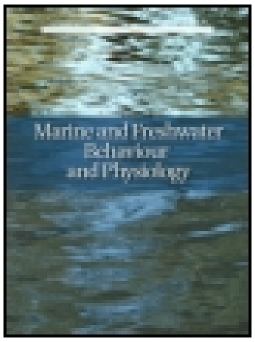

Marine & Freshwater Behaviour & Phy

ISSN: 0091-181X (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/gmfw19

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To cite this article: Anne E. Magurran , Benoni H. Seghers , Gary R. Carvalho & Paul W. Shaw (1993) Evolution of adaptive variation in antipredator behaviour, Marine & Freshwater Behaviour & Phy, 23:1-4, 29-44, DOI: 10.1080/10236249309378855

To link to this article: https://doi.org/10.1080/10236249309378855

Mar. Behav. Physiol., 1993, Vol. XXIII, pp. 29–44
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EVOLUTION OF ADAPTIVE VARIATION IN ANTIPREDATOR BEHAVIOUR

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In many species of fish, behaviour varies adaptively amongst populations in response to predation risk. One of the best examples is provided by the guppy, *Poecilia reticulata*, in Trinidad. Although separated by distances of a few km, or less, guppy populations vary in terms of predator assessment and avoidance, schooling, foraging behaviour, resource defence, female choice and mating tactics. We show that there are behavioural costs (such as lower levels of individual aggression and reduced female choice) associated with selection for a heightened antipredator response. In the majority of cases population variation in guppy behaviour can be clearly linked to the predation regime. Nevertheless, we have begun to uncover situations where there is behavioural divergence amongst populations apparently experiencing equivalent risk. We consider explanations for these differences including the possibility that they may be related to high levels of genetic divergence.

INTRODUCTION

Intraspecific variation in behaviour provides a forum for investigating evolution in action. The traditional approach has been to focus on a selective force and ascertain the extent to which a change in selection regime correlates with behavioural modification. Since untimely death due to predation has profound fitness consequences, there is little intuitive difficulty in accepting predation as an important form of selection. In addition, the relative risk of predation (at least at the level of the species of predator present in particular communities) is comparatively easy to quantify. The behavioural and evolutionary responses to a change in predation can be assessed by experiment and observation of natural populations. Consequently, there is now a large literature demonstrating that an increase in predation pressure leads to an adaptive shift in behaviour. Table 1 lists examples drawn from three species of fish—guppies, *Poecilia reticulata*, three-spined sticklebacks, *Gasterosteus aculeatus*, and European minnows, *Phoxinus phoxinus*—and illustrates the wide range of behaviours influenced by a change in predation regime.

Table 1 Adaptive variation in behaviour as a consequence of increased predation risk

Behaviour *effect of increased predation pressure*	*Species*	*Reference*
Schooling		
larger and more cohesive schools	*P. reticulata*	Seghers, 1974a Magurran and Seghers, 1991 Breden *et al.*, 1987
	P. phoxinus	Magurran and Pitcher, 1987
Evasion tactics		
more effectively integrated in high-risk populations	*P. reticulata*	Seghers, 1973
	G. aculeatus	Giles and Huntingford, 1984
	P. phoxinus	Magurran and Pitcher, 1987
Inspection and predator assessment		
increase in inspection frequency	*G. aculeatus*	Huntingford, (this volume)
	P. phoxinus	Magurran, 1986
increase in inspection group size	*P. phoxinus*	Magurran, 1990a, b
predator-specific attack cone avoidance	*P. reticulata*	Magurran and Seghers, 1990a
more efficient assessment of predator motivation	*P. reticulata*	Licht, 1989
more likely to employ tit for tat	*G. aculeatus*	Huntingford, 1992
	P. reticulata	Dugatkin and Alfieri, 1992
Response to overhead threat		
greatest in high-risk population	*P. reticulata*	Seghers, 1974b
	G. aculeatus	Giles and Huntingford, 1984
Response to alarm pheromone		
more pronounced behavioural change following exposure to Schreckstoff	*P. phoxinus*	Magurran and Pitcher, 1987 Levesley and Magurran, 1988
Acquisition of defence skills		
predisposition to respond to experience greater in high-risk populations	*G. aculeatus*	Tulley and Huntingford, 1987 Huntingford and Wright, 1989
	P. phoxinus	Magurran, 1990b
Habituation of antipredator responses		
slower in high-risk populations	*G. aculeatus*	Huntingford and Coulter, 1989
Habitat selection		
remain near surface and seek cover at edge of river	*P. reticulata*	Seghers, 1973
Foraging		
increased feeding tenacity	*P. reticulata*	Fraser and Gilliam, 1987
Female choice		
preference for less brightly coloured males	*P. reticulata*	Breden and Stoner, 1987 Stoner and Breden, 1988 Houde and Endler, 1990
avoidance of sneaky mating attempts compromised by predator avoidance	*P. reticulata*	Magurran and Nowak, 1991
Male mating tactics		
increased use of sneaky mating tactics in high risk populations	*P. reticulata*	Luyten and Liley, 1985 Luyten and Liley, 1991 Magurran and Seghers, 1990b

Table 1 Adaptive variation in behaviour as a consequence of increased predation risk (Cont.)

