Complex origins of variation in the sexual behaviour of male Trinidadian guppies, *Poecilia reticulata*: interactions between social environment, heredity, body size and age

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Abstract. Field observations have shown that there are inter-population differences in the sexual behaviour of male guppies in Trinidad. The greatest differences are between guppies that co-exist with different predators. Here, the sexual behaviour of male Trinidadian guppies was studied to determine to what extent these differences in behaviour evolved in response to selection pressure by the predators, to what extent they are an environmentally induced response to aspects of guppy biology that covary with the predators and to what extent these factors interact. To do this, male offspring of guppies from different predator localities were reared in the laboratory under conditions designed to mimic natural variation in wild populations. Two aspects of young male guppies' social environment were manipulated: (1) population demography and (2) origin (predator locality) of conspecifics. Heredity (origin of the males' parents) was responsible for only a small proportion of the variation in sexual behaviour; social environment had a much greater influence. Also, inter-population variation was found in the degree to which a male's behaviour was affected by demographic conditions and in the relationship between a male's body size and his rate of courtship. Male sexual behaviour also varied with male age and with the origin of the female being courted. Various components of male sexual behaviour (e.g. courtship, mating attempts) were influenced to different degrees by the factors examined. Therefore, inter-population differences in male sexual behaviour result from complex interactions between heritable factors, social environment, male age and male size.

Flamboyant secondary sexual characteristics, both morphological and behavioural, have evolved in response to sexual selection (e.g. Rand & Ryan 1981; Houde 1987; Andersson 1992). Predation is one agent of natural selection that can counteract the effects of sexual selection. As a result of predation pressure, sexual characteristics can be modified through changes at the genetic level (e.g. Semler 1971; Moodie 1972; Strong 1973; Endler 1978, 1980, 1983), or only at the phenotypic level, for instance, by reducing courtship or time spent searching for mates (e.g. Ryan 1985; Endler 1987; Magurran & Seghers 1990; Magurran & Nowak 1991; Travers & Sih 1991).

Field studies reveal considerable inter-population variation in the sexual behaviour of male Trinidadian guppies including differences in the rates at which males court and attempt copulations (Farr 1975; Luyten & Liley 1985; Magurran & Seghers 1994). The greatest differences are between guppies that co-occur with one major predator, *Crenicichla alta*, and those that co-occur with another major predator, *Rivulus hartii* (Farr 1975). *Crenicichla* is a large cichlid (up to 25 cm) which preferentially preys on large, sexually mature guppies; *Rivulus* is a small killifish (up to 8 cm) which preys predominantly on small, immature guppies (Seghers 1973, 1974; Liley & Seghers 1975). Guppy populations that co-occur with *Crenicichla* differ from those that co-occur with *Rivulus* in density, size distribution and sex ratio (Haskins et al. 1961; Seghers 1973; Reznick & Endler 1982; F. H. Rodd & D. N. Reznick, unpublished data). Guppies from these populations also show differences in their colour patterns, life-history traits and female mate-choice preferences (e.g. Haskins et al. 1961; Seghers 1973, 1974; Farr 1975; Liley & Seghers 1975; Endler

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1978, 1980; Reznick 1982; Reznick & Endler 1982; Luyten & Liley 1985; Houde 1988a; Stoner & Breden 1988; Houde & Endler 1990; Magurran & Seghers 1990, 1991). In addition, guppies in *Crenicichla* localities show more strongly developed schooling behaviour and are less aggressive than those in *Rivulus* localities (Seghers 1974; Farr 1975; Magurran & Seghers 1991). For many of these traits, there is evidence that the differences have a heritable basis and that they have evolved in response to predation pressure (e.g. Endler 1978, 1980, 1983; Reznick 1982; Reznick et al. 1990).

In this study, we evaluate four factors that could contribute to the differences in the sexual behaviour of male guppies in *Rivulus* and *Crenicichla* localities.

(1) The differences could have a heritable basis (Farr 1975; Luyten & Liley 1985), that is, they could have evolved in response to selection by one or both of the predators or some correlated aspect of their environments (Reznick 1982).

(2) The differences could be environmentally induced. The differences in the demographies and behaviour patterns (e.g. schooling) of guppies from *Rivulus* and *Crenicichla* localities suggest that the rates and types of interactions between individuals within a population differ (Farr & Herrnkind 1974). These differences in interactions could, in turn, influence a male's sexual behaviour (Lott 1991).

(3) The differences in the sexual behaviour of male guppies could also result from interpopulation variation in the degree to which individuals adjust their behaviour to social cues (Krebs & Davies 1987; Lott 1991). In one type of predator locality, guppies may have the flexibility to respond to changes in population demography; in the other type of locality, such flexibility might not be present.

(4) If sexual behaviour is influenced by body size or post-maturation age (Huntingford 1984; Caro & Bateson 1986), the observed interpopulation differences in sexual behaviour could be a result of differences in the average ages and sizes of males in those populations (F. H. Rodd & D. N. Reznick, unpublished data). We predicted that the reproductive strategies of male guppies would change with age because their coloration is not fully developed at maturity (personal observation) and because sexual interactions can depend on male coloration (Houde 1988b;

Kodric-Brown 1989). We also predicted that male courtship would be influenced by body size given the evidence for such a relationship in several other poeciliid species (e.g. Farr et al. 1986; Ryan & Causey 1989; Travis & Woodward 1989). Age and body size could have independent effects on male guppy behaviour because males grow little after they mature (Reynolds et al. 1993; personal observation).

We evaluated the contributions of these factors to variation in male sexual behaviour by doing a multi-factorial experiment where we reared juvenile guppies from both localities in controlled conditions and measured their sexual behaviour as adults. The juveniles were reared in laboratory populations composed of guppies that are known to differ for several behaviour patterns (i.e. from *Rivulus* and *Crenicichla* localities). The populations in which the juveniles were reared had demographies (densities, size distributions and sex ratios) that were designed to mimic differences between natural populations of guppies in *Rivulus* and *Crenicichla* localities. We evaluated the influence of age on male sexual behaviour by observing each male on three separate occasions within a few weeks of attaining sexual maturity. We also investigated the influence of male body size on sexual behaviour.

METHODS

Experimental Design

Juvenile male guppies (the test males) were reared under different social conditions and, at maturity, their sexual behaviour was observed under standardized conditions. The three main factors tested in this experiment were heredity (the origin of the test male's parents), the general behaviour of resident conspecifics (the origin of the guppies with whom the test male was reared), and population demography (the type of demography in which the test male was reared).

We established populations of guppies from *Rivulus* and *Crenicichla* localities in large aquaria in the laboratory. The demographies of these populations of resident conspecifics were designed to simulate those of guppy populations either in *Crenicichla* localities (low density, even sex ratio, high proportion of juveniles) or in *Rivulus* localities (high density, female-biased sex ratio, low proportion of juveniles; Haskins et al. 1961;

Seghers 1973; Reznick & Endler 1982). The populations were composed as follows: *Rivulus*-type demography: five adult females, three adult males, two subadults; *Crenicichla*-type demography: two adult females, two adult males, two subadults. We added one test male to each aquarium and reared him to maturity. Test males were the offspring of guppies from either *Rivulus* or *Crenicichla* localities. To disentangle the influence of the residents' behaviour from that of population demography on male behaviour, we tested all combinations of residents' origin and residents' demography; hence, male offspring of parents from both localities were reared in four types of populations for a total of eight different treatments. Two replicate tanks of each treatment were run at all times. Treatments were assigned randomly to the available aquaria.

