified. Therefore when they subsequently encounter larger fish with predatory intentions, threespine stickleback from the site where predators are abundant have a full repertoire of effective antipredator responses that is effectively absent in those from the site where predators are uncommon.

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