Population differentiation without speciation

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Population differentiation is often viewed as an important step towards speciation, and part of the rationale for conserving variation at the intraspecific level is that the potential to generate more biological diversity should be retained. Yet, speciation is not an inevitable consequence of population divergence. This paper reviews recent work on the Trinidadian guppy, *Poecilia reticulata*, a species that is renowned for its capacity for population differentiation. Guppy populations evolve rapidly, within 10^1 to 10^2 generations, as a response to changes in selection exerted by predators. The rates of evolution involved can be up to seven orders of magnitude greater than those seen in the fossil record. Sexual selection, particularly female choice, appears to reinforce the divergence that natural selection has generated. Perplexingly, however, there is no reproductive isolation (either prezygotic or postzygotic) between populations, even those that have been separated for at least 10^6 generations. Sexual conflict may be the key to explaining this absence of speciation. Male reproductive behaviour, particularly the high incidence of sneaky mating, may be instrumental in producing sufficient gene flow to prevent reproductive isolation. Sneaky mating has the potential to undermine female choice, and is known to be an important means of sperm transfer in wild populations. Sexual dimorphism, also a result of sexual conflict in guppies, may inhibit speciation in another way. Morphological differences between the sexes, that have arisen for reproductive reasons, mean that males and females are pre-adapted for different foraging niches. This, in turn, reduces the opportunity for the development of feeding polymorphisms, a mechanism that seems to have been important in the sympatric speciation of other fish species.

Keywords: *Poecilia reticulata*; Trinidadian guppy; sexual conflict; evolutionary rates; reproductive isolation

1. INTRODUCTION

It is conventional to view biological diversity as synonymous with species richness and/or species abundance (Magurran 1988; Rosenzweig 1995). In recent years, however, the concept of biological diversity has been extended to embrace the rich seam of diversity within species themselves (Barbault & Sastraprajda 1995; Gaston 1996; Mallet 1996; Butlin & Treganza, this volume). Such diversity can be cryptic and only apparent once appropriate techniques are applied, an example being the use of allozymes to uncover levels of heterozygosity (Butlin & Treganza, this volume), or it may be expressed phenotypically and manifest itself as variation in behaviour, morphology or life histories (Mallet 1996; Foster & Endler 1997).

Current conservation practice recognizes that intraspecific diversity is worth preserving in its own right. This is partly because the viability of a species may in some way be related to its variability (Bisby 1995; but see, also, Amos & Harwood, this volume). An additional consideration is that intraspecific diversity is perceived as the raw material for evolution (Barbault & Sastraprajda 1995; Mallet 1996). It stands to reason that populations that are highly differentiated are the precursors of new species. Thus it is not simply variation as such, but also the potential to generate new species and even more biological diversity, that must be conserved (Myers 1997). However, as evolutionary biologists have been discovering, the relationship between population divergence and speciation is not straightforward. Although population differentiation can be an important step on the path to speciation, speciation is by no means the inevitable outcome of even the most marked population differentiation. This paper illustrates the issue by reviewing recent work on a little fish that is increasingly being cited as a classic case of evolution in action.

2. POPULATION DIFFERENTIATION IN THE TRINIDADIAN GUPPY

Few species offer a more compelling example of population differentiation than the guppy, *Poecilia reticulata*. (Endler 1995; Magurran *et al.* 1995). The guppy is endemic to north-eastern South America and occurs in Venezuela, Guyana, Surinam and several of the Lesser Antilles, including Trinidad and Tobago (Rosen & Bailey 1963). It is, however, in Trinidad, that this species has been most intensively studied. Work by Caryl Haskins and his colleagues (Haskins & Haskins 1950, 1951; Haskins *et al.* 1961) alerted biologists to the evolutionary significance of Trinidadian populations. Half a century later interest in the Trinidadian guppy shows no signs of waning. Indeed, as the reference list of this paper testifies, the quality and quantity of contemporary research on this little fish continues to grow. Why have guppy populations in Trinidad proved so rewarding to study? Part of the answer is provided by the geography of Trinidad itself. Trinidad was, until recently (somewhere between 10^3 and 10^4 years ago (Kenny 1989, 1995; Magurran *et al.* 1995)) part of mainland South America. Sea-level changes in the wake of the last ice age created the island we know today. One legacy of these continental origins is the Northern Range mountain chain running along the northern flank of Trinidad. The Northern Range is dissected by many rivers, virtually all of which support thriving guppy populations. Some of these populations are part of a rich community of fish species, including important guppy predators such as the pike cichlid, *Crenicichla alta*. In other cases, guppies co-occur with just a few species, most notably the cyprinodont, *Rivulus hartii*. *Rivulus* is at best a minor predator of guppies. The presence of barrier waterfalls, a characteristic feature of the Northern Range, means that there can be marked changes in predation regime over very short distances. Guppies and *Rivulus* tend to be found in all but the highest reaches of a river, but larger fish, including guppy predators, are often prevented from colonizing upstream by barrier waterfalls. Evolutionary biologists thus have at their disposal replicate populations that vary in terms of an important selective factor: predation risk. It is not surprising therefore that Trinidadian guppy populations have proved invaluable in demonstrating the power of natural selection in the wild (Endler 1995).

Haskins & Haskins (1950) and Haskins *et al.* (1961) first noted the relationship between male coloration and predation regime and set the stage for a series of important papers by John Endler (see, for example, Endler 1978, 1980). This work confirmed that guppy colour patterns in different populations result from the interaction of natural selection (for increasing inconspicuousness in more dangerous sites) and sexual selection (exerted by females for males of different hues). Ben Seghers (Seghers 1973, 1974; Liley & Seghers 1975) was in turn the first to recognize that guppy populations displayed geographical variation in behaviour and morphology that could be related to variation in predation intensity. For example, he (Seghers 1974) discovered that guppies in populations that are subject to predation from a number of piscivorous species have higher schooling tendencies than those that exist in much less threatening environments. Seghers (1974) was also able to show that population differences in schooling behaviour were retained when fish were bred under standard conditions in the laboratory, thus confirming that the behaviour patterns had a genetic basis. As schooling behaviour is an important antipredator tactic (Magurran 1990; Magurran & Pitcher 1987; Neill & Cullen 1974; Pitcher & Parrish 1993), the adaptive nature of the geographic variation is evident. Subsequent investigations have revealed that Trinidadian guppy populations differ in virtually every feature that biologists have cared to examine. Endler (1995) lists 47 traits that covary with each other and with predation risk. Although such covariance provides strong evidence for the role of natural selection in shaping populations, these studies are essentially correlational. A direct causal link between predation risk and evolution is required. Trinidadian guppy populations have provided this too and what is particularly remarkable is the speed with which heritable changes arise.