Adult residents in the treatment tanks were captured, as adults, at *Rivulus* and *Crenicichla* sites in the Northern Range Mountains in Trinidad. We collected guppies in September 1988, March 1989, February–March 1990 and March–April 1991 from four *Rivulus* localities and four *Crenicichla* localities (*Rivulus* sites: two tributaries to the Quare River, and tributaries to the Arima and Aripo Rivers; *Crenicichla* sites: the El Cedro, Aripo, Oropuche and Mausica Rivers; see Rodd 1994 for details). Annual collections meant that few residents had been in the laboratory for more than 1 year. Resident fish were chosen randomly from each locality and assigned randomly to a treatment tank.

Subadult residents were laboratory-born offspring of guppies from either *Crenicichla* or *Rivulus* localities and were kept in stock tanks prior to use in this experiment. They were distinguished from test individuals by the injection of a tiny drop of acrylic paint solution into their caudal peduncle (Rodd & Reznick 1991). This procedure did not appear to influence their behaviour. They were checked weekly and replaced as they approached maturity 4–6 weeks later. The rate of turnover was probably less than that experienced in the field where mortality rates can be as high as 40% per 12-day period (D. N. Reznick, M. J. Butler & F. H. Rodd, unpublished data).

We maintained the demographies of the experimental populations throughout the experiment by removing new-born individuals and by replacing the few individuals that died with those of similar size. The compositions of the populations varied from the original design for short periods when test males had matured and were awaiting behaviour testing (see below), when female siblings of the test males were present in the tanks (as part of another experiment; Rodd 1994) and when the next round of young test males had been added. Despite these deviations, the numbers of adult females and the total densities in aquaria with a *Crenicichla*-like demography were always lower (2–3 females; 6–10 total individuals) than those with a *Rivulus*-like demography (5–6 females; 11–15 total individuals). There was little overlap in adult sex ratio (females:males; *Crenicichla*: $\bar{X}=0.76$, range$=0.4–1.0$; *Rivulus*: $\bar{X}=1.18$, range$=0.8–1.7$) or in proportion of the population composed of immature animals (*Crenicichla*: $\bar{X}=0.37$, range$=0.28–0.56$; *Rivulus*: $\bar{X}=0.24$, range$=0.17–0.33$). Despite this variation in demography over the whole experiment, there was little variation in the conditions that individual test males experienced from the time they were placed in the treatment tank to the time their behaviour testing was complete.

The treatment tanks measured 31.6×76 cm and were filled with water to a depth of approximately 31.5 cm (intermediate between average depths observed in *Rivulus* and *Crenicichla* sites; Reznick & Endler 1982). Given space limitations and the need to have several individuals per aquarium, the range of densities of guppies used here (28–52 per m²) was higher than maximum densities observed in the field (25 per m²; Reznick & Endler 1982). However, guppies do school, especially in *Crenicichla* localities, and this increases the density that guppies experience in the field (Seghers 1974; Farr 1975). All tanks were maintained at $23.5 \pm 0.5°C$ in a controlled temperature room. Natural-coloured gravel covered the bottom of the tanks and floating plants (hornwort) provided cover for small individuals.

The fish were fed liver paste (beef liver and infant cereal) once or twice a day and newly hatched brine shrimp when available. We tried to ensure that food was not a limiting factor. It was dispersed so that all individuals had access to it. High-density treatment tanks received approximately twice the ration that low-density treatment tanks received.

Test males were born in the laboratory to females from either *Crenicichla* or *Rivulus* localities that had been isolated for up to several weeks

before parturition. Mothers were held in the laboratory for up to a year and were inseminated in the wild (three pairs of broods) and/or in the laboratory (14 pairs of broods) by males from the same site and predator locality. The female was removed from the young within 24 h of giving birth. The young were reared with no more than 12 (usually six to eight) of their broodmates in a 35·5 × 20·2-cm aquarium until they were introduced into the treatment tanks.

The test males were introduced into the treatment tanks when they were 5–6 weeks old (minimum size at which they were no longer at risk of being eaten by conspecifics). Introductions of test males from *Rivulus* and *Crenicichla* localities were paired so that one test male was added to each treatment tank within a 1-week period. All males from one locality in one introduction period were from the same brood. Subsequent introductions of new test individuals were made as previously added test males reached maturity. As males approached sexual maturity, we checked them daily to determine the date of maturation and we measured their standard length at that time. Maturation was considered complete when the gonopodial hood extended beyond the tip of the fin (Reznick 1990). The mean age at maturity was 95 days (range=67–158).

To measure sexual behaviour, we tested each male with one mature female (the stimulus female) in a small aquarium (35·5 × 20·2 cm, filled to a depth of approximately 16·5 cm). The tank was placed in a darkened room and was illuminated with a 40-W bulb suspended 11 cm above the water surface. Three sides of the tank were covered with tan paper. We began testing after the morning feeding (1000 hours) and ended testing before the afternoon feeding (1600 hours). Because male sexual behaviour is variable (e.g. Baerends et al. 1955; Liley 1966), we observed the behaviour of test males on three separate occasions. Because most adult males survive less than 8 weeks in the field (D. N. Reznick, unpublished data), we first tested the males' behaviour approximately 7–10 days after they attained sexual maturity. To minimize the effects of the test procedure on subsequent tests, the last two tests were done approximately 7–10 days after the previous test. The stimulus female was a mature, presumably pregnant, wild-caught female resident living in a treatment tank other than that of the male's own treatment (home) tank. To avoid

using receptive females (Crow & Liley 1979), we did not use females being chased by male residents in their home tanks. From one test session to the next, we tested males with females from alternate localities; we tested half of the males with a female from a *Rivulus* locality first. Males were never tested with the same female twice and all females were of a similar size. We placed the stimulus female in the test tank approximately 1 h before introducing the first male to be tested that day. For each test session, we added the male to the test tank and recorded the time of his first approach to the female. After allowing an acclimatization period of 10 min from the time the male was introduced into the tank, we scored the male's behaviour for 10 min and then returned him to his home tank. We collected data on a portable computer using an event-recording program (Noldus 1991).

Because the various components of male sexual behaviour (Table I) could be influenced differentially by the factors studied and because they apparently play different roles, we recorded the frequencies of all behavioural patterns and the durations of the sigmoid and posturing displays. Biting, display jumps and full copulations with the female's cooperation were extremely rare, so those data were not analysed.

For comparison with the test males, we observed the behaviour of males captured as adults in Trinidad (14 from each of *Rivulus* and *Crenicichla* localities). They were captured at the locations described above and were tested twice, approximately 20 days apart, within 6 weeks of capture. The behaviour tests were done using the procedure described above except that we placed these males in large stock tanks, containing adult male and female guppies, before and between tests. On their first test, all males were tested with the same wild-caught female from a *Crenicichla* locality, on the second, with a wild-caught female from a *Rivulus* locality.

