ORIGINAL ARTICLE

Jonathan P. Evans · Jennifer L. Kelley
Indar W. Ramnarine · Andrea Pilastro

Female behaviour mediates male courtship under predation risk in the guppy (*Poecilia reticulata*)

Abstract Previous work has shown that under elevated predation risk, male guppies (*Poecilia reticulata*) switch from courtship to less conspicuous coercive mating attempts. This behavioural transition is traditionally interpreted as a 'risk-sensitive' response that makes males less conspicuous to predators. However, predation risk leads to behavioural changes (such as schooling and predator inspection) in females that may result in coercive mating attempts being more profitable in high-risk situations. Here, we tested the hypothesis that the switch to coercive mating by male guppies in high-risk situations is mediated by adjustments in female behaviour, rather than directly by the predator. We used replicate models resembling a known guppy predator to simulate predation risk in wild-caught guppies from a high-predation population in Trinidad. Our results revealed that males performed proportionately more coercive mating attempts when presented with a female that had been exposed previously to a model predator compared to when males were paired with non-exposed females. Total mating activity (combined rates of courtship and forced mating attempts) did not differ significantly among the two treatment groups, indicating that overall mating activity is unaffected by predation risk. Importantly, when we subsequently presented both sexes concurrently with a predator model, total mating activity and the proportion of forced mating attempts remained unchanged in the high-risk treatment. Taken together, these results indicate that the transition from courtship to forced mating attempts under elevated predation risk is mediated by changes in female behaviour, which we suggest may favour the use of coercive mating under high predation risk.

Keywords Alternative mating tactics · Guppies · Poeciliidae · Predators · Sneaky mating

J.P. Evans (✉) · A. Pilastro
Dipartimento di Biologia, Università di Padova, via U. Bassi 58/B, Padova, 35131, Italy
e-mail: jonathan.evans@unipd.it
Tel.: +39-049-8276224, Fax: +39-049-8276209

J.L. Kelley
Environmental and Evolutionary Biology,
University of St Andrews, St Andrews, Fife, KY16 9TS, UK

I.W. Ramnarine
Department of Life Sciences, The University of the West Indies, St Augustine, Trinidad and Tobago, West Indies

Introduction

Predators can have a profound influence on the behavioural decisions of their prey (Lima and Dill 1990). In particular, conspicuous activities associated with reproduction (e.g. courtship and pair bonding), which frequently lead to elevated predation risk for both sexes, are curtailed in the presence of predators (Magnhagen 1991; Sih 1994; but see Warner and Dill 2000). For example, chorusing male túngara frogs respond to simulated attacks by model bats by reducing the intensity of their calls (Ryan 1985). Similar examples of predator-mediated changes in male courtship behaviour have been reported in insects (Sih 1988), crustaceans (Koga et al. 1998) and a number of fish species (Forsgren and Magnhagen 1993; Chivers et al. 1995; Candolin 1997). Predators have also been shown to suppress female reproductive behaviour and a number of studies have demonstrated that under increased predation risk females become sexually unresponsive (Jennions and Petrie 1997) or reduce their preference for conspicuous males (Crowley et al. 1991; Godin and Briggs 1996; Gong and Gibson 1996).

In species where males alternate between distinct mating strategies, there exists the opportunity to study how individuals resolve the trade-off between mating success and the risk of mortality (Lima and Dill 1990). One species that is particularly well suited for this purpose is the guppy (*Poecilia reticulata*), a small poeciliid fish inhabiting freshwater streams throughout Trinidad. Guppies have provided some of the best examples to date of the adaptive use of alternative mating strategies

in response to predation risk (reviewed by Houde 1997). Males either court females using conspicuous displays or attempt to circumvent female choice using forced copulations in the form of 'gonopodial thrusts' (Baerends et al. 1955; Liley 1966). Although individual males employ both strategies interchangeably, the degree to which either tactic is used can depend on several factors including population demography (Rodd and Sokolowski 1995; Rodd et al. 1997), female receptivity (Liley 1966) and predation intensity (Endler 1995). In particular, studies have repeatedly shown that under elevated predation risk, male guppies switch from highly conspicuous courtship displays to more covert coercive mating attempts (Endler 1987; Magurran and Seghers 1990; Magurran and Nowak 1991; Godin 1995). This switch in male mating behaviour is also evident at high light intensities when males are presumably at greater risk from predators (Endler 1987; Reynolds et al. 1993).