3. EVOLUTION IN ACTION

A pioneering investigation of natural selection in the wild was performed by John Endler in 1976 when he collected 200 guppies from a high-risk site in the Lower Aripo River and moved them to an upstream tributary of the same river (Endler 1980). Barrier waterfalls had prevented this tributary from being colonized by guppies, or by other fish species with the exception of *Rivulus*. The transplanted guppies thrived in their new home; indeed their descendants can be found there today. Endler monitored the population for the next two years. The changes in male colour pattern were as swift as they were dramatic. There was an increase in the size of colour spots, the number of colour spots and the overall diversity of colour (Endler 1980). In other words, the males became more colourful in line with the expectation for a low-risk habitat. In these relatively benign sites females will have more opportunity to exert preferences for brighter males, and brighter males will be at a much lower risk of capture by predators. A genetic correlation between male colour pattern and female choice (Houde 1994) will reinforce the trend towards more flamboyant males.

Evolution in the Aripo introduction experiment was not confined to male morphology either. Marked changes in life history traits were also observed. Reznick & Endler (1982) noted phenotypic changes in offspring size and in the proportion of body mass devoted to reproduction. A follow-up study confirmed that the life histories of the source and transplant environments continued to diverge over the 11 years during which the experiment was monitored (Reznick *et al.* 1990) and that the changes in life history were heritable. Once again evolution was in the direction anticipated for a low-predation community. The transplanted fish were larger and older at maturity and produced fewer but bigger offspring.

Reznick & Bryga (1987) carried out an additional transplant in the El Cedro River of Trinidad. Here they found changes in male size and age at maturity after 4 years and changes in female life histories after 7 years. Reznick *et al.* (1997) estimate the mean generation time of guppies in low-predation localities to be 210 days, which is equivalent to 1.74 generations per year though Endler (1983) suggests that there can be as many as 14 generations in 23 months and Haskins *et al.* (1961) propose four generations a year.

The rate of evolution represented by these life history changes is truly remarkable. Reznick *et al.* (1997) calculated the rate of change in terms of darwins (Stearns 1992) as $(\ln X_2 - \ln X_1)/\Delta t$, where X_1 and X_2 are the values of the trait in question at the beginning and end of the time period and Δt is the length of the time period in years. Table 1 summarizes their results. They conclude that the rate of evolution they observed was on a par with that observed in artificial selection experiments, and seven orders of magnitude faster than in the fossil record. Reznick *et al.* (1997) attribute the differences in rate of evolution between the sexes to greater genetic variance for age and size at maturity in males rather than weaker selection on female traits.

Why should guppy populations evolve so rapidly? The answer lies in the fact that these transplant experiments resulted in strong directional selection, which persisted

Table 1. *The rate of evolution in natural populations of guppies in Trinidad*

(The table shows the rate of change, expressed as 10^3 darwins, in two life history traits, age at maturity and size at maturity, for both male and female guppies. Geometric mean rates of evolution in the fossil record range from 0.7–3.7 darwins (Reznick *et al.* 1997). See text for details.)

	male age	male size	female age	female size
Aripo River 18 generations	16.4	10.9	8.0	13.9
El Cedro River 7 generations	45.0	27.1	3.7	5.1
El Cedro River 13 generations	13.9	5.3	7.9	9.3

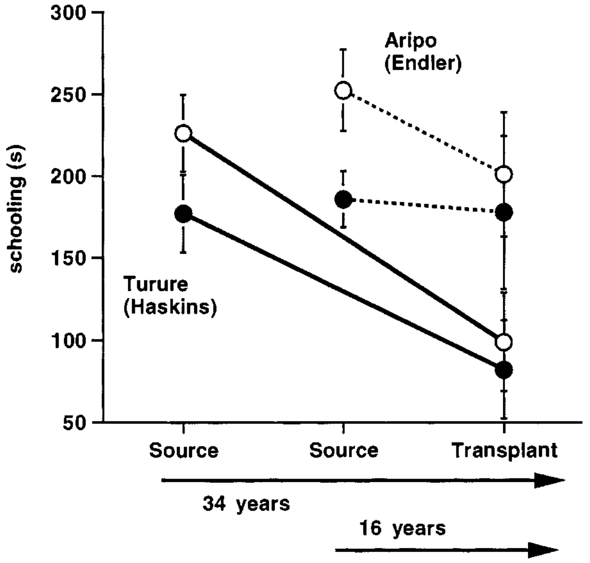

Figure 1. Evolution of antipredator behaviour in Trinidadian guppies. This figure illustrates changes in schooling tendency following a relaxation of predation regime. Two introduction experiments are compared: the Turure transplant by Caryl Haskins and the Aripo transplant by John Endler. Fish were collected from the wild and then bred, raised and tested under standard conditions in the laboratory. Schooling tendency was assessed by recording the length of time (out of 5 min) that individual fish spent in the proximity of a transparent container that housed a school of guppies of the same sex. The Aripo transplant is denoted by a hatched line, the Haskins transplant by a solid line. Open symbols represent females and closed symbols signify males. The separation of the source sites on the x-axis symbolizes the separation in time of the source and transplant populations in the two introductions. The data on which the figure is based are taken from Magurran *et al.* (1992, 1995), and the figure is redrawn from Carvalho *et al.* (1996).

for the time period over which the traits were measured. As Reznick *et al.* (1997) point out, once life histories become optimized for the prevailing conditions no more evolution is to be expected. Thus, further monitoring of the fish in the Aripo and El Cedro introductions is likely to reveal a reduction in the rate of evolution. In addition, the transplant experiments ensured that selection pressure was consistently in the same direction, unlike many natural situations were selection operates erratically as environmental conditions change.