Statistical Analyses

We used repeated-measures analyses of variance to determine whether the test males' behaviour changed between test sessions ('within subject' factor) and to examine the influence of the independent variables on the test males' behaviour ('between subject' factors; PROC GLM, SAS 1989). Data were transformed to meet the

Table I. Components of male guppy sexual behaviour*

Behaviour	Description
Approach	Male observes the female and moves towards her
Following	Male swims behind female when she moves away from him
Biting	Male nibbles in the vicinity of the female's urogenital opening
Courtship displays	
Posturing (dorsal fin erect)	Male positions himself in front of female at approximately 120° and observes her. This is the least intense courtship display
Posturing (dorsal fin folded)	As above but with dorsal fin folded
Sigmoid	Male positions himself directly in front of the female at approximately 90° to her, he arches his back and quivers. The most intense courtship display. Females are most likely to mate with a male after he performs this display
Display jump	Male darts off rapidly in one direction after the completion of some sigmoid displays
Gonopodial swing	Function not fully understood, possibly loading gonopodium with sperm
Half swing	Male moves his gonopodium forward, 90° from its resting postition
Full swing	Male moves his gonopodium fully forward, 180° from its resting position
Gonopodial thrust	Male's attempt to internally inseminate a female using his gonopodium (modified anal fin). The male contacts the female unless she moves away quickly
Copulation	Male transfers sperm to the female with his gonopodium, followed by post-copulatory jerking (male moves in front of the female and displays to her with a back-and-forth rocking motion)

*From Clark & Aronson 1951; Baerends et al. 1955; Liley 1966; Farr 1980a.

assumptions of this analysis as follows: gonopodial thrusts and total sigmoid display duration were transformed using ln(trait + 1) (Zar 1984). The other behavioural patterns were transformed using the square root of (trait + 3/8); this transformation is recommended when the data are counts of events with small sample sizes and/or some zero values (Zar 1984). It was not necessary to transform mean sigmoid duration. We used type III sums of squares because sample sizes were unequal among cells (SAS 1989). For the 'within subject' analyses, correlations between the variables were not constant over time so we adjusted the probability values using the Huynh–Feldt correction factor (SAS 1989). Because origin of the stimulus female influenced male behaviour (see below), we first considered female origin as an independent variable in these analyses. To do this, we only used the data for the first and third test sessions because each male was tested with females from the same predator locality in those two sessions. Where there were no interactions between female origin and the other independent variables, the analysis was re-run without female origin as an independent variable because including it meant the loss of one-third of the data (for the second test session) and for simplicity of presentation. A total of 116 males were tested, however, because of logistic difficulties, some individuals were not tested at 7–10-day intervals. Therefore, for these analyses, to limit the amount of overlap in age between sessions, we excluded individuals whose post-maturation ages, at the time of testing, fell outside the following periods: test 1: 3–13 days (mean=7); test 2: 10–21 days (mean=15); test 3: 18–34 days (mean=23). The data for 87 individuals were used in these analyses; each treatment was represented by at least seven individuals.

We tested males with stimulus females from the same predator locality as the residents in his home tank and with females from the other predator locality. This allowed us to ask how males responded to familiar and unfamiliar types of females. We did a repeated-measures ANOVA using, for each male, data from two test sessions: one with a female from a *Crenicichla* locality and one with a female from a *Rivulus* locality. Here, we used the data for the last two test sessions because they showed fewer age-related differences from each other than when compared with data for the first test session (see below). Data were transformed as for the previous analyses.

Information about responsiveness to variation in the environment can be lost using only ANOVA (Sultan 1987). Therefore, we used multiple

Table II. Tests for homogeneity of slopes of courtship behaviour (ln(trait) minus ln(standard length)) versus body size (ln(standard length))

	df	Mean square	F	P	r^2
Posturing (fin down)					
All males*	7	2·33	1·96	0·07	0·18
Error	96	1·19			
Rivulus locality males only†	3	0·09	0·08	0·97	0·21
Error	49	1·24			
Crenicichla locality males only†	3	1·03	0·90	0·45	0·16
Error	54	1·15			
Rivulus versus *Crenicichla*‡	1	10·67	9·16	0·003	0·09
Error	108	1·16			
Sigmoid display					
All males*	7	15·49	2·21	0·05	0·24
Error	96	1·04			
Rivulus locality males only†	3	0·93	1·01	0·40	0·34
Error	42	0·92			
Crenicichla locality males only†	3	1·77	1·57	0·21	0·12
Error	54	1·13			
Rivulus versus *Crenicichla*‡	1	4·16	3·52	0·063	0·03
Error	108	1·18			

*Comparison between the slopes of the behaviour–size relationships for all eight treatments.

†Comparison between the four treatments of test males with parents from the indicated locality.

‡Comparison between test males with parents from *Rivulus* and those with parents from *Crenicichla* localities.

regressions to investigate the relative influences of mature female, mature male and immature conspecifics on male sexual behaviour. It was possible to do these analyses because of short-term deviations from the original experimental design (see above). We used data for the third test session only so that these analyses would be representative of the males' fully developed behaviour (see below). To ensure that the assumptions of this test were met, we checked residuals and tolerances and verified that correlations between the numbers of guppies in each category were not significant (Sokal & Rohlf 1981; Zar 1984). Next, we checked for interactions of the origins of the stimulus female and the residents with the other independent variables. Where there was none, we re-ran the analyses without those variables. Next, terms for interactions among the independent variables that were not significant were excluded from the regression (PROC GLM, SAS 1989). Where the numbers of adults had a significant influence on a behaviour pattern, we did a separate multiple regression to determine the relative importance of the total number of adults versus their sex ratio. Data were transformed as described above.

To test for allometric relationships between male body size and sexual behaviour, we asked whether any behaviour patterns were correlated with body length (ln(standard length); Farr et al. 1986). Because male body size varied among treatments (Rodd 1994), we transformed each trait using ln(trait) − ln(standard length) so that trait-size relationships would be independent of inter-treatment differences in body size (Mosimann & James 1979; Farr et al. 1986). To ensure that behaviour patterns were as fully developed as possible, we analysed only data for the third test session. We first checked for an influence of the origin of the stimulus female on the trait–length relationship and for interactions between the female's origin and the other parameters. Because none was found, we dropped female origin from these analyses. Where slopes of the trait–size relationships were homogeneous among the treatments, we used ANCOVA with ln(body size) as the covariate (PROC GLM, SAS 1989). For the frequencies of both sigmoid and posturing (dorsal fin folded) displays, the slopes of the size–trait relationships were heterogeneous among treatments (Table II). For both traits, the greatest

differences were between treatments with males whose parents came from different predator localities. Therefore, we conducted separate tests for homogeneity of slopes for males with parents from each predator locality. Because there were no differences within either set of four treatments, we combined data for each locality and compared the overall patterns for sons of *Rivulus* locality guppies and sons of *Crenicichla* locality guppies.

RESULTS

Influence of Parental Origin (Heritable Factors)

The frequencies of approaching the stimulus female ($F_{1,53}=5.51$, $P=0.023$) and of full gonopodial swings were influenced by the origin of a male's parents (Table III). For gonopodial thrusts, there was an interaction between all four main factors (demography and origins of the parents, residents and stimulus female; $F_{1,53}=5.16$, $P=0.027$) with the only pattern between treatments being a difference between males with different parental origins ($P<0.006$ for the least-squares means comparisons between treatments; SAS 1989). Males from *Crenicichla* localities performed all of these behaviour patterns (approaches, full swings and thrusts) more frequently than males from *Rivulus* localities (Table IV).

Male Choosiness

We asked whether some males were more choosy than others. First we established that there was variation in the number of stimulus females that males attempted to mate with during their three test sessions. However, there was no difference between treatments in the number of females that a male attempted to copulate with, that is, we found no evidence that males from some treatments were more choosy than others (intercept: $\chi^2=239.9$, $df=1$, $P<0.0001$; for each independent variable and for each interaction among them: $\chi^2<1.9$, $df=1$, $P>0.17$; PROC CATMOD, SAS 1989).

