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Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*)

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Abstract In the guppy (*Poecilia reticulata*), males have two alternative mating tactics. Individual males may either display to a receptive female prior to attempting to copulate with her or attempt to quickly sneak-copulate with a female without first displaying to her or without a prior receptive response from her. In this study, I experimentally investigated the effects of simulated local increases in the risk of predation (in the form of a cichlid fish predator model in situ) on the mating tactics used by free-ranging male guppies in two typical macrohabitats (riffle and pool) of a Trinidadian river. Focal male guppies displayed to females significantly less often on average, and conversely attempted sneak copulations more often, in the presence of the predator model than in its absence; this pattern was similar for both habitats. These fish therefore performed a lower proportion of sigmoid displays and increased their sneaky mating attempts when the apparent risk of predation had increased locally. This predator-mediated response is consistent with a trade-off between mating success and risk of mortality due to predation. The results are the first to confirm risk-sensitive mating behaviour in free-ranging male guppies within a population, and demonstrate the potential importance of predators in influencing the relative use of alternative mating tactics in this species on a microgeographical scale in the wild.

Key words Fish · Guppy · *Poecilia* · Predation risk · Mating tactic

Introduction

Within species, males may attempt to fertilize the eggs of females using alternative reproductive strategies and tactics (Gross 1984; Krebs and Davies 1993; Taborsky 1994). These may be genetically fixed, with individuals using only one tactic throughout their lifetime, or conditional, with any individual potentially using any one or more of the available tactics depending on its phenotype or prevailing social and environmental conditions (Gross 1984; Krebs and Davies 1993). Among environmental factors which may affect the cost of mating, and thus a male's choice of one particular mating tactic over other ones, is the risk of predation. In general, animals engaged in mating activities may be more vulnerable to predation than otherwise, owing mainly to their breeding coloration, conspicuous courtship displays, mate searching and assessment, or mating itself (Lima and Dill 1990; Magnhagen 1991). Although predators are known to affect the reproductive behaviour of animals in diverse ways (reviewed in Lima and Dill 1990; Magnhagen 1991), little is known about their direct effects on alternative mating behaviours in males (e.g. Endler 1987; Magurran and Seghers 1990; Magurran and Nowak 1991). Here, I examine the effects of simulated local increases in predation risk on the occurrence of alternative mating tactics in free-ranging Trinidadian male guppies (*Poecilia reticulata*).

Alternative male mating behaviours are common in fishes (Gross 1984; Farr 1989; Taborsky 1994). In the sexually dichromatic guppy, a live-bearing species with internal fertilization and a promiscuous mating system, males have two alternative mating tactics (Liley 1966; Farr 1989). They may either court a receptive female prior to attempting to copulate with her using their modified anal fin (the gonopodium) or attempt to inseminate a female quickly and without first displaying to her or without a prior receptive response from her. The courtship tactic consists of the male arching its body into an S-shape, with unpaired fins closed or extended, and oscillating the long axis of the body both horizontally and vertically in front of a female. This display, termed the sigmoid display, may last several seconds (Luyten and Liley 1985) and is highly

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conspicuous to females and presumably to predators. The alternative 'sneaky copulation' tactic, termed gonopodial thrusting, involves a male approaching a female from behind and quickly thrusting its gonopodium towards her gonopore in an attempt at insemination. Such a mating attempt is very brief (typically < 1 s, Clark and Aronson 1951) and relatively inconspicuous. Individual males are able to adopt either mating tactic (Magurran and Seghers 1990).

Although the mating success of male guppies depends largely on female choice (e.g. Houde 1987, 1988; Kodric-Brown 1993), most male courtship displays are ignored by females because they are choosy and receptive only as virgins and for a short period following parturition (Liley 1966). Males may circumvent female choice, however, by using the gonopodial thrusting tactic (Liley 1966; Luyten and Liley 1991; Kodric-Brown 1993). The relative pay-offs of these two alternative mating tactics are unknown for any guppy population. However, available evidence suggests that courting males are more successful on average at achieving fertilizations than males using gonopodial thrusting (Clark and Aronson 1951; Liley 1966; Farr 1980a; Houde 1988; Kodric-Brown 1993). Although males may be more likely to achieve matings by courting females than by sneak copulation, they probably incur greater costs in terms of energetic expenditure and predation risk by using the former tactic over the latter.