Evolution will also occur, albeit at a slower rate, under weaker selection. The very first guppy transplant experiment in Trinidad was performed by Caryl Haskins in 1957 when he collected 200 guppies from a high-predation site in the Caroni drainage and moved them to a low-risk (and prior to his experiment, guppy-free) stream in the Turure River of the Oropuche drainage. This transplant was never published and might have been overlooked were it not for serendipitous sampling of the Turure River during an investigation of the genetic diversity of guppy populations in Trinidad (Shaw *et al.* 1991). This, and a subsequent study (Shaw *et al.* 1992), revealed that guppies in the Turure River bore the genetic signature of the Caroni drainage even though they were geographically part of the Oropuche drainage. From the genetic data it was possible to conclude that the descendants of the founder fish had not only colonized the Upper Turure River but also moved downstream below the barrier waterfall and replaced the indigenous guppy population in the Lower Turure River.

The guppies that were introduced to the Upper Turure experienced a reduction in predation risk. There are costs of devoting too much time and energy to antipredator behaviour (Magurran & Seghers 1991), but these are much less than the costs of failing to employ appropriate predator evasion tactics when required. As there is often variation in the incidence of predation risk during ecological time, for example as predator population densities change, there may be good adaptive reasons why antipredator behaviour should be retained over an evolutionary timescale. Indeed, the costs of antipredator behaviour might be so low in any case that it diminishes only as a consequence of non-adaptive decay resulting from accumulating mutations, which reduce the incidence of the relevant genes in the population. For these reasons we might anticipate that antipredator behaviour is lost much more gradually than colour patterns are modified or life histories change. Nonetheless, evolution of antipredator behaviour is apparent over the time frame provided by the Haskins experiment. The 34 years that elapsed between the introduction and its rediscovery were marked by a significant (heritable) decrease in the schooling tendencies of both male and female guppies (see figure 1). Schooling, as was noted earlier, is an effective antipredator behaviour and varies adaptively in Trinidadian guppy populations (Seghers 1974; Magurran & Seghers 1994*b*). By Reznick *et al.*'s (1997) calculations, 34 years represent approximately 60 generations. An equivalent investigation of Endler's Aripo introduction 16 years after the transplant had occurred revealed only a non-significant trend towards a lower schooling tendency (Magurran *et al.* 1995; Carvalho *et al.* 1996; figure 1).

Each of these studies leads to the same conclusion: that guppy populations in Trinidad show marked evolution over a time period that is not only short in evolutionary terms, but also comprehensible in human ones. This occurs for traits that might be expected to be relatively resistant to evolutionary change (antipredator behaviour in the above example) as well as for ones for which rapid evolution is to be anticipated.

4. THE RELATIONSHIP BETWEEN REPRODUCTIVE ISOLATION AND POPULATION DIFFERENTIATION

Given the speed and magnitude of evolutionary change in Trinidadian guppy populations it seems reasonable to suppose that they are in a state of incipient speciation. After all, as was noted above, such populations differ more, in a variety of traits, than some well-established species. It is therefore perplexing to discover that this is not the case. Molecular analyses (Carvalho *et al.* 1991; Fajen & Breden 1992; Magurran *et al.* 1995) reveal that guppy populations in the Caroni and Oropuche drainages diverged in the order of 500 000 years ago. This translates into a minimum of one, and possibly two, million generations. Despite this long separation there is no evidence that these populations are reproductively isolated. Magurran *et al.* (1996) examined female preferences in guppies from the Tacarigua River (Caroni drainage) and the Oropuche River (Oropuche drainage). These fish were as likely to solicit matings from males from the alien drainage as from their own (figure 2*a*). It could be argued that an evolutionary history of predation risk tends to diminish female choice (Iwasa & Pomiankowski 1991, 1994; Pomiankowski *et al.* 1991; Pomiankowski & Iwasa 1993), and it was the case that fish in the study by Magurran *et al.* (1996) came from populations that co-occur with *Crenicichla* and other predators. However, another study (Endler & Houde 1995), which included fish from a variety of predation regimes and drainages, also indicated that females do not actively discriminate against males from genetically divergent populations. Figure 2*b* illustrates the outcome for those comparisons, which examined female choice across the Caroni/Oropuche divide. In none of the three cases, including the one in which both populations of fish came from low-risk localities, do females treat males from the other drainage as less (or more) attractive than males from their own population. When the 11 populations in their study were taken into account, and all native and alien data pooled, there is some evidence that females are significantly more attracted to males from their own population than those from different populations ($t_{1318}=2.74$, $p<0.01$; Endler & Houde 1995). However, in only 5 out of the 11 populations is the preference for native over alien males significant and neither drainage nor predation risk affect the strength of the response. These results may be of statistical significance, but their biological significance is less clear. Matings between fish from different drainages also produce viable offspring (Endler & Houde 1995; Endler 1995) so there is, to date, no evidence that postmating isolation operates either.

5. WHY HAVE GUPPIES NOT SPECIATED?

How can we reconcile the evident potential for speciation in the guppy with the reality that it is not occurring? Endler (1995) lists three reasons why guppies have failed to speciate. These are ephemeral habitat gradients, the decline of female preferences in high predation areas and