Influence of Social Environment: Residents and Demography

Many of the behaviour patterns we measured were influenced by the origin and demography of the resident population (Table III). The main courtship display, the sigmoid, was marginally influenced by both aspects of the males' social environment (Fig. 1, Table III). Males reared with *Rivulus* locality residents in a *Crenicichla*-type demography (low density) did sigmoids more often and for longer durations than did males reared with those residents in a *Rivulus*-type demography (high density; sigmoid frequency: $P=0.004$ for the comparison of least-squares means for *Rivulus* locality guppies reared in the two demographies; total duration of all sigmoids performed during a test session: $P=0.05$). Males reared with guppies from *Crenicichla* localities had the same low frequency and duration of sigmoids as males in the latter condition (*Rivulus* residents in a *Rivulus* demography), regardless of the population demography. Because body size influences the performance of sigmoid displays (see below; Reynolds 1993), we analysed sigmoids with an ANCOVA with body size as a covariate. The results described above remained unchanged.

We did multiple regression analyses to determine what aspect of the demography was exerting an influence on male behaviour (see Methods). For all test males, the frequency of gonopodial thrusting increased with increasing densities of mature males. For males with parents from *Rivulus* localities, the numbers of adults influenced the frequency with which they performed courtship displays (sigmoids and fin-down posturing; Table V). The rate of display decreased as the number of mature females in the home tank increased and the rate increased with the number of mature males in the home tank. Separate analyses showed that the sex ratio of adults was determining the rate of display, not their total numbers. Males performed fewer courtship displays when the sex ratio was female biased. For males from *Crenicichla* localities, relative numbers of conspecifics did not significantly influence display rates. However, those males followed the stimulus female more frequently as the number of mature males in their home tank increased.

Influence of the Origin of the Stimulus Female

Analyses with the origin of the stimulus female included as a main effect in the ANOVAs showed that it had an infuence on three patterns of behaviour: number of approaches made towards the female, gonopodial thrusts and half swings.

Table III. Repeated-measures ANOVA on sexual behaviour: between-individual effects

Behaviour	Factor	Mean square	F	P^*
Time to first approach	Parents	1·04	0·06	
	Residents	14·00	0·84	
	Demography	2·19	0·13	
	P × R	31·89	1·90	
	P × D	1·93	0·12	
	R × D	34·20	2·04	
	P × R × D	25·17	1·50	
	Error†	16·76		
Following	Parents	5·93	3·15	0·08
	Residents	0·50	0·27	
	Demography	2·71	1·44	
	P × R	7·02	3·73	0·06
	P × D	0·15	0·08	
	R × D	0·67	0·36	
	P × R × D	2·85	1·51	
	Error	1·88		
Posturing (fin folded)	Parents	8·38	2·09	
	Residents	6·03	1·50	
	Demography	8·38	2·09	
	P × R	0·59	0·15	
	P × D	4·08	1·02	
	R × D	7·07	1·76	
	P × R × D	4·97	1·24	
	Error	4·01		
Sigmoid display	Parents	0·00	0·00	
	Residents	2·87	1·35	
	Demography	8·67	4·08	0·05
	P × R	4·77	2·25	
	P × D	0·62	0·29	
	R × D	7·93	3·73	0·06
	P × R × D	4·08	1·92	
	Error	2·12		
Duration of all sigmoid displays	Parents	0·20	0·07	
	Residents	1·70	0·58	
	Demography	12·79	4·35	0·04
	P × R	4·19	1·42	
	P × D	1·12	0·38	
	R × D	10·42	3·55	0·06
	P × R × D	5·77	1·96	
	Error	2·94		
Gonopodial full swing	Parents	6·22	5·71	0·02
	Residents	0·62	0·57	
	Demography	2·25	2·07	
	P × R	0·07	0·07	
	P × D	0·52	0·48	
	R × D	1·21	1·11	
	P × R × D	0·99	0·91	
	Error	1·09		

Effects of three experimental factors on male behaviour: origin of the male's parents (P), origin of the residents (R), and demography of the population (D). Results for behaviour patterns influenced by the origin of the stimulus female are presented in the text.

*Probability values greater than 0·1 are not shown.

†$df=1$ for all main effects and interactions. For the error terms, $df=74$ for time to first approach and $df=77$ for all other behaviour patterns.

Table IV. Least-squares means ($\pm$ SE) of behaviour patterns per 10-min period for the third behaviour test as a function of treatment

Treatment			Behaviour patterns		
P	R	D	Time to first approach	Approach	Following
C	C	C	56·88 (23·00)	4·38 (1·13)	4·75 (1·55)
C	C	R	80·92 (26·56)	5·17 (1·31)	5·83 (1·79)
C	R	C	73·75 (32·53)	8·38 (1·61)	4·75 (2·19)
C	R	R	66·50 (37·56)	6·43 (1·72)	4·86 (2·34)
R	C	C	73·23 (25·52)	5·43 (1·21)	3·50 (1·66)
R	C	R	89·28 (34·78)	3·71 (1·72)	5·14 (2·34)
R	R	C	164·80 (29·10)	5·50 (1·44)	1·00 (1·96)
R	R	R	108·90 (29·10)	7·54 (1·37)	3·09 (1·87)
			(N=82)	(N=85)	(N=85)
P	R	D	Posturing (fin folded)	Mean posturing display duration (fin folded)	Posturing (fin erect)
C	C	C	14·00 (2·65)	3·72 (2·58)	2·19 (0·71)
C	C	R	13·58 (3·06)	7·91 (2·35)	0·33 (0·82)
C	R	C	18·50 (3·75)	2·62 (5·77)	0·00 (1·01)
C	R	R	11·14 (4·01)	5·30 (2·88)	0·57 (1·08)
R	C	C	11·57 (2·83)	10·42 (3·33)	1·21 (0·76)
R	C	R	11·28 (4·01)	1·03 (5·77)	2·43 (1·08)
R	R	C	12·60 (3·35)	8·16 (2·58)	2·30 (0·90)
R	R	R	11·00 (3·19)	2·24 (5·77)	0·27 (0·86)
			(N=85)	(N=26)	(N=85)
P	R	D	Sigmoid display	Duration of all sigmoid displays	Gonopodial half swing
C	C	C	7·56 (1·68)	1·93 (0·68)	4·44 (0·78)
C	C	R	4·58 (1·94)	3·07 (0·68)	5·33 (0·90)
C	R	C	7·12 (2·38)	1·33 (0·97)	6·50 (1·10)
C	R	R	3·14 (2·55)	2·38 (0·68)	2·57 (1·18)
R	C	C	3·07 (1·80)	2·44 (0·68)	4·28 (0·83)
R	C	R	3·00 (2·55)	—	4·86 (1·18)
R	R	C	8·00 (2·13)	2·48 (0·48)	1·30 (0·99)
R	R	R	4·00 (2·03)	—	3·36 (0·94)
			(N=85)	(N=13)	(N=85)
P	R	D	Gonopodial full swing	Gonopodial thrust	Sample sizes
C	C	C	6·94 (1·01)	4·25 (1·07)	24
C	C	R	6·75 (1·17)	6·33 (1·24)	17
C	R	C	6·75 (1·43)	3·12 (1·52)	11
C	R	R	4·43 (1·53)	1·71 (1·62)	11
R	C	C	6·07 (1·08)	2·71 (1·62)	15
R	C	R	5·14 (1·53)	1·71 (1·62)	9
R	R	C	4·90 (1·28)	1·00 (1·35)	14
R	R	R	3·54 (1·22)	2·82 (1·29)	15
			(N=85)	(N=85)	

Sample sizes for each treatment are given in the final column. These analyses were done on untransformed data using the same ANOVA model as for the analyses presented in Tables III and VII.