Behaviour *effect of increased predation pressure*	*Species*	*Reference*
Aggression		
individual aggression reduced	*G. aculeatus*	Huntingford, 1982 Bakker and Feuth-De Bruijn, 1988
	P. reticulata	Ballin, 1973 Magurran and Seghers, 1991

BEHAVIOURAL DIVERGENCE: TRINIDADIAN GUPPIES

Population variation amongst guppy populations in Trinidad (Figure 1) is especially well documented. Not only is the species a very tractable organism for laboratory study, but there is also a clear gradation of predation regime within, as well as across, many rivers. As Table 1 reveals, there are population differences in a wide range of behaviours. A further extensive literature details the way in which predation influences guppy sexual selection (Endler, 1983) and life history (Reznick and Endler, 1982). Additional evidence for the pivotal role of selection in inducing population differentiation has been provided by experiments in which guppies transplanted across predation regimes within the same drainage rapidly evolve colour patterns and life history attributes appropriate to their new location (Reznick *et al.*, 1990).

Despite the wealth of information on population variation in Trinidadian guppies two areas have been little explored. First, few studies have considered behavioural changes contingent upon selection for more efficient predator avoidance. For instance, the ability to find food or mates may be compromised by the need to avoid predators. Second, there has been little attempt to explain variation that does not fit the adaptive model. In this paper we begin to address these issues.

For convenience we divide the Trinidad predation regimes into three main categories: sites with a range of piscivores including the pike cichlid (*Crenicichla alta*), an important guppy predator (Haskins *et al.*, 1961); sites with *Rivulus hartii* only (a minor predator which primarily targets juvenile guppies (Seghers, 1978; Liley and Seghers, 1975); and sites with *Macrobrachium crenulatum*, a freshwater prawn (often found in association with *R. hartii*) which is known to predate guppies (Endler, 1991). See Figure 1 for details.

BEHAVIOURAL TRADE-OFFS IMPOSED BY EFFECTIVE PREDATOR AVOIDANCE

Competition for Limited Resources

One interesting outcome of the studies of adaptive variation is that an increase in risk may modify behaviours not directly related to predator avoidance. For instance, well developed antipredator behaviour may reduce an individual's options for securing limited resources. Although schooling is an effective defence against