The behavioural transition by male guppies from courtship to coercive mating in high-risk situations has been interpreted as a risk-sensitive response designed to make them less conspicuous to predators (Endler 1987). However, Magurran and Nowak (1991) provided an alternative hypothesis by suggesting that the increase in coercive mating by males under elevated predation risk could be the result of them exploiting the females' preoccupation with observing and evading predators (see, also, discussions by Magurran and Seghers 1990; Godin 1995). Magurran and Nowak (1991) noted that when both sexes were faced with a predator, females tended to show more enhanced anti-predator responses (notably predator inspections and increased schooling) than males, which they argue was due to the disparity in risk among the sexes in high-risk locations. This stems from the fact that predators such as *Crenicichla alta* (the pike cichlid) and *Hoplias malabaricus* (a predatory characin) tend to favour females over males because they are larger and therefore more profitable as prey items (Liley and Seghers 1975; Pocklington and Dill 1995). Furthermore, studies have confirmed that following predator exposure, females tend to reduce their overall level of sexual activity and switch their mating preferences in favour of duller (i.e. less conspicuous) males (Godin and Briggs 1996; Gong and Gibson 1996; Gong 1997). Thus, in high-risk situations, predator-induced changes in female behaviour may increase the relative efficiency of coercive mating attempts, given the reduced probability of achieving copulations through courtship. Additionally, preoccupation with predator avoidance is likely to divert the attention of females away from avoiding unsolicited mating attempts, thus making the coercive strategy more profitable in high-risk situations (Magurran and Seghers 1990).

In this paper we tested the hypothesis that males switch from courtship to forced mating attempts in response to changes in female behaviour following the experimental manipulation of predation risk. Our study examined the mating strategies of individual males when: (1) the female alone was exposed to a simulated predation threat, and (2) when both sexes were exposed simultaneously to the threat. The experiment was designed to examine the mating strategies of individual males in both contexts and compare these findings with those from a control experiment in which neither sex was exposed to the threat. We considered total male mating activity (= total number of sigmoid displays and gonopodial thrusts) and the proportion of mating attempts devoted to gonopodial thrusting, and determined whether either parameter was affected when only females were exposed to the simulated threat, and whether any observed effect was maintained (or enhanced) when both sexes were simultaneously exposed to the threat. To simulate predation risk in this experiment, we used several replicate models resembling a known guppy predator. Such models are known to stimulate antipredator behaviour in guppies (Magurran and Seghers 1994a) and make it possible to standardise the perceived level of risk among trials.

Methods

Origin and maintenance of experimental fish

The fish used for this experiment were collected from the Tacarigua River (grid reference PS 787 804) in Trinidad's Northern Range in January 2002. This site is characterised by high levels of piscivorous predation, exerted by several cichlid (e.g. *Crenicichla alta*, *Aequidens pulcher*) and characid species (*Astyanax bimaculatus*, *Hemibrycon taeniurus* and *Hoplias malabaricus*) (see Magurran and Seghers 1994b for further details of the biological and physical characteristics of this site). Approximately 150 adult and 60 juvenile fish (ca. 6 weeks old) were collected using a one-person seine and returned to the laboratory (University of West Indies, Trinidad). The adult fish were housed (ca. 1:1 sex ratio) in six holding aquaria (45×30×30 cm filled to a depth of 22 cm, containing gravel and *Elodea* aquatic weed) for 2 weeks prior to the experiment. The juveniles were placed separately in one large (120×45×45 cm) tank. All fish were fed each morning on a diet of commercially prepared flake food.