P: Origin of test male's parents (*Rivulus* or *Crenicichla*); R: origin of residents in experimental tank (*Rivulus* or *Crenicichla*); D: demography of residents (*Rivulus* or *Crenicichla*).
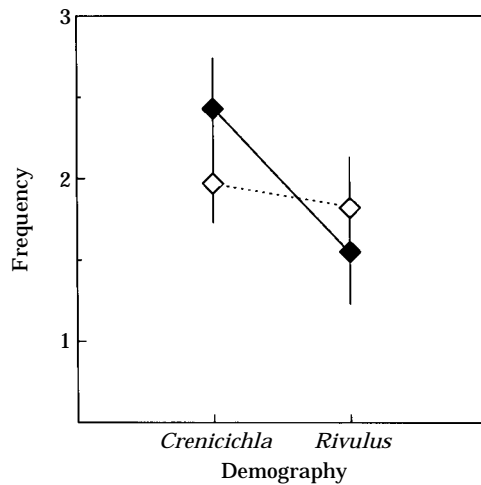
Figure 1. Least-squares mean ($\pm$ SE) frequency of sigmoid displays performed during a 10-min test session plotted against the demography of tank residents for males reared with residents from *Rivulus* ($\blacklozenge$) or *Crenicichla* ($\lozenge$) localities. Data were transformed as square root (trait $+ 3/8$) and are for the third test session only.

Females from *Crenicichla* localities were approached more often by males reared with *Rivulus* locality residents than by males reared with *Crenicichla* locality residents ($F_{1,53}=7.74$, $P=0.008$). For gonopodial thrusts and half swings, there was an interaction between the origin of the stimulus female and the other main factors but there was no obvious pattern in the responses to the treatments. In a comparison of males' responses to familiar versus unfamiliar females, we found that females from *Rivulus* localities elicited more courtship displays for longer periods from all males than did females from *Crenicichla* localities (Table VI).

Because one stimulus female was used for several tests in succession, it was possible that the female's behaviour changed throughout the day and that males responded to this change. However, we found no temporal trends in three of the most important behaviour patterns (sigmoids, display posturing and gonopodial thrusts).

Influence of Age: Post-maturation Development of Sexual Behaviour

Many behaviour patterns changed over the males' three test sessions (Table VII). These

changes could be a result of the development of the behavioural trait and/or a result of increasing familiarity with the test situation. To determine the importance of familiarity, we compared the performance of recently captured wild males during two test sessions with that of the test males during their first two test sessions using a repeated-measures ANOVA (PROC GLM, SAS 1989). For all test males, from one test session to the next, there were significant increases in the frequencies of sigmoid (Fig. 2) and posturing displays, and in the total time spent performing sigmoid displays. Wild males also displayed more often and for longer durations in the second test session than in the first (number of sigmoids: $F_{1,26}=30.43$, $N=28$, $P=0.0001$; number of display posturings (fin closed): $F_{1,26}=13.03$, $P=0.0013$; total duration of courtship displays: $F_{1,26}=17.84$, $P=0.0003$). This change in the behaviour of wild males between trials indicates that familiarity with the test situation played a role in the increases in test males' behaviours (note: our measurement of 'familiarity' for wild males was inflated because they were tested with *Rivulus* locality females second and males tend to court those females more than ones from *Crenicichla* localities; see above). However, wild males performed more sigmoid displays during the second test session than test males did in the second or even in the third sessions (for the interaction between test session and type of male (wild versus test): $F_{1,110}=10.94$, $N=115$, $P=0.0013$). Therefore, the increase in the frequency of sigmoid displays with increasing age for test males appears to be due to both development and familiarity with the test situation. As additional evidence for the role of development, we observed that some test males performed incomplete sigmoid displays when they first matured.

Males reared with *Crenicichla* locality fish showed a tendency to increase the frequency with which they performed gonopodial thrusts over the three test sessions ($F_{2,90}=2.84$, $N=50$, $P=0.064$); those reared with *Rivulus* locality fish showed no change over time ($F_{2,64}=1.69$, $N=37$, $P=0.193$; Fig. 2). Wild males showed no change in thrusting over time ($F_{1,26}=0.85$, $N=28$, $P=0.36$).

Influence of Body Size

For several behaviour patterns, we found evidence for relationships between the performance

Table V. Multiple regression analyses with tank residents (by sex and age category and by number and sex ratio) as the independent variables and frequency of the behavioural trait in the third test session as the dependent variable

| Behaviour | *Crenicichla* locality | | | | | *Rivulus* locality | | | | |
	df	Mean square	F		Slope	df	Mean square	F		Slope
Display posturing										
(dorsal fin folded)										
Mature females	1	0·67	0·26	NS		1	10·78	4·53	*	− 0·42
Mature males	1	2·04	0·78	NS		1	13·92	5·84	*	+0·60
Immatures	1	0·81	0·31	NS		1	5·36	2·25	NS	
Error	58	2·60				46	2·38			
Total no. adults	1	4·63	1·86	NS		1	5·04	2·16	NS	
Adult sex ratio†	1	7·27	2·93	NS		1	21·57	9·23	**	− 2·21
Total no. × sex ratio	1	7·07	2·84	NS						
Error	58	2·48				47	2·34			
Sigmoid display										
Mature females	1	1·18	0·69	NS		1	9·89	6·05	*	− 0·40
Mature males	1	1·52	0·89	NS		1	7·45	4·55	*	+0·44
Immatures	1	0·03	0·02	NS		1	0·18	0·11	NS	
Error	58	1·71				46	1·64			
Total no. adults	1	6·80	4·04	*	− 0·14	1	0·38	0·24	NS	
Adult sex ratio	1	0·15	0·09	NS		1	12·10	7·73	**	− 1·66
Error	59	1·68				47	1·57			
Gonopodial thrust										
Mature females	1	0·50	0·61	NS		1	1·56	2·91	NS	
Mature males	1	4·57	5·62	*	+0·26	1	5·26	9·82	**	+0·37
Immatures	1	1·49	1·83	NS		1	1·13	2·11	NS	
Error	58	0·81				46	0·54			
Total no. adults	1	3·22	3·90	*	+0·09	1	4·18	7·56	**	+0·12
Adult sex ratio	1	1·91	2·31	NS		1	4·15	7·51	**	− 0·97
Error	59	0·83				47	0·55			
Following										
Mature females	1	1·68	1·20	NS		1	0·62	0·57	NS	
Mature males	1	9·06	6·48	*	+0·36	1	1·36	1·25	NS	
Immatures	1	1·36	0·97	NS		1	4·50	4·13	*	− 0·36
Error	58	1·40				46	1·09			

Analyses were run separately for males with parents from *Crenicichla* and *Rivulus* localities.
†Ratio of adult females:adult males.
*$P<0.05$; **$P<0.01$.

of the behaviour pattern and body size. For two courtship displays (sigmoids and posturing with the dorsal fin folded), there was variation in the trait–length relationships between treatments, with the origin of the male's parents responsible for most of the variation (Table II). Males from *Rivulus* localities showed the typical positive courtship–body size pattern with large males (17·5–19·8 mm) displaying more often than small males (15·3–17·4 mm) which, in some tests, did not display at all. The pattern was allometric for posturing displays (rate of displaying increased at a faster rate than body size) but not for sigmoid displays (Table VIII). In contrast to this, males

from *Crenicichla* localities had a negative courtship–body size relationship with small males (14·9–17·4 mm) tending to display more often than large males (17·5–20·1 mm). This negative relationship was marginally significant for posturing displays but was not significant for sigmoid displays.