Field observations have revealed that male guppies in populations exposed to high fish predation pressure display to females less often, and exhibit gonopodial thrusting more often, on average, than males in populations with lower risk of predation (Farr 1975; Luyten and Liley 1985; Magurran and Seghers 1994; but see Farr 1975 for exceptions). In the laboratory, males from different populations generally reduce their display rate, and, conversely, increase their rate of thrusting, in the presence of a fish predator (Endler 1987; Magurran and Seghers 1990; Magurran and Nowak 1991). These studies suggest that individual males are sensitive to the perceived threat of predation and adjust their behaviour accordingly. However, males may also have modified their mating decisions in response to predator-mediated changes in female behaviour (Magurran and Nowak 1991) or to ambient light intensity (Endler 1987; Reynolds 1993; Reynolds et al. 1993), which varies over time and between sites and affects male conspicuousness to both females and predators (Endler 1991, 1995). Despite the above, the effects of short-term changes in predation risk within populations on the mating decisions of free-ranging male guppies remain unknown. How animals respond to such local selection pressures within their lifetime can affect their fitness (e.g. Lima and Dill 1990; Endler 1995).

In the current study, I experimentally investigated for the first time the effects of simulated local increases in predation risk (in the form of a cichlid fish predator model in situ) on the mating tactics used by free-ranging male guppies within a Trinidadian population. Assuming that displaying is a higher risk–higher gain tactic than gonopodial thrusting, I predicted lower average courtship rates and higher gonopodial thrusting rates by males in the vicinity of the predator model compared with males in the absence of the model, with local ambient light intensities held constant statistically.

Material and methods

I observed the mating behaviour of free-living male guppies at two sites in the Quaré River, Trinidad, West Indies (10° 41' 25" N, 61° 11' 51" W) between 8 to 13 March 1993. Guppies in this river are exposed to relatively intense predation pressure from a number of predatory fishes, including the pike cichlid *Crenicichla alta* (Magurran et al. 1992; J.-G. J. Godin, personal observation). Two representative macrohabitats, one riffle and one pool, were chosen for observations. The riffle (c. 9 m wide × 50 m long) had about 50% canopy cover, its substratum consisted of rocks, gravel and some leaf litter, and water velocity was low (< 10 cm/s) nearshore where behavioural observations were made. Killifish (*Rivulus hartii*) and blue acara cichlid (*Aequidens pulcher*), known guppy predators (Liley and Seghers 1975), were occasionally observed at this site. The pool (c. 7 m wide × 20 m long) was located about 250 m downstream of the riffle. Its centre contained several large boulders and rocks, whereas the shallower nearshore areas had a mixed gravel and sand substratum with interspersed rocks. The pool had about a 5% canopy cover, and water flow was negligible nearshore where observations were made. Several predatory cichlids (*Crenicichla alta, Aequidens pulcher, Cichlasoma bimaculatum*), characins (*Astyanax bimaculatus*) and killifish were observed daily in the pool, with at least the pike cichlids being resident. Ambient predation risk to guppies thus appeared greater in the pool than in the riffle. Guppies in both these habitats occurred in mixed-sex shoals, as they typically do in Trinidadian streams and rivers (Magurran and Seghers 1991, 1994). The adult sex ratio in the Quaré River (near the two study sites) is 1 male : 1.85 females (J.-G. J. Godin, unpublished data collected March 1991).

To investigate the potential effect of an apparent increase in the local risk of predation on the mating tactics of male guppies, free-living fish at both sites were presented in situ with a model of a pike cichlid for pre-determined periods. A fish predator model was used to standardize a simulated predatory threat, and because attacks on guppies by their natural predators are infrequently observed (Endler 1987; J.-G. J. Godin, personal observation). The model was constructed from body filler material using a mold made from a freshly sacrificed 14 cm pike cichlid. Glass eyes were fixed into the model, which was painted realistically and coated thinly with fibreglass resin. The model was suspended into the water column from one end of a 1 m clear Plexiglas rod with two monofilament nylon lines. Guppies respond to such predator models and live fish predators in a qualitatively similar manner (Magurran and Seghers 1990, 1994; Dugatkin and Godin 1992).