Experimental apparatus

The apparatus was designed to introduce and retract a model predator into an experimental arena and subsequently to allow a test male to enter the arena for behavioural assays. We prepared four replicate test tanks (45×30×30 cm) for this purpose (see Fig. 1). Each tank was divided in two by a black plastic partition. On one side of the partition (right hand side in Fig. 1A) we fixed a black plastic 'start box' with a trap door leading into the main behaviour arena (Fig. 1B). A second trap door, which was positioned on the other side of the partition just below the start box, allowed entry of a model predator (Fig. 1B). Both doors were connected to a monofilament line on a pulley, which made it possible for an observer to raise and lower them from a remote location. In the main arena of each experimental tank (30×30×30 cm; left hand side of Fig. 1A), we placed natural rocks and gravel from the river. Each experimental tank was filled to a depth of 22 cm with conditioned freshwater (Stress Coat, Aquarium Pharmaceuticals, Chalfont, Penn., USA). Aeration and water filtration was provided by a small water filter placed in the smaller compartment (i.e. not the test arena – see below) of the experimental tank (see Fig. 1A).

In the high-risk treatment, a hand-made pike-shaped model (length 115 mm, width 17 mm, widest depth 22 mm) was suspended on a monofilament line, which passed through the entire tank,
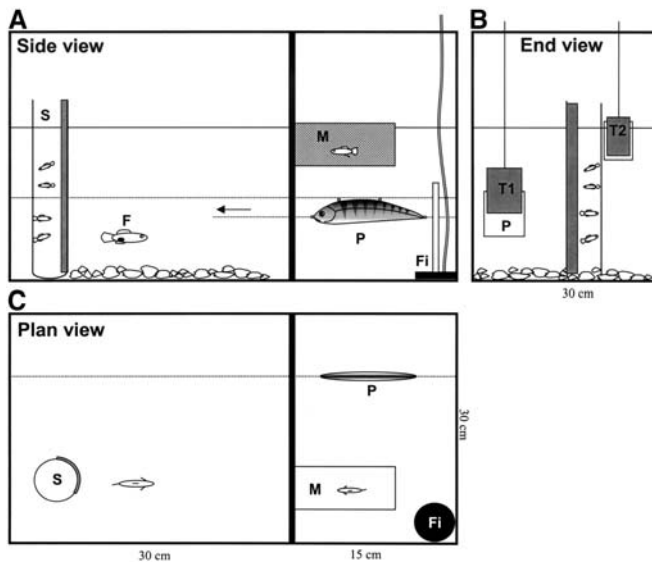
Fig. 1 Experimental design, showing (**A**) side view, (**B**) end view and (**C**) plan view of the experimental tank (the diagram depicts the high-risk treatment). *S* School bottle containing four juveniles; *M* male's start box containing an experimental male; *F* experimental female in main test arena; *P* model predator; *Fi* water filter; *T1, T2* trapdoors for model predator and test male respectively

while in the low-risk treatment the line remained empty. The models, which were hand painted (see Fig. 1A), were chosen because of their resemblance to the pike cichlid (*Crenicichla alta*), an important guppy predator in the Tacarigua River (Magurran and Seghers 1994b). Before embarking on the field trip, we tested several potential predator models on captive (wild-caught and first generation captive born) fish originating from the Tacarigua River and selected the model ('Terminator', Abu Garcia Products, Spirit Lake, Iowa, USA) that elicited the strongest antipredator behaviour (J.P. Evans and J.L. Kelley, unpublished results). A pulley system (operated from a remote location) was used to move the predator model (high risk treatment) or the empty monofilament line (low risk treatment) through the open trap door and into the main behaviour arena of the experimental tank (see below). We reduced the possibility of pseudoreplication by selecting at random one of four replicate models for each high-risk trial (see Kroodsma et al. 2001) and by randomly assigning each of the four tanks with respect to treatment.