For all males, there were negative allometric relationships between body size and the mean duration of sigmoids ($r= − 0.238$, $F_{1,68}=5.33$, $P=0.024$) and between body size and the frequency of following behaviour ($r= − 0.304$, $F_{1,103}=9.23$, $P=0.003$). There was no significant relationship between body size and frequency of

Table VI. Repeated-measures ANOVA on the influence of the stimulus female (female with whom the male was tested) on male courtship behaviour

Origin of the residents in the treatment tank:	*Crenicichla*		*Rivulus*				
Origin of the test female:	*Crenicichla*	*Rivulus*	*Rivulus*	*Crenicichla*	df	F	P
Behaviour							
Sigmoid display	1·74	1·78	2·11	1·57	1,88	3·32	0·072
	(0·18)	(0·17)	(0·22)	(0·20)			
Mean duration of	1·46	1·64	1·79	1·15	1,88	4·55	0·036
sigmoid displays	(0·21)	(0·21)	(0·25)	(0·25)			
Mean duration of	2·33	2·99	3·02	2·28	1,51	11·41	0·001
display posturing	(0·19)	(0·21)	(0·23)	(0·25)			
(fin folded)							

Statistical parameters are shown for the interaction between the origins of the stimulus female and the residents in the male's home tank. Least-squares means (± SE) of transformed data for males in each category are shown.

gonopodial thrusts but, in six of the eight treatments, the slopes were negative.

Wild-caught Males

There were no differences between males captured in *Rivulus* localities and those captured in *Crenicichla* localities for any of the behaviour patterns scored except the number of approaches ($F_{1,26}=4·77$, $N=28$, $P=0·04$; *Crenicichla*: $\bar{X}=4·5$; *Rivulus*: $\bar{X}=6·0$) and the duration of display posturing with the dorsal fin folded ($F_{1,11}=6·75$, $N=13$ (test sessions where at least one display was performed), $P=0·02$; *Crenicichla*: $\bar{X}=11·6$ s; *Rivulus*: $\bar{X}=5·5$ s).

DISCUSSION

Influence of Parental Origin (Heritable Factors)

Laboratory-reared offspring of guppies from the two predator localities showed differences in some behavioural traits. Hence, some of the variation in their sexual behaviour appears to have a heritable basis. However, contrary to the predictions and findings of previous studies (Farr 1975; Luyten & Liley 1985), we found no evidence for a genetic basis for the observed variation in courtship (sigmoids, posturing). We only found such evidence for the difference in the frequencies of attempted copulations (gonopodial thrusts), full gonopodial swings, and approaches made towards the stimulus female. Male offspring of guppies from *Crenicichla* localities performed all of these

behaviour patterns more frequently than those from *Rivulus* localities. Our results for gonopodial thrusts are consistent with field observations (Farr 1975; Luyten & Liley 1985; Magurran & Seghers 1994). A possible explanation for higher levels of all of these activities (approaches, swings and thrusts) in *Crenicichla* locality males is that these males are less discriminating when choosing a mate than those from *Rivulus* localities because mature male guppies in the former suffer higher mortality rates than those in the latter (Hubbell & Johnson 1987; D. N. Reznick et al., unpublished data). However, we found no indication that males differed in their choosiness. Other possible explanations include differences in the responses of females to males from the two types of populations, differences in the intensity of male–male competition and differences in the strategies that males use to attain matings.

Luyten & Liley (1985) found a difference, where we did not, between laboratory-reared *Rivulus* and *Crenicichla* locality guppies in the rate at which they performed the most intense courtship display, the sigmoid display. However, uncontrolled factors in their experiment, such as density and male age (see below), might be responsible for the difference that they observed.

Our results suggest that some differences in male sexual behaviour have a heritable component. However, further experiments are necessary to determine whether maternal effects (e.g. female energy reserves or hormonal status) contributed to these differences (Wahlsten 1979; Reznick & Yang 1993). In domestic strains of guppies, Farr

(1980, 1983) found that non-genetic maternal effects had little or no impact, when compared with the influences of Y-linked and autosomal genes, on the rates at which males performed gonopodial thrusts and sigmoid displays. If the inter-population differences in male behaviour do have a genetic basis, predators could have been responsible for their evolution either directly (e.g. Seghers 1973; Farr 1975; Endler 1987; D. N. Reznick et al., unpublished data) or indirectly by changing the demographies of the two types of guppy population (Reznick & Endler 1982; F. H. Rodd & D. N. Reznick, unpublished data) and hence affecting the intensity of sexual selection (e.g. Cade & Cade 1992; McLain 1992). It seems unlikely that differences in predation pressure per se have caused an increase in these behaviour patterns in *Crenicichla* locality males since the opposite pattern has usually been observed (i.e. intense predation pressure usually causes a decline in activity; e.g. Strong 1973; Travers & Sih 1991); however, differences in the cues used by the predators to detect their prey (e.g. colour versus motion, single individuals versus those in a group) could be involved (Endler 1987).

Influence of Social Environment: Origin of Conspecifics (Residents and Stimulus Female)

We evaluated the hypothesis that predators are indirectly responsible for phenotypic variation in male sexual behaviour by creating differences in the social environment of guppies. By rearing males with conspecifics from either *Rivulus* or *Crenicichla* localities, we found that general differences in the biology of guppies from the two predator localities influenced two behaviour patterns, the frequencies of sigmoid displays and gonopodial half swings. These differences in the behaviour of the test males could have arisen in a number of ways. First, the test males could have imitated the behaviour of the resident adult males (e.g. Tooker & Miller 1980; Caro & Bateson 1986; Böhner 1990). However, because we found no differences between wild-caught males from *Rivulus* and *Crenicichla* localities for these behaviour patterns, it is unlikely that this is a primary cause of the differences. Second, males from different localities may show different levels of male–male competition and the test males might have been inhibited by these interactions (Farr 1980b; Magurran & Seghers 1991). However, we rarely saw overt aggression in the treatment tanks. Third, the differences in male behaviour could be a physiologically based response to variation in social interactions where interactions with conspecifics influence hormone levels which, in turn, influence behaviour (Hannes & Franck 1983; Hannes 1984; Hannes et al. 1984; Groothuis 1992). Finally, males may have modified their behaviour in response to differences between adult female residents from *Rivulus* and *Crenicichla* localities (Haskins & Haskins 1949; Baerends et al. 1955; Farr 1980c; Kodric-Brown 1989). During our behaviour tests, males did respond differently to females from the two predator localities. Therefore, a male's sexual behaviour may be influenced both by the type of females present during his development and by the type of female being courted. Males could be responding to differences in the females' behaviour which could vary because, for example, females from different localities use different criteria when choosing a mate (Farr 1980a; Houde 1988a; Stoner & Breden 1988; Houde & Endler 1990). Or males could be responding to subtle morphological differences between females and/or to the putative differences in pheromones produced by females from different localities (Snyder 1978, cited in Luyten & Liley 1991).

Influence of Social Environment: Population Demography

The demography of the population experienced during development influenced male sexual behaviour. This was true even though each male was tested with a single female. The only universal pattern was that males increased their rate of gonopodial thrusting as the density of mature males in their home tank increased. Farr (1976) found a similar pattern when he varied the numbers of mature male guppies present at the time of testing. As competition for females increased, males increased their rate of attempted copulations (Farr 1976).