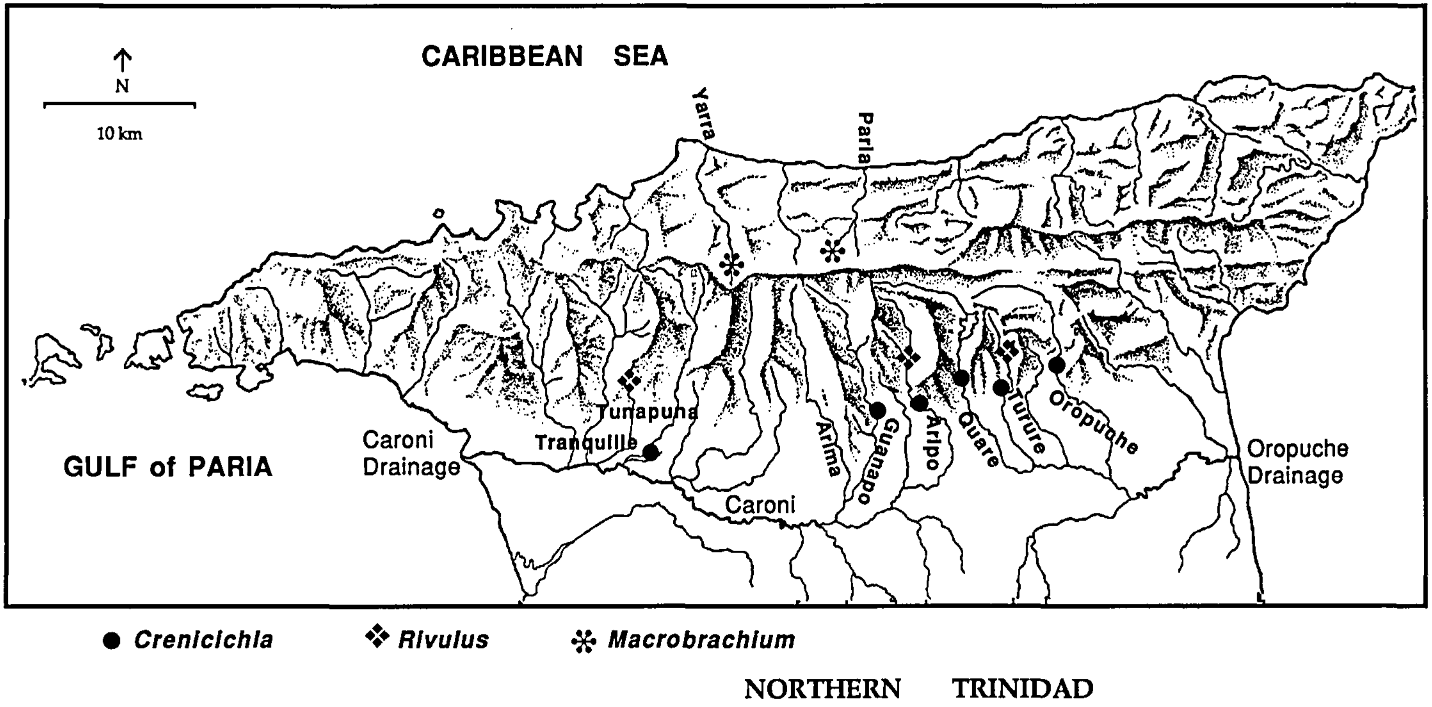

Figure 1 Location of study populations in Trinidad. The predator status of each site is indicated.

predation (Magurran, 1990a), it depends on coordination amongst school members and may restrict individual competition. We tested the hypothesis that levels of individual aggression will be reduced in fish with a high schooling tendency by comparing the behaviour of male guppies from 8 populations. Schooling behaviour was measured in the wild using the elective group size technique (Magurran and Pitcher, 1987). The observers watched quietly at the side of a stream and recorded the size and composition of adult guppy schools. Schools were defined as groups of fish in which individuals were within 5 body lengths of their nearest neighbour. As many as possible, but at least 30, different schools were recorded at each site. The median group size in the distribution of individuals against group size was taken as the measure of schooling tendency. EGS scores ranged from 1, for populations such as Paria (where there is only minimal risk from fish predators) to 21 for Tranquille (where guppies coexist with at least 12 predatory fish species (Magurran and Seghers, 1991)). Aggression, measured in the context of food patch defence, varied across populations with Paria and Tunapuna being significantly more aggressive and Tranquille guppies significantly less aggressive than the other populations (Figure 2).

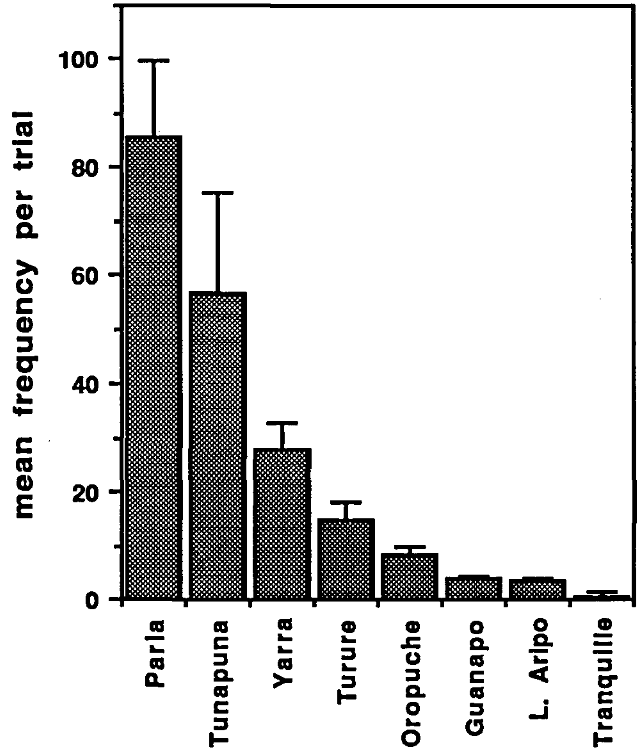

Figure 2 Mean (and SE) frequency of aggression in groups of 8 (wild) male guppies competing for a small food patch. Aggression was measured in the laboratory where the frequency of aggressive acts was recorded for a period of 20 minutes. Numbers of replicates (each with different fish) were as follows: Paria (n=5), Tunapuna (n=6), Yarra (n=6), Lower Turure (n=6), Oropuche (n=5), Guanapo (n=6), Lower Aripo (n=5), Tranquille (n=6). Aggression scores varied significantly (1 way ANOVA $F_{7,37}=49.0$, $P<0.001$). Redrawn from Magurran and Seghers (1991).