A typical experimental trial consisted of paired, consecutive 10-min observation periods that were separated by less than 5 min. During the first 10-min (control) period, the aforementioned Plexiglas rod (without the predator model attached) was extended and held stationary (by hand) over the riffle/pool, about 40 cm above the water surface, to control for external disturbances. This was done by an assistant located on shore. From an adjacent vantage point on the river's bank, I recorded (on audio tape) the number of sigmoid courtship displays and gonodopodial thrusts exhibited by focal male guppies towards females within an area of about 2 m^2 (predetermined by using natural features of the substratum such as rocks), centred on the tip of the Plexiglas rod. A given focal male was chosen haphazardly within this area and followed until he swam out of the area. The time over which the focal male was observed was noted, and then another focal male was chosen and its behaviour similarly recorded. This process was repeated for several focal males per trial. Adult males are readily distinguished from the drab females by their conspicuous colour patterns. To obtain estimates of local adult guppy density, my assistant concurrently recorded on audio tape the number of adult guppies ($\geq$ 1 cm total length) of both sexes instantaneously present in a 1 m^2 area below the Plexiglas rod at 30-s intervals during the 10-min period. During the second, paired 10-min (experimental) trial, the predator model was presented to the guppies in the same delineated area as for the matched control trial described above. The model was submerged into shallow water (15–30 cm depth) about 1 m from the shoreline, approximately 5 cm above the substratum, and held relatively stationary there. The behaviour of focal male guppies and guppy density were recorded as described above. The presence of the predator model in the pool (but not in the riffle) attracted resident, territorial pike cichlids who repeatedly approached to within 0.25–2 m of the model during each trial, thereby raising further the local risk of predation. At the end of a matched pair of trials, ambient light intensity (irradiance, μE/m^2 per s) was recorded at the water surface using a Landing Instrument Model LI-185 radiometer and water temperature noted. Fifteen such paired trials were carried out at each of the two selected sites. Observations were made between 0900 and 1700 hours, which includes the peak periods of guppy mating activities and fish predator activity (Endler 1987). At both sites, water temperatures (24–26 °C) and ambient light intensities ($\bar{x} \pm$ SD: riffle = 789 ± 979 μE/m^2 per s, pool = 951 ± 1004 μE/m^2/s, $t = 0.45$, $df = 28$, $P > 0.60$) were similar and water clarity was excellent.

From the transcribed data, standardized frequencies (number per minute) of sigmoid display and gonopodial thrust were calculated separately for each focal male. These frequencies were then normalized (by log$_{10}$ transformation) for each male and averaged over all focal males for each 10-min trial, thus yielding an average per capita sigmoid frequency and thrust frequency per trial. Since guppy mating behaviour varies with time of day and ambient light intensity (Endler 1987; Reynolds 1993; Reynolds et al. 1993), the behaviour frequency data were analysed with ambient light intensity (associated with each paired trials) held constant statistically using the ANCOVA. Fish density was estimated as the total number of adult guppies sighted within the pre-selected 1 m^2 area of the riffle/pool in any given instantaneous scan. This number was then logarithmically transformed and averaged over the 21 scans to yield a mean instantaneous local guppy density for a given 10-min observation period. There was no a priori reason to expect that the rates of male display and gonopodial thrust would vary systematically with fish density, as Farr and Herrnkind (1974) previously found no effect of density on mean male courting rate in laboratory guppy populations.

Since the movements of individual guppies between macrohabitats (e.g. between pools) in Trinidadian streams appears limited (Seghers 1973), the data obtained from guppies at the riffle and pool sites in this study are likely to be independent. Within macrohabitats, it is possible that some guppies were observed repeatedly during a given trial and subsequent trials, but this is unlikely given the high densities of guppies at both sites (see below). Nonetheless, the data collected on different trials may not truly be independent in the statistical sense. This is an inevitable consequence of observing large numbers of unmarked, mobile animals in the field. An attempt was made to alleviate this potential problem by: (1) limiting the number of trials at a particular site to a maximum of three per day and by separating consecutive trials at the same site by at least 1 h, (2) ensuring that a given focal male guppy left the observation area before another one was observed in any given trial, (3) using only the per capita mean for each of the sigmoid and thrust frequencies per trial in statistical analyses (thereby avoiding pseudoreplication), and (4) using repeated-measures statistical tests to analyse the data obtained from paired trials within sites.