There was variation among males in the degree to which they modified their courtship displays in response to population demography. Males whose parents were from *Rivulus* localities showed greater differences in their responses to variation in population demography than those whose parents were from *Crenicichla* sites. In addition, males reared with *Rivulus* locality residents

Table VII. Repeated-measures ANOVA: within-subject effects (the influence of test session on behaviour)

Behaviour	Factor	Mean square	F	$P*$
Time to first approach	Test	1·01	0·07	
	Test × Parents	58·25	4·10	0·02
	Test × Residents	7·39	0·52	
	Test × Demography	0·88	0·06	
	T × P × R	36·01	2·53	0·08
	T × P × D	2·85	0·20	
	T × R × D	3·60	0·25	
	T × P × R × D	14·07	0·99	
	Error	14·22		
Approach	Test	0·59	1·01	
	Test × Parents	1·97	3·40	0·04
	Test × Residents	2·19	3·78	0·02
	Test × Demography	0·19	0·33	
	T × P × R	0·03	0·05	
	T × P × D	0·42	0·73	
	T × R × D	0·20	0·35	
	T × P × R × D	0·59	1·02	
	Error	0·58		
Following	Test	1·57	1·51	
	Test × Parents	0·59	0·57	
	Test × Residents	2·75	2·65	0·07
	Test × Demography	1·59	1·53	
	T × P × R	0·16	0·16	
	T × P × D	0·09	0·08	
	T × R × D	0·81	0·78	
	T × P × R × D	0·74	0·71	
	Error	1·04		
Posturing (dorsal fin folded)	Test	56·14	27·61	0·0001
	Test × Parents	0·68	0·33	
	Test × Residents	2·00	0·99	
	Test × Demography	5·99	2·95	0·06
	T × P × R	1·35	0·66	
	T × P × D	3·84	1·89	
	T × R × D	2·39	1·17	
	T × P × R × D	3·83	1·89	
	Error	2·03		
Sigmoid	Test	18·02	22·61	0·0001
	Test × Parents	0·74	0·93	
	Test × Residents	0·59	0·75	
	Test × Demography	1·09	1·37	
	T × P × R	0·86	1·07	
	T × P × D	0·77	0·97	
	T × R × D	1·34	1·68	
	T × P × R × D	0·36	0·45	
	Error	0·80		
Total duration of all sigmoid displays	Test	25·57	23·00	0·0001
	Test × Parents	0·97	0·86	
	Test × Residents	2·27	2·04	
	Test × Demography	1·47	1·32	
	T × P × R	0·37	0·33	
	T × P × D	1·59	1·43	
	T × R × D	1·09	0·98	
	T × P × R × D	0·58	0·52	
	Error	1·11		

Table VII. (*Continued*)

Behaviour	Factor	Mean square	F	P*
Gonopodial half swing	Test	0·04	0·08	
	Test × Parents	0·03	0·07	
	Test × Residents	0·02	0·05	
	Test × Demography	0·37	0·77	
	T × P × R	0·26	0·54	
	T × P × D	0·68	1·43	
	T × R × D	0·29	0·61	
	T × P × R × D	1·48	3·13	0·05
	Error	0·47		
Gonopodial full swing	Test	0·93	1·54	
	Test × Parents	1·49	2·46	0·09
	Test × Residents	1·58	2·62	0·08
	Test × Demography	0·52	0·85	
	T × P × R	0·16	0·26	
	T × P × D	0·90	1·49	
	T × R × D	0·04	0·07	
	T × P × R × D	0·80	1·32	
	Error	0·60		
Gonopodial thrust	Test	0·73	1·37	
	Test × Parents	0·39	0·73	
	Test × Residents	1·59	2·99	0·05
	Test × Demography	0·17	0·32	
	T × P × R	0·46	0·86	
	T × P × D	0·25	0·48	
	T × R × D	0·06	0·12	
	T × P × R × D	0·98	1·85	
	Error	0·53		

Factor designations are as noted in Table III, except test (T) represents test session.
*Probability values not shown were greater than 0·1. *P*-values were adjusted using the Huynh–Feldt correction factor. $df=2$ for all main effects and interactions. Error term: time to first approach, $df=148$; all others, $df=154$.

showed variation in their courtship displays with changes in population demography but ones reared with *Crenicichla* locality residents did not. The variation shown by males reared with *Rivulus* locality residents is probably attributable to differences in behaviour exhibited by those residents when they are held at different densities. Therefore, guppies from *Rivulus* localities showed greater plasticity in courtship behaviour in response to changes in social conditions than guppies from *Crenicichla* localities.

Differences in the relative costs and benefits of phenotypic plasticity for guppies in the two localities might account for the differences in the amount of behavioural flexibility that they exhibit. Sexual behaviour is thought to be relatively costly both energetically and in terms of the increased risk of predation (Endler 1987). Therefore, it should be beneficial to perform sexual behaviour only when there is a high probability of inseminating a female. The costs of plasticity (i.e. the costs of having the ability to adjust behavioural responses to the conditions at hand) could include the time required to learn how and when to perform the behaviour, errors in its performance because it is not developmentally canalized, the time needed to assess current circumstances and modify behaviour accordingly, and the cost of maintaining the complex 'machinery' required to provide plasticity (Johnston 1982; Alcock 1989; Lott 1991; Newman 1992). The costs of delays and errors may be higher in *Crenicichla* sites because of the greater mortality rates of mature males there (D. N. Reznick et al., unpublished data). The benefits of plasticity may be considerably less in *Crenicichla* sites than in *Rivulus* sites because of less heterogeneity in guppy demography in time and space (Levins 1968; F. H. Rodd & D. N. Reznick, unpublished data), greater levels of food
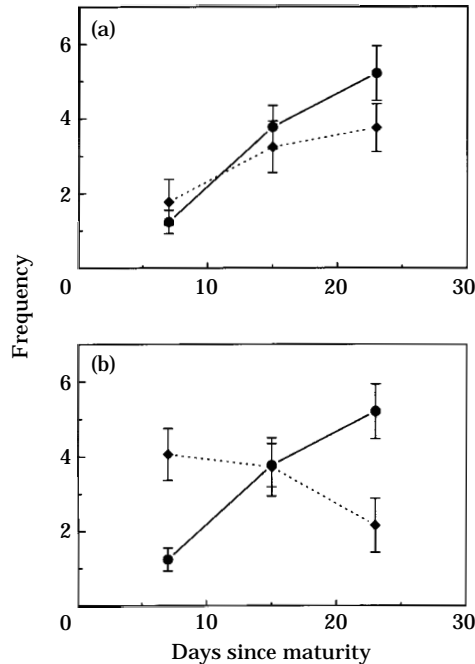
Figure 2. Least-squares mean (± SE) frequencies of sigmoid displays (●) and gonopodial thrusts (◆) performed during a 10-min test session plotted against mean male age in days since sexual maturity for males reared with residents from (a) *Crenicichla* and (b) *Rivulus* localities.

Table VIII. Relationship between courtship behaviour (ln(trait) minus ln(standard length)) and body size (ln(standard length))

	Posturing	Sigmoid displays
***Crenicichla* locality males**		
Pearson correlation coefficients	− 0·229	− 0·158
P-values	0·073	0·220
Regression equation		
Intercept	16·79	9·92
Slope	− 3·82	− 2·67
***Rivulus* locality males**		
Pearson correlation coefficients	0·333	0·200
P-values	0·018	0·164
Regression equation		
Intercept	− 29·98	− 19·23
Slope	5·22	2·98

Crenicichla localities. Therefore, higher costs and fewer benefits of behavioural flexibility may be responsible for the reduced levels of plasticity expressed by guppies from *Crenicichla* localities. It seems unlikely that there is insufficient genetic variation for plasticity available in *Crenicichla* localities (Carvalho et al. 1991; Newman 1992; D. N. Reznick, unpublished data). Finally, it is possible that the variation in plasticity is an artefact of some other difference in the biology of these guppies.