Experimental procedure

On the morning of each behavioural trial, a 1.5-l water bottle containing four unsexed juvenile fish was placed in the behaviour arena (hereafter referred to as the test arena). One side of the school bottle was covered with a black plastic 'blind' (6×24 cm) to prevent the school fish from seeing the predator model when it was introduced into the test arena. We used juvenile and not adult fish for the school to avoid the possibility of sexual interactions between members of the school and the focal male and female. Immediately after placing the school bottle in the test arena, an adult male was chosen at random from one of the holding tanks and placed in the black plastic start box (Fig. 1A), from which he had no visual access to any other part of the tank (i.e., the male could not see into the test arena or the area of the tank containing the model predator). A small section of netting was placed on top of the box to prevent the male escaping. A female was then selected at random from a holding tank (different from the test male's to avoid familiarity among the male and female) and placed in the test arena. Each female usually spent between 10–15 min explor-

ing the test arena before engaging in normal foraging and schooling activities (see below).

Female schooling and inspection behaviour
during the exposure period

When the female was fully settled, the door for the model predator (T1, see Fig. 1B) was gently raised and the model ('high risk' treatment) or the empty monofilament line ('low risk' treatment) was introduced into the test arena for 10 min. In the high-risk treatment, the model was initially placed in the centre of the test arena and at 2-min intervals thereafter it was moved slowly forwards and backwards along the monofilament line (5 cm in each direction). Preliminary trials confirmed that gentle movement of the predator model in this way elicited strong antipredator responses (notably schooling and inspection, but also darting movements away from the model). In the low risk (control) treatment, the empty monofilament line was moved at 2-min intervals in exactly the same way as the high-risk treatment. Thus, any disturbance (which was not observed) to the female caused by the line moving through the test arena was standardised in both treatments.

The time that each female spent schooling and the number of inspections performed were recorded as soon as the predator model entered the test arena. Schooling times were determined by measuring the length of time that the focal female spent within two body lengths of the juveniles in the bottle (see Magurran et al. 1994). In practice, whenever the female was in close proximity to the bottle she interacted visually with the school fish. An inspection event was characterised by visual fixation on the model predator whilst slowly swimming or 'gliding' towards it (Seghers 1973). Frequently, the test fish turned laterally towards the model and swam in a series of arcs along the side of it (this behaviour is termed 'avoidance drift') (Seghers 1973). Following an inspection, the female quickly darted or 'jumped' away and often returned to the school. Observations of female and male behaviour (see below) were performed behind a blind to avoid disturbing the fish.

Male mating behaviour

After the 10-min exposure period the model predator (or the empty monofilament line) was retracted and the trapdoor (T1) was closed. The door to the male's start box (T2) was then raised gently allowing the male (which had not previously seen the model predator) to swim into the main test arena. In the majority of trials the test male swam into the test arena as soon as the door was raised. If the male did not enter the test arena within 10 min the trial was aborted. Behavioural observations commenced as soon as the male performed his first mating attempt. As a measure of male sexual behaviour we considered the number of sigmoid displays (courtship attempts) and gonopodial thrusts (coercive mating attempts) performed by the test male during a 10-min period. Sigmoid displays were recorded when the focal male moved in front (or to one side) of the female, arched his body in a pronounced S-shaped posture and quivered (Baerends et al. 1955; Liley 1966). Gonopodial thrusts were recorded when the focal male attempted or succeeded in making physical contact with the female's genital pore without her cooperation or prior display (Baerends et al. 1955; Liley 1966).

After observing the male for 10 min we opened the 'predator door' (T1) and reintroduced the model into the test arena (or moved the empty line through the test arena in the low risk treatment). We then recorded male behaviour (as above) for a further 10 min. Thus, in the high-risk treatment we were able to record the mating behaviour of individual males in two contexts: (1) in the presence of a female that had been exposed previously to a simulated (and standardised) threat, and (2) in the presence of both the female and the model predator. Similarly, in the low-risk treatment, male behaviour towards non-exposed females was measured in both periods in the absence of the predator model (all other

variables, such as the door opening and the line moving through the tank, remained constant in both treatments). Thus, the low-risk treatment controlled for the possibility that male behaviour changes over time independently of the simulated predation threat. In both treatments, we also measured female schooling and inspection behaviour (described above for the exposure period) during the two 10-min periods in which we recorded male behaviour.