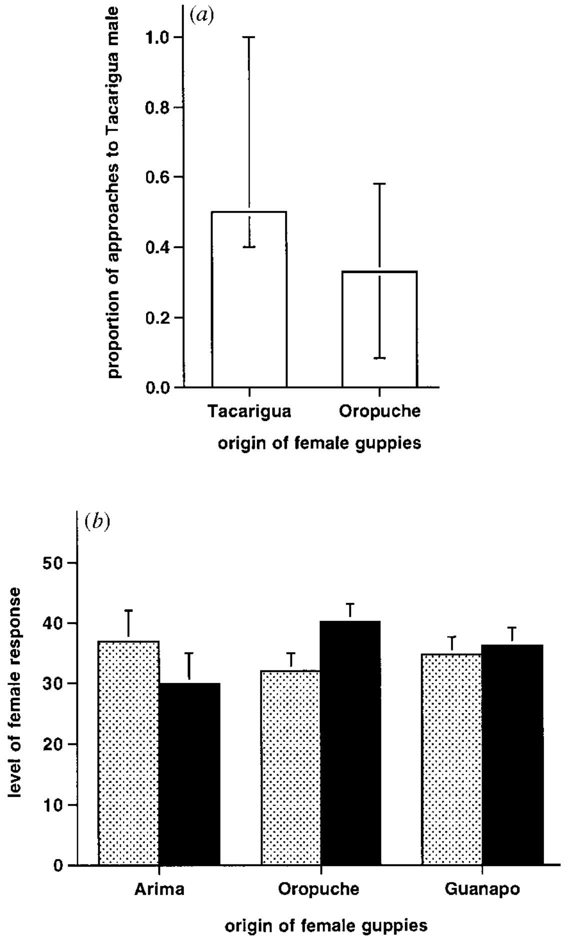

Figure 2. Female guppies do not appear to discriminate against males from genetically divergent populations. (*a*) Summarizes a study (Magurran *et al.* 1996) in which virgin female guppies from the Tacarigua River (Caroni drainage) and Oropuche River (Oropuche drainage) were given the opportunity of mating with males from both rivers. The graph shows the median proportion of approaches (plus quartiles) by both sets of females to males from the Caroni drainage. This approaching, or gliding, behaviour is a strong indicator of female preference (Liley 1966). There was no significant difference between the two sets of females in their preference for Caroni males (Mann–Whitney test, $n=10$, $z=0.24$, $p=0.80$). (*b*) Endler & Houde (1995) also carried out an extensive analysis of Trinidadian guppies in which female preferences for males from their own population were contrasted with their preferences from males from alien populations. Some of the comparisons examined female choice between the Caroni and Oropuche drainages. These are shown here. A female's response was measured as the fraction of a male's sigmoid displays that persuaded her to cease other activities and glide unambiguously towards him. As females were virgin at the outset they remained receptive to male courtship for the duration of the trial. The mean female response (following an arcsin transformation) and standard error are illustrated for three populations: females from Arima 6 (a low predation site in the Caroni drainage) in relation to males from their own population and males from Quare 6 (a low predation population in the Oropuche drainage); females from Oropuche 1 (a high predation population in the drainage of the same name) with their own males and males from Guanapo 6 (a medium predation site in the Caroni drainage); and females from Guanapo 6 in relation to Guanapo 6 males and males from Oropuche 1. Stippled bars represent the female's own drainage.

the scale of the selection regimes. Over part of their range in Trinidad guppies do indeed occur in ephemeral habitats. These tend to be low-order streams in the upper reaches of rivers and form the classic low-predation, *Rivulus*, sites that have proved indispensable to biologists. Other short-lived guppy habitats include pools, ditches and wetlands, which may be subject not merely to natural perturbations, but also to human ones, such as pollution and drainage. It is therefore possible that guppy habitats do not persist for long enough for reproductive isolation to arise. An additional factor is that the environmental boundaries, such as barrier waterfalls or riffles, that help separate populations and prevent gene flow may be even more transitory than the habitats themselves. However, the impressive speed with which guppy populations evolve in response to selection (within 10^1 to 10^2 generations) implies that events that are ephemeral in geological terms (occurring, for example, over 10^3 or 10^4 years) are unlikely to be the sole reason why speciation has not taken place. Furthermore, as noted above, molecular analyses of populations in the Caroni and Oropuche drainages indicate that reproductive isolation has not arisen even when there has been ample time for it to have done so. This contrasts starkly with the case of cichlids in the African Great Lakes of Victoria, Malawi and Tanganyika (Meyer *et al.* 1990; Meyer 1993). Each of these lakes is home to large numbers of endemic cichlids, some of which are very recent in origin. For example, Lake Nabugabo has been isolated from Lake Victoria for only about 4000 years yet has five endemic cichlids (Greenwood 1965). Some Lake Malawi cichlids may even have speciated within the last few hundred years (Owen *et al.* 1990), and Johnson *et al.* (1996) deduce, on the basis of sediment cores, that Lake Victoria was dry some 12 500 years ago and that all its 500 cichlid species must have evolved since then.

Can female preferences provide the answer instead? It has already been noted that females from high-predation regimes may be less choosy than their counterparts from safer localities. After all, it seems plausible that females that do not need to spend much time evading predators will have more opportunities to appraise the merits of potential mates. Unfortunately, data from Trinidadian guppy populations provide only partial support for this idea. Endler & Houde (1995) used the amount of variance in female responsiveness (to males) explained by male traits as a measure of the strength of preference. The average values for females (exposed to males from their own population) were 54% for low-predation (*Macrobrachium*) populations versus 33% for high-predation (*Crenicichla*) populations. *Macrobrachium* is a genus of freshwater prawns abundant in Trinidad, particularly in rivers that drain the northern slopes of the Northern Range. The most widespread species, which can act as a minor guppy predator, is *M. crenulatum*. *M. crenulatum* typically occurs with *Rivulus*. However, when Endler & Houde (1995) carried out the same analysis for the two other low-risk (*Rivulus* only) sites in their investigation the strength of preference was only 27%. There is no doubt that low-risk localities in northern flowing drainages are characterized by strong female preferences, but caution is needed before concluding that low-risk populations in other drainages behave in an identical fashion. In addition, low-risk sites tend to be more oligotrophic than high-risk ones, with the result that fish, of both sexes but particularly females, need to devote a greater proportion of their time to foraging (Magurran & Seghers 1994*c*).

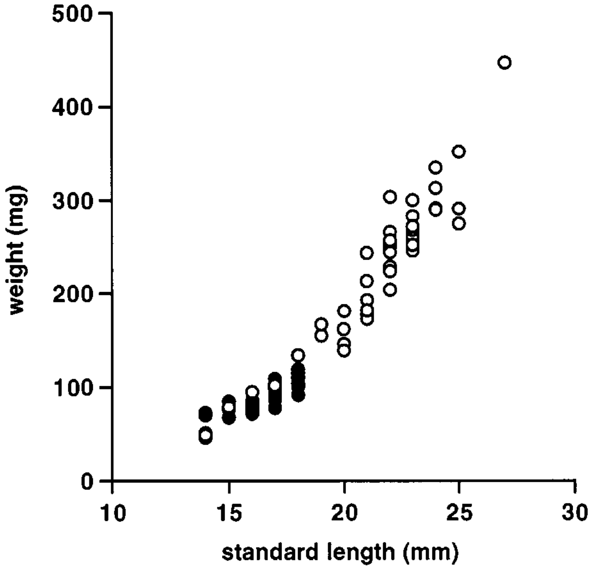

Figure 3. The weight/length relationship for guppies in the Upper Tunapuna (low risk) population. Data were collected during the 1994 dry season. Females are represented by open symbols, males by closed ones. Note that females are generally larger than males.