There was a significant inverse relationship between the ranked level of aggression (measured in the laboratory) and schooling tendency (measured in the wild) in males from the 8 populations ($r_S=-0.90$, $P<0.01$: Figure 3). These results, together with those obtained by Huntingford (1982) for sticklebacks, point towards a trade-off between antipredator behaviour and resource defence. A motivational link between antipredator behaviour and intraspecific aggression could provide an economical method of achieving this type of behavioural compromise (Huntingford, 1982; Magurran and Seghers, 1991). The behavioural consequences of trade-offs imposed by predation are explored in more detail by Magnhagen later in this volume.

Risk Sensitive Courtship

Tactics of courtship and mate choice can also be shown to vary adaptively in response to predation risk. Male guppies have essentially two ways of achieving a mating. They may either perform sigmoid displays in an attempt to persuade a receptive female to mate or opt for sneaky mating tactics. Females from low-risk populations prefer more brightly-coloured males (Stoner and Breden, 1988; Houde and Endler, 1990) while high-risk males show greater behavioural versatility under threat. One of our studies (Magurran and Seghers, 1990b) compared the courtship behaviour of males from two Trinidadian populations. Lower Aripo fish (see Figure 1) occur sympatrically with a range of piscivores including the pike cichlid, *C. alta*. Barrier waterfalls have prevented the upstream migration of these predators so that Upper Aripo guppies (which are genetically similar to their downstream

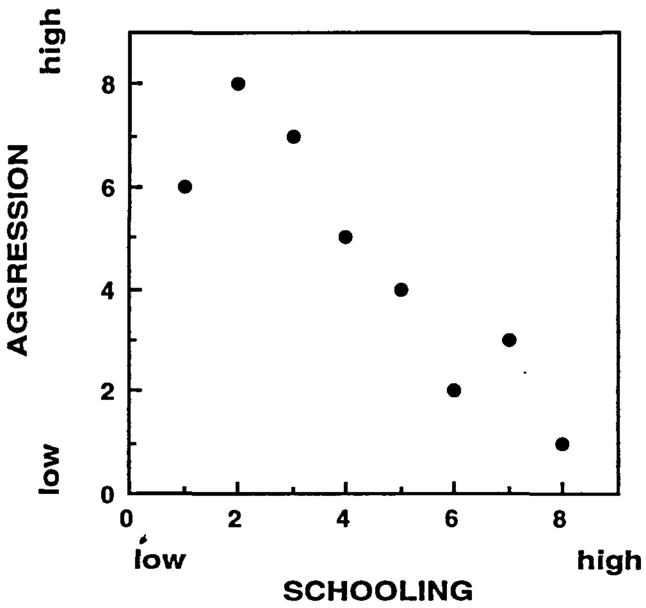

Figure 3 Relationship between (ranked) schooling tendency and aggression for male guppies from 8 Trinidadian populations. Redrawn from Magurran and Seghers (1991).

counterparts—see Figure 10) are subject to reduced risk. Upper Aripo males displayed risk-reckless courtship behaviour and did not reduce their sigmoid display rate or otherwise modify their courtship behaviour when threatened by two characins (*Astyanax bimaculatus*) which are potential predators (Liley and Seghers, 1975). The courtship behaviour of the Lower Aripo males was, by contrast, risk sensitive. These fish performed a lower proportion of sigmoid displays and increased their level of sneaky mating attempts in the presence of predators (Figure 4). Interestingly, males from upstream sites such as the Upper Aripo are more successful (in terms of actual inseminations) when mating in clear predator-free waters whereas downstream males do better in turbid (and potentially risky) conditions (Luyten and Liley, 1991).

Male behaviour under risk is not simply a direct reaction to danger but also an exploitation of female antipredator behaviour. In a subsequent study we focused on male/female interactions as a response to threat. Two high risk populations, Lower Aripo and Oropuche, (both from sites with high densities of the pike cichlid, *C. alta* (Douglas and Endler, 1982)) were investigated. Fish were tested in groups of 10 (5 adults of each sex). The behaviour of each individual was monitored for 5 min in a low risk (undisturbed) situation and in the presence of a threatening, but non-attacking, blue acara (*Aequidens pulcher*). Data were collected for 20 individuals of each sex and population. Males from both populations significantly reduced their display rate (Wilcoxon signed-ranks test, LA: z=3.18, *P*<0.01; Oro: z=2.02, *P*<0.05) and increased their sneaky mating attempts (LA: z=1.97, *P*<0.05; Oro z=3.25,