Following the final observation period the male and female were caught and their standard lengths (±0.5 mm) were measured. We confirmed that male and female body size did not differ significantly between the experimental groups (males: t_{37}=0.015, P=0.99; females, t_{37}=0.898, P=0.375). Test males and females were released into a post-experimental tank where they took no further part in subsequent trials. The fish in the school bottle were released into the holding tank containing the 60 juveniles. For each trial, we randomly selected juveniles from this tank for the 'school fish' and therefore some juveniles may have been used as school members more than once. However, our experimental design ensured that all juvenile fish used in the experiment were naïve of the treatment group, and all were assigned at random to the experimental treatment groups. The water in the experimental tanks was kept at 25°C (±1°C). All behavioural trials took place between 0800 and 1400 hours and light/dark cycles followed natural diurnal patterns (12 h:12 h, provided by 40 W fluorescent tubes). A total of n=28 trials were performed for each treatment, from which we obtained behavioural data from n=19 males for the high-risk treatment and n=20 for the low-risk treatment (n=17 trials were aborted due to the male not leaving the start box within 10 min of the start of the trial). In 7 replicates we failed to obtain schooling data from individual females during one of the three consecutive trials (within each replicate) and therefore sample sizes for schooling times can sometimes vary between analyses. Proportional data were arcsine transformed and all probabilities are two–tailed. Statistical analyses were performed using SPSS 10.1.4.

Results

Our analysis revealed that the presence of the predator model had a clear effect on female schooling behaviour. Females assigned to the high-risk group performed at least one predator inspection in 76.5% of the predator exposure trials (mean inspections=2.35±0.55 SE, range=0–7). Females in the high-risk group spent significantly more time schooling than their counterparts assigned to the low-risk group (repeated measures AN-OVA: between treatment groups, $F_{1,30}$=34.09, P<0.0001) and altered their behaviour among successive treatment periods in the high-risk group according to the presence or absence of the predator model (repeated measures ANOVA: within subjects, $F_{2,60}$=11.90, P<0.0005, interaction, F=6.46, P<0.003; Fig. 2). This was confirmed when schooling times for the three periods were analysed separately for each of the two experimental groups (repeated measures ANOVA: high risk group: $F_{2,26}$=12.375, P<0.0002; low-risk group: $F_{2,34}$=1.742, P=0.19). Importantly, females in the high-risk group schooled significantly more during the two test periods in which the predator model was in the tank (Fig. 2).

The total number of mating attempts performed by males (= no. thrusts + no. sigmoid displays) did not differ significantly between the treatment groups or between the two successive male behaviour trials within each group (repeated measures ANOVA: between treatment groups, $F_{1,36}$=0.719, P=0.402; within subjects,
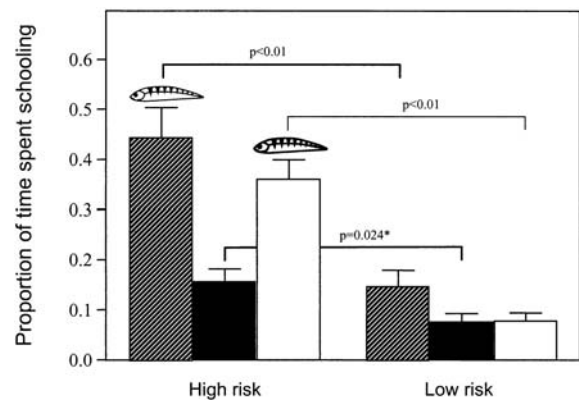