Endler's final explanation is that the distance over which gene flow occurs is large in relation to the scale at which selection takes place. Endler (1977, 1995) has estimated the scale of gene flow as 0.75 km of river. Trinidadian rivers are relatively short with discontinuities in predation regime occurring at intervals of a few kilometres or less. Thus, although behaviour and other traits can evolve rapidly as a consequence of selection exerted by predators, a steady influx of genes from populations under other selection regimes may undermine differentiation. Gene flow must be the key to understanding why speciation has not occurred in Trinidadian guppy populations, but what are the factors that bring it about? To answer this question it is necessary to look more closely at the guppies themselves.

6. SEXUAL DIMPORHISM

One of the most striking features of guppies is their marked sexual dimorphism. Female guppies are larger than males. In Trinidadian populations, female standard lengths usually exceed 20 mm, often by considerable margins. The comparative figures for males are 13–18 mm (Liley & Seghers 1975). These length differences translate into much larger differences in body mass (see figure 3). Sexual dimporhism in size is largely a consequence of reproductive biology. Females continue to grow after maturity and their fecundity is related to their body size (Reznick 1983), which is in turn a consequence of their foraging efficiency (Magurran & Seghers 1994*a*). Feeding rate is correlated with size in females but not in males (Dussault & Kramer 1981). This is undoubtedly because male growth is determinate and virtually ceases after sexual maturity. Although there is some evidence that male body size is used as a criterion of quality during female choice (Reynolds & Gross 1992), greater weight is placed on tail length and particularly on colour pattern (Endler & Houde 1995). The trade-off between body size and reproductive success thus differs dramatically between the sexes.

Even more impressive are the colour differences. Females have a cryptic beige coloration, presumably as a defence against predation. It is the males, however, that prompt some of the local Trinidadian names for the species—'red tails' or 'seven colours'—and have led to guppies becoming one of the most popular of aquarium fish. It is probably no coincidence that, in their classification, Endler & Houde (1995) recognized seven colour categories: fuzzy black, black, orange (including red), yellow, silver, blue and bronze-green. Haskins & Haskins (1950) first realized the significance of male colour patterns in sexual selection. Since then a series of papers have documented patterns of female preference and male coloration and the guppy is now firmly established as a model species for testing ideas about sexual selection and female choice (see Endler 1978, 1980, 1983; Endler & Houde 1995; Houde 1987, 1988, 1997; Houde & Endler 1990; Breden & Stoner 1987; Kodric-Brown 1985). Endler & Houde (1995) found that females in most of the populations they investigated had a preference for orange/red. Caretonoid colours (orange, red and yellow) are honest indicators of foraging efficiency (Kodric-Brown 1989) and parasite load. In addition, females may use display rate as indicators of male fitness (Nicoletto 1991, 1993). Sensory drive models (Endler 1991, 1992), which predict that the environment in which the signallers live, as well as the precise nature of their sensory systems will help shape sexual selection, can also be invoked to explain geographic variation in male coloration (Endler & Houde 1995).

Like other poeciliids, the guppy has internal fertilization and the female gives birth to live young (Wourms 1981). Wild females typically produce broods of between two and eight young once a month (Reznick & Endler 1982; Reznick & Miles 1989). This is an ovoviviparous species, in other words one in which the female provides no additional nourishment to her offspring after fertilization (Thibault & Schultz 1978). She does, however, make a major energetic investment during egg production (Reznick 1983; Reznick & Yang 1993; Reznick & Miles 1989). The resources devoted to each offspring, relative to the male's investment in his gametes, ensures that the female is the choosy sex in this species. Females can store sperm and need only a single mating to produce broods over many months (Winge 1937). They are receptive to male courtship only infrequently, that is either as virgins or in the first 24–48 h following parturition (Liley 1966; Crow & Liley 1979). As a female's reproductive output is determined by the size and number of broods she can produce during her life, at other times her priorities are predator avoidance and foraging (Magurran & Seghers 1994*c*).

Whereas a female's reproductive success is ensured if she has mated successfully and manages to survive, a males fitness will depend on the number of females he inseminates. Because of female choice (Houde 1987, 1988; Houde & Endler 1990), and possibly also as a result of male–male competition (Kodric-Brown 1992) and mate copying (Dugatkin 1992; Dugatkin & Godin 1992), some males will achieve many more matings than others. Males use a modified anal fin, or gonopodium, as an intromittent organ (Constanz 1989) to transfer sperm to females and adopt two mating tactics. They can either employ a sigmoid display in which the body is arched into a characteristic 's' shape and the fins are extended and quivered (Liley 1966), or they may dispense with courtship and opt for sneaky mating during which the gonopodium is thrusted towards the females genital pore (Luyten & Liley 1985). Sigmoid displays test the receptivity of females and exhibit a male's colours to their best advantage. If a sigmoid display fails to elicit any response, or if two or more males are pursuing the same female, sneaky mating is used instead. All males adopt both tactics though they vary in the extent to which they use them (Magurran & Seghers 1990*b*) as well as in their overall level of reproductive activity (Matthews *et al*. 1997).

7. THE BATTLE OF THE SEXES

Many aspects of the biology and behaviour of female guppies reinforce the population differences that natural selection has generated. For example, females, probably as a consequence of their increased investment in anti-predator behaviour, have a higher schooling tendency than males. And, as a study of wild guppies in the Tacarigua River in Trinidad revealed (S. W. Griffiths and A. E. Magurran, unpublished data), they prefer to associate with familiar schooling partners. In these choice tests fish were given the opportunity of schooling with same-sex individuals from their own school (that is the one they belonged to in the wild) or a different one. Females exerted a clear preference for fish from their natural school. Males did not. Given that it takes in the order of 12 days for female guppies to develop preferences for familiar individuals (Griffiths & Magurran 1997*a*), the existence of such behaviour among wild fish (Griffiths & Magurran 1997*b*) indicates that guppy schools are not transitory social groups. Rather it appears that the wild schools are based around female alliances and that their structure remains stable over time. Males, on the other hand, seem to move between schools as mating opportunities become available. This is reflected in their greater mobility over the short term (see figure 4). Mark–recapture studies (D. N. Reznick, personal communication) also indicate that males are more likely to emigrate than females. It is not yet known whether guppy schools represent kin groups. A previous study using multilocus genetic fingerprinting indicated that individual members of wild guppy schools were more closely related than the average for the population (Magurran *et al*. 1995), but that the level of relatedness within schools was low, in the range of 4th order relatives (Lynch 1988). However, the schools in Magurran *et al*. (1995) were analysed without regard to gender. With hindsight it is clear that sex differences in behaviour have important implications for patterns of kinship within schools. The tendency of females to remain in cohesive groups (as well as the ability of guppies to school from birth (Magurran & Seghers 1990*a*)) leaves open the possibility that they could be related, whereas the mobility of males means that they are probably not.