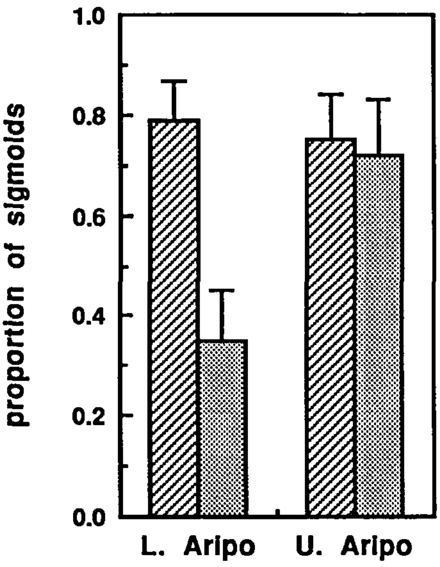

Figure 4 Courtship behaviour of Lower Aripo and Upper Aripo male guppies in the absence (stripes) and presence (stipples) of predators. The mean (and 95% confidence limits) proportion of mating attempts that involved sigmoids is shown for both experimental conditions. Each male was observed for 5 min and could be recognised by his unique colour pattern. There were n=30 males per population. Redrawn from Magurran and Seghers (1990b).

$P<0.01$)—Figure 5—in the presence of the predator. Females made fewer attempts to avoid the advances of males when under threat (LA: $z=3.41$, $P<0.001$; Oro: $z=3.60$, $P<0.001$) and received more gonopodial thrusts as a consequence (LA: $z=3.12$, $P<0.01$; Oro $z=3.26$, $P<0.01$)—Figure 6. Most inspections of the predator are initiated and led by female guppies. This provides males with an excellent opportunity for attempting a sneaky mating while the females are otherwise preoccupied (Magurran and Nowak, 1991).

Females in the experiments would have been, like the majority of females in the wild, in a sexually non-receptive phase. Such fish continuously try to avoid the unceasing mating activity of males. This male avoidance behaviour is prejudiced by the presence of predators.

NON-ADAPTIVE VARIATION?

Schooling

The schooling tendency and inspection tactics of most populations of guppies can be predicted from prevailing predation risk. We have, however, discovered a number of cases where there are substantial levels of behavioural divergence within given predation regimes. Two comparisons underline this point. The upstream sections of the Paria and Yarra rivers contain high densities of the freshwater prawn, *M. crenulatum* (Douglas and Endler, 1982). Laboratory studies show that Yarra fish have substantially higher levels of schooling than Paria fish (Figure 7).

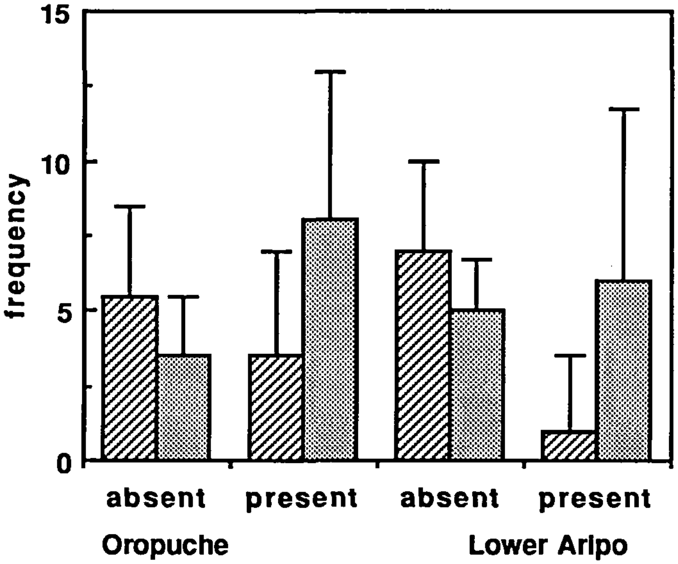

Figure 5 Male courtship behaviour as a response to risk. Median frequencies (and upper quartile) of sigmoid displays (stripes) and gonopodial thrusts (stipples) are shown.

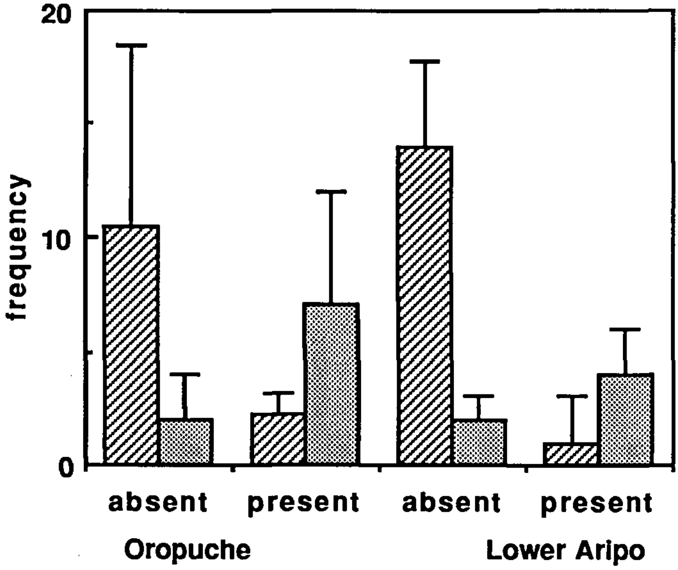

Figure 6 Female behaviour as a consequence of risk. Median number (and upper quartile range) of times that females avoided males (stripes) and received thrusts (stipples) per 5 minutes is indicated.