Fig. 2. The mean proportion of time (±SE) that females spent schooling during the three test periods in the high- and low-risk treatments. *Dashed bars* During initial exposure period (no male present); *filled bars* during first male behaviour trial; *open bars* during second male behaviour trial (predator model present in high-risk treatment). *After correcting for multiple comparisons (Bonferroni, α=0.05/3) the two behaviour periods (*filled bars*) do not differ significantly between treatments (Student *t*-test). The diagram of the model denotes the exposure periods when the model was present in the test arena
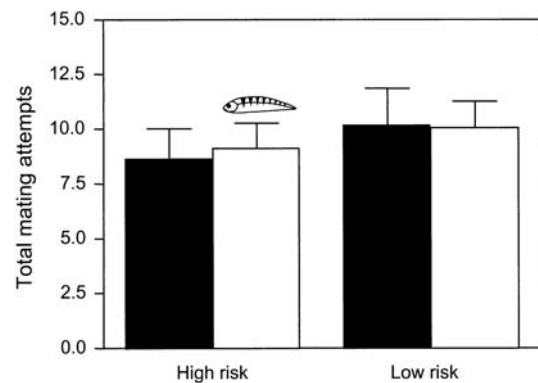
Fig. 3 The mean number (±SE) of mating attempts (= sigmoid displays + gonopodial thrusts) performed by focal males during the 10-min observation periods compared within and between treatments. *Filled bars* First behaviour period (no model present in either treatment); *open bars* second behaviour period (predator model present in high-risk treatment). The diagram of the model denotes the exposure period when the model was present in the test arena

$F_{1,36}$=0.007, P=0.934, interaction, F=0.078, P=0.781; Fig. 3). However, the proportion of gonopodial thrusts [= thrusts / (sigmoids + thrusts)] performed by males was significantly higher in the high-risk group (repeated measures ANOVA: between treatment groups, $F_{1,34}$=19.52, P<0.0001, Fig. 4). There was no significant difference in the proportion of thrusts between the two successive behavioural trials within either treatment group (repeated measures ANOVA: $F_{1,34}$=0.014, P=0.907, interaction, F=0.617, P=0.438, Fig. 4), confirming that in the high-risk group the increased reliance on coercive mating by males following female only ex-
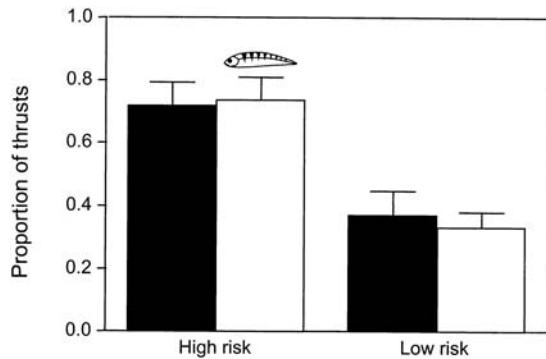
Fig. 4 The mean proportion (±SE) of thrusts [= no. thrusts / (no. sigmoid displays + no. thrusts)] compared within and between treatments. *Filled bars* First behaviour period (no model present in either treatment); *open bars* second behaviour period (predator model present in high-risk treatment). The diagram of the model denotes the exposure period when the model was present in the test arena

posure to the model did not change when the predator model was reintroduced into the test arena.

Discussion

Our results indicate that male guppies perform proportionally more gonopodial thrusts and fewer sigmoid displays when presented with a female that has been exposed previously to a simulated predation hazard. Total mating activity (combined rate of courtship and gonopodial thrusting) remained unchanged both within and between treatments but the proportion of thrusts was significantly higher during both trial periods in the high-risk treatment. Importantly, we did not detect a significant difference in male mating behaviour between the two successive behavioural trials in the high-risk treatment. Our results therefore support the hypothesis that the shift from courtship to coercive mating is mediated by changes in female behaviour (Magurran and Nowak 1991; and see Godin 1995) rather than a result of males displaying 'risk-sensitive' behaviour in response to predators (Endler 1987; and see discussion by Houde 1997, p. 100).

Our finding that female schooling behaviour did not differ (significantly) between the treatment groups following the initial exposure period (filled bars, Fig. 2) suggests that males did not use schooling as a cue to switch from courtship to forced mating attempts. Thus, males probably exploit other changes in female behaviour associated with a recent predator encounter. For example, in the period following the initial predator exposure we observed that females were relatively inactive and remained visually fixated on the area of the tank in which the predator had previously appeared. These behavioural cues may cause males to alter their mating strategy and exploit the female's preoccupation with predator vigilance. During the second exposure period,

in which the male, female and the model were present (in the high-risk treatment), our qualitative observations suggested that males also tended to exploit female inspection behaviour rather than react in a risk-sensitive way towards the model (see below).