An important consequence of the tendency of females to associate with familiar schooling partners, irrespective of

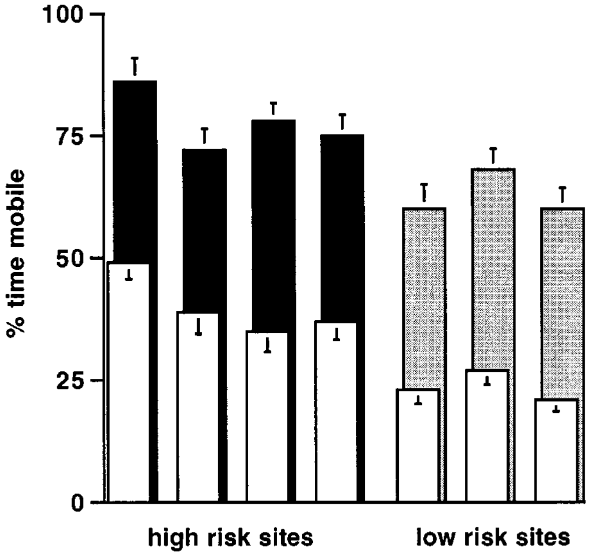

Figure 4. Males are more mobile than females. This graph illustrates the proportion of time that wild fish of both sexes spend actively swimming. Mean values (and standard error) are shown. Thirty individuals were recorded per population. There were four high-risk (*Crenicichla*) localities (in the Aripo and Tacarigua Rivers) and three low-risk (*Rivulus*) localities (in the Aripo and Tunapuna Rivers) in the study. Females are represented by open bars, males by closed ones. Data were collected as part of the investigation described in Magurran & Seghers (1994*c*).

whether they are related or not, will be the reduction of gene flow. This ought to be reinforced by female preferences for males of certain colour patterns (Houde 1987, 1988, 1997; Houde & Endler 1990), always assuming that these preferences can be exercised in the wild, and by mate-copying (Dugatkin 1992; Dugatkin & Godin 1992), as long as it operates in nature to the extent to which it is seen in the laboratory (see also Lafleur *et al.* 1997). Lande (1981) recognized that a genetic correlation between sexually selected traits (in males) and preferences (by females) could result in rapid speciation. Such a genetic correlation occurs in guppies (Houde 1994). In short, female partner preferences, of both the social and sexual kind, facilitate the evolution of reproductive isolation (see, also, Butlin & Treganza, this volume; Coyne & Orr, this volume).

Although female guppies appear to show strong site fidelity there are infrequent occasions on which they can move considerable distances from their place of birth. This might happen, for instance, during a hurricane or tornado (there are anecdotal accounts of fish landing in people's gardens in Trinidad in the course of such events) or after a flood. Unsuccessful predation attempts may also occasionally result in fish movement. Sperm storage (Winge 1937) means that a single adult female translocated in this way has the potential to found a new population. It is already known, for example, that a single female can produce up to 41 offspring from six successive broods without reinsemination and also that guppies in more naturally isolated populations show a greater capacity to store sperm (Carvalho *et al.* 1996). It is impossible to confirm that any wild guppy populations are the product of such extreme founder effects, though the genetic evidence reveals a number of cases where there are severe population bottlenecks that probably resulted from chance colonizations of a similar kind (Carvalho *et al.* 1996). There is, however, a well-documented case of a single guppy female founding a viable population. This occurred in 1981 when Professor J. S. Kenny, the then Head of the Zoology Department at the University of the West Indies in Trinidad, collected one pregnant female from a wild population and placed her in an ornamental pond. Her descendants thrived. When the allozymic structure of the population was examined a decade later it became clear that a marked reduction in heterozygosity and significant genetic divergence had occurred (see figure 5). Indeed, the differentiation between the source and transplanted populations was greater even than that between the Caroni and Oropuche drainages (Carvalho *et al.* 1996). Although the role of founder effects in speciation remains controversial (Barton 1989) the ability of single females to found populations, and the genetic consequences that follow, have important implications for differentiation.

Females may facilitate population differentiation and speciation, but males almost certainly hinder it. There are essentially two ways in which male behaviour will increase gene flow. The first, as already noted, is greater male mobility relative to females. The second, and possibly more important, factor is mating behaviour. One of the most striking features to the observer of a wild guppy population is the incidence of sneaky mating behaviour. A typical female is subjected to an average of one sneaky mating attempt per minute (figure 6; see, also, Magurran & Seghers 1994*c*; Magurran *et al.* 1995). It is likely that very few of these mating attempts are successful, yet the ardour with which males pursue females and the time and energy that they invest in attempting copulations implies that, in evolutionary terms, this is an important strategy. We now know that males that engage most persistently in sneaky courtship have highest reserves of sperm (Matthews *et al.* 1997). We also know that some 15% of wild females, who are at a stage in their reproductive cycle during which they are not receptive to male advances, have sperm in their gonopores that could only have come from sneaky matings (I. M. Matthews and A. E. Magurran, unpublished data). Sperm competition is an inevitable outcome of the mating system of the guppy, though as yet, the fate of sperm obtained from sneaky matings is unknown. However, if even a small fraction of sneaky matings result in paternity, female choice will be undermined and gene flow facilitated. Male pursuit of reproductive success could well be the key to understanding why guppy populations have not speciated, even though many of the ingredients for rapid speciation seem to be present. Parker & Partridge (this volume) note that speciation will be more rapid in circumstances where females generally win mating contests than is situations where males do. Trinidadian guppies seem to offer an excellent example of the evolutionary consequences of this battle of the sexes.