Results

A total of 493 focal male guppies were observed, each for an average of 36.1 s (SD range = 18.3–71.1, $n = 275$, log$_{10}$ data) in the riffle and 49.2 s (SD = 27.3–88.7, $n = 218$) in the pool. Although the times spent observing focal males differed between sites ($F_{1,489} = 26.99$, $P < 0.001$, two-way ANOVA), they did not differ between control (predator model absent) and experimental (model present) trials ($F_{1,489} = 1.35$, $P = 0.25$). Overall, adult guppy density was greater ($F_{1,28} = 23.75$, $P < 0.001$, repeated-measures ANOVA) in the pool (12.8 ± 4.7 fish/m^2) than in the riffle (11.3 ± 3.4), and greater during trials with the model predator present than during control trials in the riffle (paired $t = 2.38$, $df = 14$, $P = 0.03$) but not in the pool (paired $t = 1.83$, $df = 14$, $P > 0.05$). On average, 9.2 and 7.3 focal males were observed per 10-min trial in the riffle and pool, respectively. All focal males observed exhibited at least one sigmoid display towards females or attempted at least one gonopodial thrust, with 52.1% of them performing $\geq$ two mating attempts.

Neither the mean rates of male display nor gonopodial thrust varied with guppy density ($F_{1,26} = 0.87$ and 3.11, respectively, both $P > 0.05$, repeated-measures ANCOVA), but both were affected by ambient light intensity ($F_{1,26} = 33.02$ and 5.98, respectively, both $P < 0.02$). With ambient light intensity (as a covariate) therefore held constant statistically, male sigmoid frequencies were significantly higher overall in the pool than in the riffle (Fig. 1; $F_{1,27} = 15.87$, $P < 0.001$, repeated-measures ANCOVA), but rates of gonopodial thrusts did not differ between sites ($F_{1,27} = 0.92$, $P > 0.30$). In both the riffle and pool, males employed sigmoid displays significantly more often than gonopodial thrusts in attempting to mate with females, in both the absence and presence of the predator model (Fig. 1). Males courted females (with sigmoid displays) significantly less often, on average, in the presence of the predator model compared with its absence (Fig. 1; $F_{1,27} = 34.58$, $P < 0.001$), and this response to an apparent increase in predation risk was similar at both sites (interaction term, $F_{1,27} = 1.42$, $P > 0.20$). Conversely, males significantly increased their rate of sneaky mating attempts (gonopodial thrusts), on average, in the presence of the predator model compared with its absence (Fig. 1; $F_{1,27} = 32.35$, $P < 0.001$), and this predator-mediated response was also similar at both sites (interaction term, $F_{1,27} = 0.46$, $P > 0.50$). Therefore, when expressed as a proportion of total mating attempts (sigmoids plus thrusts), and with the covariate (light intensity) held constant, males exhibited proportionately fewer sigmoid displays on average ($F_{1,27} = 15.26$, $P < 0.001$, repeated-measures ANCOVA on arcsine transformed data) in the presence of the predator model ($\bar{x}$ = 75.8%, SD = 46.0–96.0) than in its absence ($\bar{x}$ = 97.1%, SD = 91.6–99.7). These