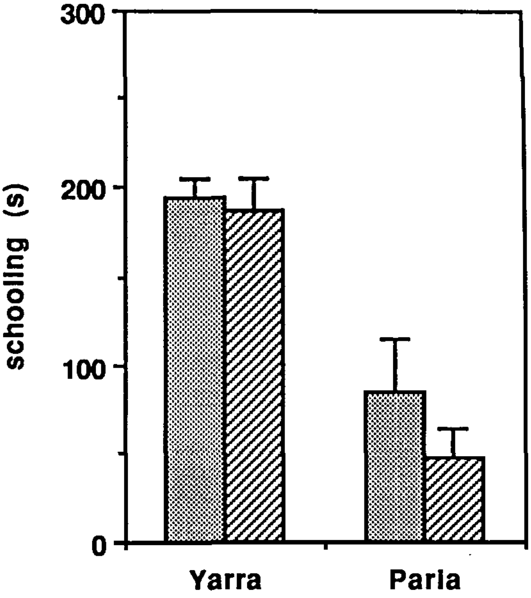

Figure 7 Mean (and SE) schooling tendency of Paria and Yarra guppies. Females are denoted by stipples, males by stripes. There were n=6 replicates of Paria fish per sex and n=8 replicates of Yarra fish. All fish were bred and raised in the laboratory. In this test the focal fish was allowed to associate freely with 4 individuals of the same sex and population. Schooling behaviour was measured by recording the number of seconds out of 5 minutes that the focal fish spent within 5 body lengths of its nearest neighbour. Males and females were tested separately. The portion of the Yarra River where the guppies originated is also known as the Limon River.

Likewise, Oropuche and Lower Aripo guppies (Figure 8) have equivalent levels of predation but quite different schooling tendencies. The low schooling scores of the Oropuche fish cannot be attributed to reduced numbers of predators since our own observations, and those of other workers (for example Douglas and Endler (1982)) point to high densities of *C. alta* in this river. The elevated schooling of female guppies is probably related to an increased perception of risk—see Magurran and Nowak (1991) for a discussion.

A comparison of four populations, Paria and Yarra, Guanapo and Oropuche also showed that inspection tactics are determined by schooling tendency rather than predation regime. Guanapo guppies (from the Caroni drainage) resemble Lower Aripo fish in their behaviour.

	High Fish Predation	*Prawn Predation*
High Schooling	Guanapo	Yarra
Low Schooling	Oropuche	Paria

In females, for example, there is a significant negative relationship (Figure 9) between schooling tendency and the proportion of solo inspections (data with arcsin transformation: $F_{1,28}=658.67$, $P<0.001$)

Since schooling behaviour offers important protection against predators such as the pike cichlid (Magurran, 1990a) it is not clear why levels of schooling are reduced in Oropuche fish. Similarly, it is difficult to explain why Paria and Yarra guppies

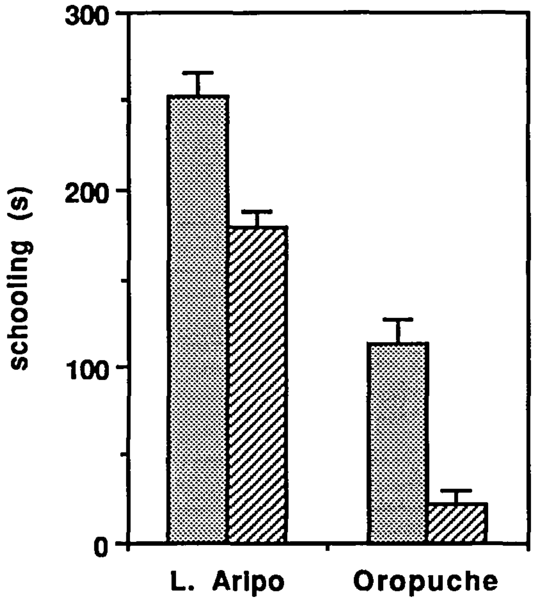

Figure 8 Mean (and SE) schooling tendency of guppies from the Lower Aripo and Oropuche Rivers. Females are denoted by stipples, males by stripes. All fish were bred and raised in the laboratory. There were 24 replicates (i.e. tests using separate focal fish) for each sex and population. In this test schooling behaviour was recorded as the number of seconds that a focal fish spent within 5 body lengths of a clear plastic bottle containing 6 guppies of the same sex.