8. SEX AND SYMPATRIC SPECIATION

There are other ways in which the battle of the sexes may constrain differentiation. It has recently been recognized that phenotypic variation within populations may represent adaptations to particular ecological conditions (Robinson & Wilson 1994). For example, individual members of a species

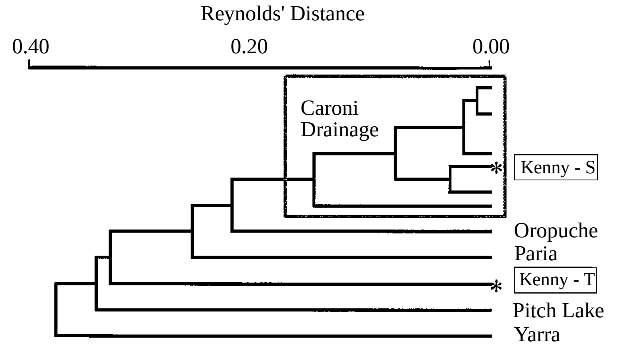

Figure 5. Genetic consequences of an extreme founder effect. This figure shows a dendrogram of Reynolds' (Reynolds *et al.* 1983) genetic distances between samples of guppies from Trinidad. The dendrogram is a consensus tree based on bootstrapping (see Carvalho *et al.* 1996 for details). Calculations (UPGMA) are based on frequencies of 37 alleles across 25 gene loci. A clear separation between the Caroni and Oropuche drainages is evident. The genetic divergence between the Kenny source (Kenny-S) and Kenny transplant (Kenny-T) populations after 10 years is even more impressive. Redrawn from Carvalho *et al.* (1996).

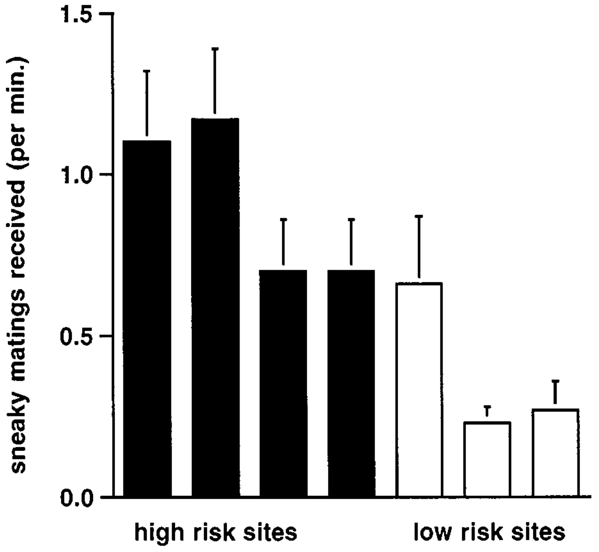

Figure 6. Wild female guppies in Trinidad are subjected to a constant barrage of sneaky mating attempts. This graph illustrated the mean frequency (and standard error) of sneaky matings experienced by females in seven Trinidadian guppy populations (see figure 4 for details). The figure is redrawn from Magurran *et al.* (1995).

may develop distinct morphs associated with feeding specializations. Most often two forms develop: a benthically feeding one with a deep body and a downward pointing mouth, and a pelagic form with a more fusiform shape better suited to manoeuvring and chasing mobile prey. Feeding morphs are most prevalent in low-diversity systems where there are few specialized foraging competitors. Robinson & Wilson (1994) documented coexisting benthic and pelagic morphs in 38 lacustrine species of fish. These include whitefish (Coregonidae: Lindsay 1981; Todd *et al.* 1981), sunfish (Centrarchidea: Ehlinger & Wilson 1988), cichlids (Cichlidae: Meyer 1990*a*,*b*) and sticklebacks (Gasterosteidae: McPhail 1984, 1994). Such morphs may be a consequence of phenotypic plasticity in that the environment in which the fish develops plays a central role in shaping its feeding behaviour and body plan (Meyer 1987). For example, Wainright *et al.* (1991) found that the proportion of gastropod molluscs in the diet of pumpkinseed sunfish (*Lepomis gibbosus*) during ontogeny could be related to variation in the jaw morphology of the adult fish. Alternatively, feeding polymorphisms may have a genetic basis and will be expressed in offspring irrespective of the environment in which they develop (McPhail 1984; Schluter & McPhail 1992). In many cases, however, genetic and environmental factors interact during the development of such polymorphisms (Skúlason & Smith 1995). There can also be selection for phenotypic plasticity in its own right. This appears to be especially prevalent in unstable habitats (Skúlason & Smith 1995).

One of the most dramatic examples of trophic polymorphism of all is provided by the arctic charr, *Salvelinus alpinus*. This species has a circumpolar distribution and occurs primarily in arctic and subarctic lakes and rivers, which have otherwise impoverished fish faunas (Johnson 1980). Sympatric forms of arctic charr have been identified in a number of localities, including Loch Rannoch in Scotland (Gardner *et al.* 1988) and Lake Hazen in Canada (Reist *et al.* 1995). It is, however, in the Icelandic lake, Thingvallavatn, that the most impressive morphological divergence occurs. This lake supports four distinctive forms of charr (Skúlason *et al.* 1989, 1992, 1993; Skúlason & Smith 1995; Snorrason *et al.* 1994). These are a large benthivorous morph, a small benthivorous morph, a pelagic planktivorous morph and a piscivorous morph. The morphs differ markedly in appearance and size, occupy different habitats and distinct feeding niches. This diversification, driven by intraspecific competition for limited food resources, can lead to reproductive isolation (Snorrason *et al.* 1994). Laboratory tests indicate that a number of behavioural differences between the morphs are genetically based (Skúlason *et al.* 1993). The morphs also vary in age and size at sexual maturity, spawning coloration and spawning time (Skúlason *et al.* 1989). It appears that these differences have arisen in less than 2000 generations (Snorrason *et al.* 1994). African cichlids also provide strong evidence for sympatric speciation. Schliewen *et al.* (1994) found monophyletic species flocks in two volcanic crater lakes in Cameroon. These lakes are small, 4.15 and 0.6 km^2, and ecologically monotonous. There are no obvious barriers to gene flow among mobile creatures such as cichlids, yet the lakes are home to 11 and 9 endemic species, respectively. Schliewen *et al.* (1994) argue that ecological diversification may have played a key role in speciation after colonization and highlight the fact that in one lake, Bermin, the basal lineages of the flock separate the pelagic and benthic feeders. Such ecological diversification sets the stage for assortative mating, which is a prerequisite for reproductive isolation.