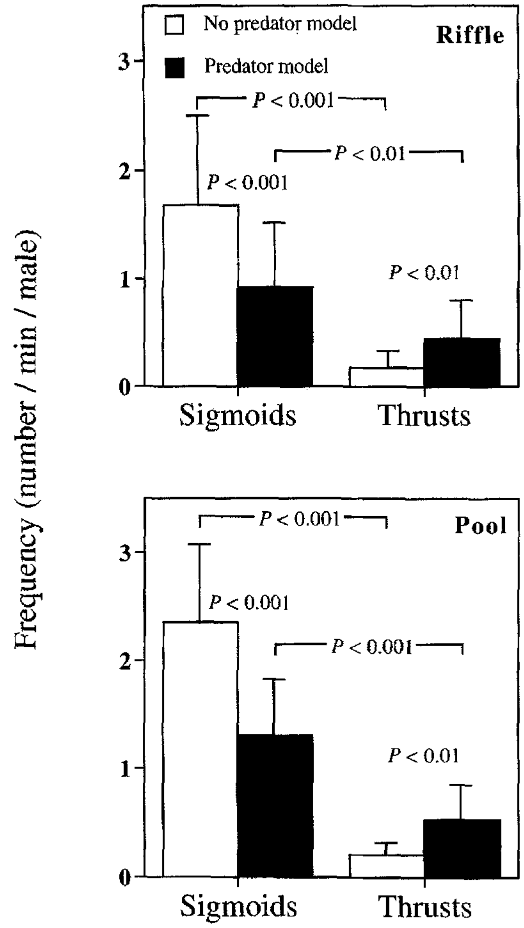

Fig. 1 Mean (+ SD) per capita frequency of sigmoid displays and gonopodial thrusts performed by focal male guppies in the presence and absence of a fish predator model introduced into both a riffle and a pool in the Quaré River, Trinidad. Within each habitat, mean scores were compared with the paired *t*-test, and the statistical significance (*P* value) of all paired comparisons is shown. Means are based on 15 paired trials (predator model absent and present) for each stream site separately

data were pooled over both sites because there was no significant site effect ($F_{1,27} = 0.31$, $P > 0.50$) or site × predator treatment interaction ($F_{1,27} = 0.07$, $P > 0.80$).

Of those individual males ($n = 262$) who were observed to perform ≥ two mating attempts, the majority used exclusively or almost exclusively (i.e. ≥ 90% of mating attempts) sigmoid displays, with the remaining males clearly using both sigmoid displays and gonopodial thrusts in varying proportions (Fig. 2). Only a small number of males used exclusively the thrusting tactic. An apparent increase in predation risk resulted in proportionally more males using a mixed mating strategy of sigmoids and gonopodial thrusts ($D_{138,124} = 0.320$, $P < 0.001$, Kolmogorov-Smirnov two-sample test; Fig. 2).

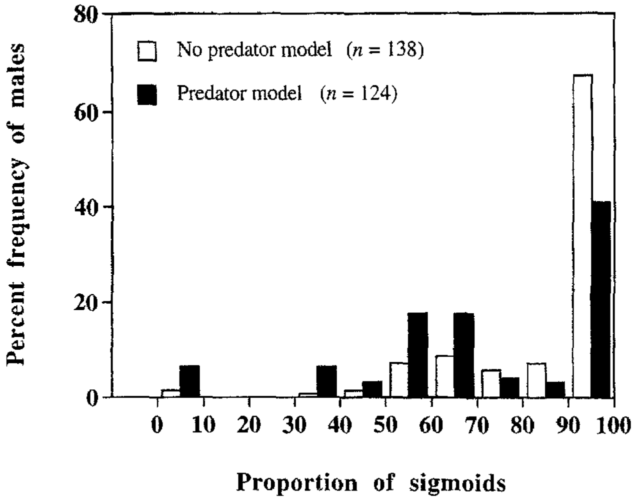

Fig. 2 Percentage frequency of focal males performing sigmoid displays in varying proportion of their respective total mating attempts (sigmoid displays plus gonopodial thrusts), in both the absence and presence of the predator model. The sample sizes shown denote the numbers of focal males observed which exhibited two or more mating attempts. The data were pooled over the two study sites

Discussion

This study has demonstrated that free-ranging male guppies do not stop attempting to mate with nearby females when the local risk of predation has apparently increased, but rather adjust their mating behaviour. Average per capita rates of sigmoid display performed by males decreased, whereas their average rates of gonopodial thrust increased, when the predator model was present compared to when it was absent at both stream study sites. My findings further indicate that this predator-mediated shift in the occurrence of alternative mating tactics resulted from individual males exhibiting proportionately more gonopodial thrusts and fewer sigmoid displays under increased predation hazard. These field results corroborate the laboratory results of Endler (1987), Magurran and Seghers (1990) and Magurran and Nowak (1991), using Trinidadian guppies originating from different populations.