Sons of guppies from *Rivulus* localities increased the frequencies of performing sigmoid displays as the density of mature males in their home tanks increased. Again, as perceived competition for mates increased, males responded by increasing their sexual activity (Farr 1976). Several studies have shown that males that are more active than rival males, both in the rates at which they display and attempt to mate, will generally have the highest reproductive success (Farr 1980a, 1989; Bischoff et al. 1985; Houde 1988a). Domestic guppies also increased courtship when they were tested with increasing numbers of adult males (Farr & Herrnkind 1974; Farr 1976). However, just as guppies from *Rivulus* localities showed this response, while guppies from *Crenicichla* localities did not, there was variation among domestic guppies in the degree to which they adjusted their displays (Farr 1976, 1980a).

Sons of guppies from *Rivulus* localities decreased their rate of display to the single stimulus female as the density of mature females in their home tank increased. In addition, they decreased their rate of display as the number of females per male increased. As the rate of encountering potential mates increases, males may become more choosy (Hubbell & Johnson 1987; Shelly & Bailey 1992) or they may change their mating strategy (fewer displays per gonopodial thrust).

We have discovered that males do alter their sexual behaviour in response to population demography. This means that the differences in demography between guppy populations in *Rivulus* and *Crenicichla* localities are responsible for some of the inter-population differences in male sexual behaviour. Because the predators in these localities have contributed to these differences in demography (Reznick & Endler 1982; F. H. Rodd & D. N. Reznick, unpublished data), they are indirectly responsible for some of the inter-population variation in male behaviour.

availability (D. N. Reznick & M. J. Butler, unpublished data), and/or less intense sexual selection (Houde 1988a; Stoner & Breden 1988) in

Influence of Age: Post-maturation Development of Sexual Behaviour

Males showed significant changes in the frequencies and durations of many behaviour patterns during the first month after they reached maturity. Because male guppies grow little after they mature (Reynolds et al. 1993; personal observation), these changes were not a result of differences in body size. Comparative observations on wild-caught adult males showed that changes in some of the test males' behaviour patterns were the result of increasing familiarity with the test situation, but others were the result of both familiarity and post-maturation development.

Our findings are relevant for natural populations because few wild males survive for more than a few months after they reach maturity (D. N. Reznick, unpublished data). Because the age structures of the populations of adult males in *Rivulus* and *Crenicichla* sites are probably different (D. N. Reznick, unpublished data), these ontogenetic changes in sexual behaviour could be an important source of inter-population variation in male reproductive behaviour.

All test males increased the rate at which they performed sigmoid displays over time. Factors that could be contributing to this change are practice (Clark & Aronson 1951), increasing testosterone levels with age (Hildemann 1954), and a greater investment in sexual activity as reproductive value decreases with age (Fisher 1958; Trivers 1972; Huntingford 1984; Petrie 1992). A fourth possibility is that, in the wild, the risk of predation is so great to mature males, because of their bright coloration and obvious displays, that it is to their advantage to delay the onset of both for a few weeks after maturation until they have had the opportunity to attempt to mate with a few females (Endler 1978, 1980, 1983, 1987).

Males reared with *Rivulus* locality guppies changed their mating strategy over time. Newly mature males displayed very little per mating attempt, that is, they used a sneak strategy. Because the coloration of many males is still quite dull when they reach maturity (personal observation) and females often prefer males with bright coloration (Houde 1988b; Kodric-Brown 1989), young males' may sneak copulations because this is their only means of mating (Endler 1987; Houde 1988a; Kodric-Brown 1989). As young males aged, they performed more displays per mating attempt, suggesting that they were more likely to try to elicit female cooperation in the mating. In contrast to this pattern, males reared with *Crenicichla* locality guppies showed little change in the sigmoid:thrust ratio over time. We suspect that this difference (*Rivulus* versus *Crenicichla*) in age-specific strategy may have arisen because of inter-population differences either in the females' responses to maturing males (see above) or in male–male interactions.

Influence of Body Size

We found that male body size had an effect on several behaviour patterns. The effect of size was independent of that of age since males grow little after they mature (Reynolds et al. 1993; personal observation) and because the males were tested at approximately the same age. Since the average size of mature male guppies differs between *Rivulus* and *Crenicichla* localities (Seghers 1973; Reznick & Endler 1982; Reznick 1989), the influence of body size on behaviour is likely to contribute to the inter-population variation in the sexual behaviour of male Trinidadian guppies.

For sons of guppies from *Rivulus* localities, there was a positive allometric relationship between body size and the frequency of an important component of courtship, posturing displays. Large males displayed more often than small ones. Positive allometric relationships between courtship and body size have been observed for several other poeciliid species (Constanz 1975; Hughes 1985; Woodhead & Armstrong 1985; Farr et al. 1986; Travis & Woodward 1989; Ryan & Causey 1989). This relationship often arises where large males are preferred by females and these males court females and solicit their cooperation in mating (e.g. Hughes 1985; Ryan & Wagner 1987; Bisazza & Marin 1991; Reynolds & Gross 1992).

In contrast to the pattern we observed for *Rivulus* locality males, there was a weak, negative relationship between body size and the rate of performing posturing displays, for sons of guppies from *Crenicichla* localities. As far as we know, a negative relationship has not been reported for any poeciliid species besides guppies. Reynolds et al. (1993) found a negative courtship–size relationship for guppies from a *Crenicichla* locality not used in this study. However, they observed this relationship only at high light levels where

large males reduced their rates of display below those performed at low light levels. All of our tests were done at high light levels. Because *Crenicichla* forage most actively for guppies when light levels are high (Endler 1987), it is possible that selection pressure by *Crenicichla* is responsible for this unusual pattern. However, the inter-population differences in the body size–courtship relationship could also have arisen because of variation in female mate-choice criteria (e.g. body size versus display rate; Houde 1988a; Stoner & Breden 1988; Houde & Endler 1990; Reynolds & Gross 1992; Reynolds 1993).

In the field, male guppies frequently encounter solitary females and thus our test situation is realistic for natural populations in the short term. Studies on other poeciliids, however, have shown that the presence of mature males during the test procedure can influence size-specific courtship behaviour, depending on the male's genotype (Ryan & Causey 1989; Travis & Woodward 1989; Zimmerer & Kallman 1989). Therefore, when male guppies encounter a female in the midst of other guppies, size-specific courtship patterns could change.

Conclusions

Farr (1975) and Magurran & Seghers (1994) found that males in *Rivulus* localities performed fewer sigmoid displays than males in *Crenicichla* localities. We found no evidence that this variation has a genetic basis, however, we did reproduce their observations in the laboratory by manipulating the demography of the population that males experienced as juveniles. Therefore, population demography must play a role in determining males' reproductive strategies in the field. In fact, Luyten & Liley's (1985) contradictory finding that males in a *Rivulus* locality performed more sigmoids than those in a *Crenicichla* locality could have been a result of an uncharacteristic demography of the guppies at one of their sites. The density of guppies at their *Rivulus* locality was unusually low. Given that the demographies of guppy populations are heterogeneous in time and space (Reznick & Endler 1982; F. H. Rodd & D. N. Reznick, unpublished data), it is not surprising that there is considerable variation in the sexual behaviour of guppies in natural populations. However, the situation is made even more complicated by the influence of the behaviour of conspecifics on male behaviour, by variation in males' sensitivity to social cues and by variation in their responsiveness to internal cues such as body size and age. Therefore, male sexual behaviour represents an interplay between genetic, social and physiological influences. Add to this males' responses to environmental factors such as light intensity (Endler 1987; Reynolds 1993), the presence of predators (Magurran & Seghers 1990; Magurran & Nowak 1991) and food availability (P. N. Ross, personal communication), all of which will influence males' behaviour in nature, and the sexual behaviour of male guppies becomes very complex indeed.

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