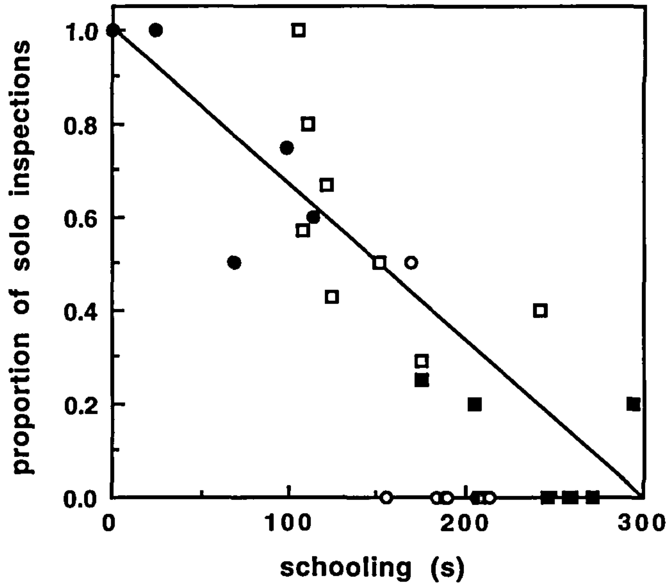

Figure 9 Proportion of solo inspections by female guppies in relation to schooling tendency (defined as seconds spent within 5 body lengths of conspecifics during a 5 min trial). The four populations are denoted as follows: Paria (solid circle); Yarra (open circle); Oropuche (open square); Guanapo (closed square).

behave so differently. Intriguingly, this behavioural divergence is paralleled by considerable genetic divergence.

GENETIC DIVERGENCE

Analysis of biochemical genetic variation among guppy populations in N. Trinidad using allozyme electrophoresis (Carvalho *et al.*, 1991) demonstrates high levels of genetic differentiation amongst populations from different rivers. Significant differences in allele frequencies (see Carvalho *et al.* (1991)) exist between the Oropuche and Lower Aripo, and Paria and Yarra populations. Figure 10 illustrates this extreme divergence between populations in terms of an overall similarity statistic, Nei's (1972) Genetic Similarity I (Oropuche – Lower Aripo I = 0.926; Paria – Yarra I = 0.886). The values of I shown are very low compared to most inter-population values within other fish (for example Buth *et al.* (1991) observed that I > 0.94 in 78% of comparisons). For comparison of levels of differentiation found between guppy populations in the same river a sample from the Upper Aripo (data from Carvalho *et al.* (1991)) is also included in Figure *10*. The genetic similarity of the Guanapo and Lower Aripo population is I = 0.956.