Guppies occur in a wide variety of habitats in Trinidad ranging from the species-rich, often turbid, waters of the lowlands to the species-poor communities found in clear mountain streams (Kenny 1995). The mountain populations live in oligotrophic sites and spend a large proportion of their time foraging (Magurran & Seghers 1994*c*). There are few fish competitors for food and, presumably, strong selection for efficient foraging. Females have offspring to provision and males inseminations to procure. In the diverse lowland communities, on the other hand, there are many potential competitors for feeding sites, but as these localities are more productive, foraging occupies a smaller proportion of the time budget (Magurran & Seghers 1994*c*). Habitat use in predator-rich communities is also constrained by risk (Seghers 1973). Robinson & Wilson (1995) tested the idea that guppies reared under different feeding conditions would develop appropriate morphologies. Treatments included a floating food regime and one in which fish were forced to forage benthically. Male guppies exposed to surface food developed longer bodies and skulls and took on the fusiform shape often seen in pelagic morphs, whereas bottom feeders became deeper-bodied. Interestingly, females did not show any plasticity in body form, even in skull morphology. This led the authors to suggest that there could be sexual dimorphism in this species in their degree of phenotypic plasticity.

Robinson & Wilson (1995) used fish descended from guppies collected in 1988 from the Upper Turure, a low-predation, low-diversity mountain stream. These fish seem to be ideal candidates for demonstrating induced morphological diversity. However, as was noted above, Caryl Haskins transplanted guppies from a high predation site in the Caroni drainage to the Upper Turure in 1957 so the fish that Robinson & Wilson (1995) investigated were ultimately derived from a lowland, and possibly less phenotypically plastic stock. It would be interesting to test the hypothesis that the diversity of the community, as well as its productivity, is associated with the potential for morphological diversity in guppy populations.

However, it could also be argued that discrete feeding morphologies, in the classic sense, are unlikely to occur in guppies. This is because different morphs already exist, reflecting the separate reproductive agendas of the two sexes. Females, by virtue of their perpetual pregnancies, are deep-bodied and thus pre-adapted for benthic foraging. Females are also much larger than males and therefore able to deal with a wider range of food items. Males need to move rapidly through the water in search of copulations. Sneaky mating calls for agility, especially as a competing male may inseminate the female first. A streamlined, fusiform body plan is an essential requirement for a male guppy.

It might be expected therefore that, in the wild, particularly in oligotrophic low-diversity sites, females will forage benthically and males will show a greater tendency towards pelagic feeding. An investigation of the behaviour of guppies in the Upper Tunapuna, a mountain stream in Trinidad's Northern Range, supported this hypothesis. The majority of females were bottom-feeders, picking algae and small invertebrates off the substrate. Many males fed benthically too, but a significantly greater proportion (Wilcoxon test, $z=2.8$, $p<0.01$; figure 7) fed in open water. To do this they held station in the current and ingested small particles of food. There was no evidence of surface-feeding in either sex. However, *Rivulus*, which also occurs in the Upper Tunapuna, is well-adapted for surface-feeding and probably outcompetes guppies in this foraging mode. In the light of these results it is perhaps not surprising that Robinson & Wilson (1995) could detect no phenotypic plasticity in the female guppies in their investigation. They were also, it seems, correct in concluding that guppies are sexually dimorphic in this trait.

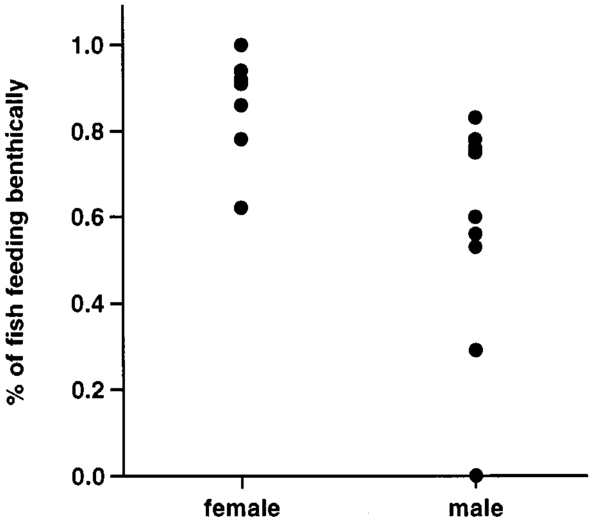

Figure 7. Male and female guppies differ in their foraging behaviour. This graph shows the proportion of fish in ten isolated pools of the Upper Tunapuna River (low risk) feeding benthically (on the bottom) as opposed to pelagically (in mid-water). Each pool was carefully scanned and the feeding location of all foraging fish noted. Clear, shallow water and good visibility meant that fish could be observed without difficulty. No fish were seen to feed from the surface during the study, although this behaviour is apparent on occasions at other localities. A total of 233 females and 123 males were recorded. These data were collected during June 1997.

9. CONCLUSIONS

Sexual selection has long been identified as a significant evolutionary force. Some of the earliest papers on Trinidadian guppies (Haskins & Haskins 1949, 1950) focused on sexual selection as a potential reproductive isolating mechanism. Yet, it is only recently that the evolutionary consequences of sexual conflict, which is the inevitable outcome of differential investment in offspring by the two sexes, have become apparent. In some circumstances sexual conflict may fuel evolution (Rice 1996; Rice & Holland 1997), in others it seems to constrain it (Magurran 1996). The empirical insights gleaned from the Trinidadian guppy system dovetail with the theoretical ones gained from the modelling approach of Parker & Partridge (this volume). Females will, it seems, typically act as a force in favour of reproductive isolation, males as a force against it. This paper has highlighted two ways in which the battle of the sexes can inhibit speciation. First, the pursuit of copulations by males seems to be a potent force in maintaining gene flow between populations that might otherwise become reproductively isolated as a result of natural selection and female choice. Second, sexual dimporhism, which is itself a consequence of sexual conflict, reduces the opportunity for the development of feeding polymorphisms that could open the door to sympatric speciation. Many details of the relationship between sexual conflict and speciation remain to be resolved and the topic seems guaranteed to offer profitable lines of research for future investigators.

What is clear is that sexual conflict plays a major role in determining whether population differentiation does translate into speciation.

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