Male sigmoid display rates were higher on average in the pool than in the riffle in the current study. The reverse was expected, as the pool contained more fish predators than the riffle and was thus a potentially riskier habitat for displaying males. This unexpected result could have been obtained owing perhaps to different spectral quality of light between the open-canopy pool and partially-shaded riffle, which may have resulted in the pool males being less conspicuous (and thus less at risk) to predators than riffle males overall (Endler 1991; see also Endler 1995).

Collectively, the above and current studies indicate that individual male guppies can use either the display or the thrusting mating tactic, and that the decision to adopt one tactic over the other can be influenced by the local risk of predation. At least four, non-mutually exclusive proximate mechanisms may explain the observed predator-mediated shift from mainly displaying to females towards proportionately more sneaky copulation attempts in my field study. First, male guppies could have responded directly to their perceived level of predation risk locally and appropriately reduced, in a risk-sensitive manner, their use of the presumably more risky sigmoid display. Second, male guppies could have exploited the antipredator behaviour of females by increasing their sneaky copulation attempts whilst the latter were preoccupied with observing and approaching the predator model (and live predators nearby), and thus not avoiding thrusting males as often as they would have otherwise. Such a shift in mating tactic is an indirect response to predation risk and has been previously observed in male guppies under laboratory conditions (Magurran and Nowak 1991). Third, males could have shifted to using preferentially sneaky copulations over the more energetically and risky courtship displays under predation hazard as an indirect response to females reducing their sexual responsiveness towards them and their mating preferences when risk is increased (Godin and Briggs, in press). Lastly, males could have used ambient light intensity as an indirect cue of the level of predation risk (Endler 1987, 1991) and reduced their display rate at the higher light intensities, under which they are presumably more conspicuous to predators (Endler 1987, 1991; Reynolds 1993; Reynolds et al. 1993). Because paired control and predator present treatments were separated by less than 5 min (and thus were carried out under similar light conditions) and ambient light intensity was statistically controlled for in the data analysis, this differential light-risk hypothesis does not explain my results.

Any one of the first three proximate mechanisms above could have contributed to free-living male guppies reducing their rate of sigmoid display, and conversely increasing their rate of gonopodial thrusting, in the presence of the predator model in the current study. It is likely that all three mechanisms were operating. Further experimentation would be required to ascertain their relative importance in generating the observed predator-mediated shifts in male mating tactics. Nonetheless, male guppies in the Quaré River adjusted their mating tactics in response to an apparent local increase in predation risk in a manner consistent with a trade-off between mating success and mortality due to predation. The observed shift away from using visually conspicuous mating displays to less conspicuous sneaky copulation attempts under predation hazard would thus appear adaptive. Male guppies in the wild further minimize their risk of predation by courting females preferentially at times of the day when light intensities are low (Endler 1987), and thus when they are less conspicuous to their predators (Endler 1991). In a few other species, males have been shown to similarly reduce their use of conspicuous acoustic and visual mating signals when the risk of predation is high (e.g. Ryan 1985; Hastings 1991; Magnhagen 1993), but at the cost of lost mating opportunities.

Although differences among guppy populations in the average rates of male sigmoid display and gonopodial thrust have a genetic basis (Farr 1980a; Luyten and Liley 1985), the differential use of these two mating tactics by individual males within populations appears largely conditional on their phenotype (Farr 1980b; Kodric-Brown 1993; Reynolds 1993; Reynolds et al. 1993), the behaviour of females (Liley 1966; Farr 1980b; Magurran and Nowak 1991) and of competing males (Farr 1980a), and (or) prevailing environmental factors, including predation risk (Endler 1987, 1995; Magurran and Seghers 1990; Luyten and Liley 1991; Magurran and Nowak 1991; Reynolds 1993; Reynolds et al. 1993). Such flexible mating behaviour in male guppies allows them to adjust their behaviour rapidly to changing social and environmental conditions locally. However, any situation or factor, such as predation risk, which favours the use of gonopodial thrusting over sigmoid display by male guppies is likely to reduce opportunities for females to exert mate choice and will thereby reduce the intensity of intersexual selection (Endler 1995). The consequences of shifts in the relative frequency of use of alternative male mating tactics in any population on the evolution of male traits via female mate choice, and of female preferences for such traits, are unknown and therefore merit further study.

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