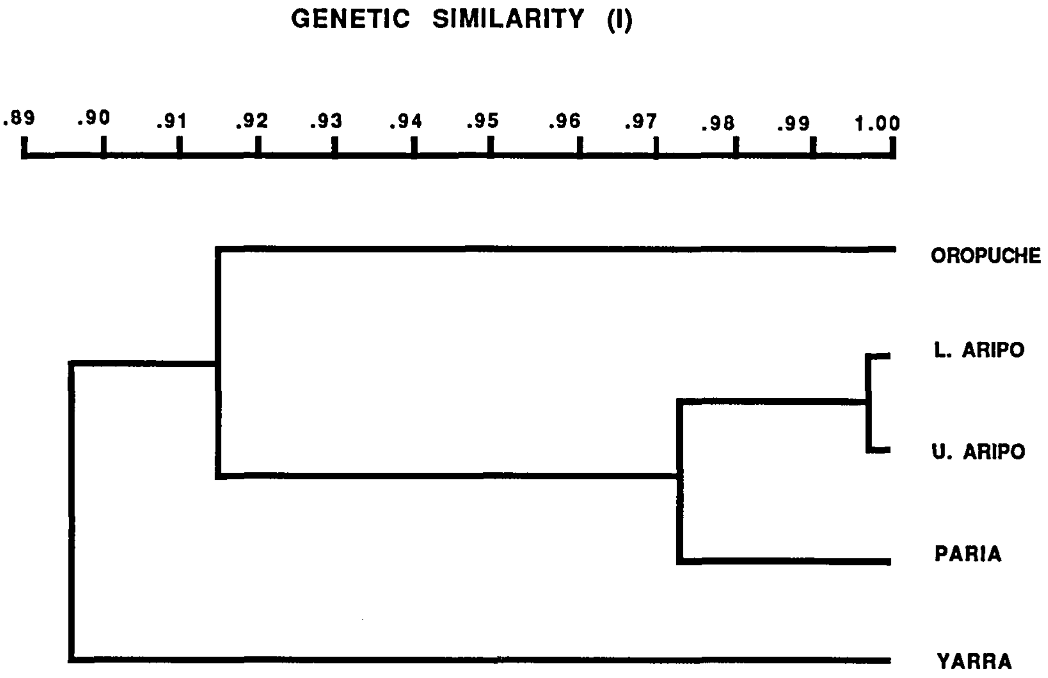

Figure 10 Dendrogram of mean genetic identities between five populations of *Poecilia reticulata* in N. Trinidad. Calculations (UPGMA–cophenetic correlation = 0.954) are based on 35 alleles at 23 loci. Redrawn from Carvalho *et al.* (1991).

DISCUSSION

Two previous studies, one on life-history tactics, the other on male coloration, have rejected the notion that either historical factors, or watershed differences contribute to observed patterns of variation.

Douglas and Endler (1982) performed a multivariate comparison (using the Mantel procedure) of 41 guppy sites in Trinidad. They assessed male colour patterns in the context of predation regime, altitude and watershed. Four alternative evolutionary models were put forward. Models 1 and 2 proposed that colour patterns vary clinally and patchily and could not be rejected. Model 3 considered the effect of distance while Model 4 explicitly tested historical factors by comparing sites within the same watersheds. Neither was supported by their analysis. Thus, there appears to be no evidence that colour patterns cluster within watershed independently of predation regime.

Strauss (1990) reanalysed Reznick and Endler's (1982) data using principal components analysis. He found a large amount (17%) of residual variation after adjusting for female body size and predation effects. This residual variation could not be attributed to drainage system or to geographical proximity. Again, the phylogenetic history of a population seems to play little part in shaping its life history tactics. Interestingly, however, a recent assessment of the life history tactics of Paria and Yarra guppies (Rodd and Reznick, 1991) points towards substantial differences in fecundity.

Why do we observe watershed differences in some aspects of behaviour when they appear to be absent from investigations of other traits? One hypothesis which could explain the surprising difference between the Yarra and Paria populations is the relative geographical isolation of each population from areas of high predation from other fish species. Although the lower portions of both rivers contain a wide variety of predators, notably *Eleotris pisonis* (Endler, 1991a), a high waterfall on the lower section of the Paria serves as a complete barrier to these predators thereby protecting the entire guppy population in this river.

By contrast, the situation in the Yarra River is quite different: the lower Yarra guppies are exposed to predators and have well-developed antipredator behaviour. Although the predators do not occur in the upper portions of the Yarra (where the present study is focused), gene flow between adjacent demes presumably links subpopulations along the entire length of the river. Consequently, behavioural adaptations may not be as finely tuned to local conditions as they are in the Paria, where gene flow from high predation populations is virtually impossible.

The difference between the Oropuche and Lower Aripo also eludes simple answers. Since the predisposition to respond to experience varies across populations of other fish species (for example minnows, *P. phoxinus* (Magurran, 1990b)) it could be that Oropuche and Lower Aripo fish react differentially to early behavioural cues. Experiments are required in order to disentangle the effects of inheritance and early experience.

Another possibility is that different behaviour patterns could be equally successful in terms of long term reproductive fitness. Thus, Oropuche guppies could be trading-off schooling against some other (as yet unknown) behaviour or life-history tactic. Finally, behaviour could genuinely be less malleable than colour or life-history traits. It may, for example, be that genetic constraints, arising as a legacy from founding events or past histories, limit the extent to which natural selection can induce change.

CONCLUSIONS

Intraspecific variation in morphology, behaviour and life-history tactics provides some of the most compelling evidence for natural selection in the wild (Endler, 1985). The work we report here does not undermine the importance of selection in inducing adaptive variation in behaviour. Indeed, most of the behaviour patterns described can be unequivocally linked to the prevailing predation regime. We have, however, uncovered a number of examples where population differences cannot be explained purely in terms of current selection pressures (at least as they have been hitherto understood). In particular we have shown that there can be considerable variation in schooling and associated behaviours of fish occurring in similar ecological communities. At present we do not know whether the different behaviour patterns are equally successful (in terms of reproductive fitness) or whether sub-optimal strategies are retained in some populations and represent a genetic legacy from the founding fish. Nevertheless, our investigation does underline the importance of considering stochastic as well as deterministic factors when attempting to explain observed behavioural variation.

ACKNOWLEDGMENTS

Financial support from the Royal Society and the Natural Environment Research Council (UK) is gratefully acknowledged.

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