The observation that males maintain high levels of sexual activity in the presence of an apparent predation hazard is consistent with the idea that they trade-off the risk of predation against future reproductive success (for similar examples see Candolin 1998; Cooper 1999; Hazlett and Rittschof 2000). Since males have limited opportunities to achieve copulations through courtship (females are sexually receptive for only 2–3 days per month), we hypothesise that an increased opportunity to obtain successful copulations through gonopodial thrusting under predation risk will have sufficient fitness value to promote this kind of risk-taking in nature. Indeed, during our observations of male behaviour we noted several incidences in which males continued to attempt gonopodial thrusts while the female was inspecting the model (i.e. when both fish were extremely close to the model predator). Although we did not quantify male antipredator behaviour in this experiment, it was evident during the high-risk trials that males were far more 'risk-reckless' than females, and usually only spent time with the school fish in order to interact (sexually) with the female while she was schooling (see also Magurran and Nowak 1991). We therefore suggest that the shift towards coercive mating by male guppies in dangerous situations is likely to be an adaptive strategy that results in higher reproductive success for males, in spite of the risks associated with engaging in mating activity under predation risk.

Previous work has demonstrated that under elevated predation risk, female guppies become sexually unreceptive and reduce their preferences for conspicuous males (Godin and Briggs 1996; Gong and Gibson 1996). This switch in female mating preferences under predation risk, coupled with a corresponding increase in antipredator behaviour (Magurran and Nowak 1991; this study), is likely to reduce the effectiveness of male courtship and favour the use of coercive mating in high-risk situations. However, this argument depends on the effectiveness (and therefore the potential benefits to males) of coercive mating in nature. Until recently, gonopodial thrusting was considered to be a relatively inefficient mating strategy in terms insemination success (Houde 1997), despite the observation that females inhabiting high-predation populations are subject to approximately one forced mating attempt per minute (Magurran and Seghers 1994b). However, a recent survey of eight natural populations in Trinidad (J.P. Evans, A. Pilastro, and I.W. Ramnarine, unpublished data) has confirmed that gonopodial thrusting is likely to be far more important than previously thought, with up to 60% of females containing sperm in the gonoducts arising from forced copulations (see also Pilastro and Bisazza 1999; Matthews and Magurran 2000).

The results presented in this study are consistent with the findings from a number of previous studies demon-

strating flexibility in male mating behaviour in response to changes in predation risk. In studies of captive (Endler 1987; Magurran and Nowak 1991), wild-caught (Magurran and Seghers 1990) and free-ranging guppies (Godin 1995), researchers consistently report that males perform proportionately fewer sigmoid displays and more coercive mating attempts under increased predation risk. However, our results differ from those presented in one study that attempted to disentangle the effect of male versus female exposure to predation risk (Dill et al. 1999). Dill et al. (1999) provided captive male and female guppies separately (and concurrently) with information about predation risk and reported a general decline in male mating activity (both forced mating attempts and courtship) following female only exposure to a simulated predation threat. Possible reasons for the differences between their results and other studies were discussed by the authors and include the fact that they used virgin males and females (which are highly motivated to copulate) for their study. Furthermore, companion fish were not used in Dill et al.'s design, thus preventing social interactions (notably schooling) between the focal individuals and other fish. Thus, females were not able to engage in behaviours that probably reduce their susceptibility to predation (Magurran 1990), but (we suggest) increase their vulnerability to gonopodial thrusting (see also Magurran and Nowak 1991). A further possible explanation for the discrepancy between our results and those obtained by Dill et al. (1999) is that we used wild-caught, rather than captive-bred fish (in their study, fifth to eighth generation). Recent work suggests that the anti-predator behaviour of wild-caught fish differs significantly from their captive-bred counterparts originating from the same population (J.L. Kelley and A.E. Magurran, unpublished data, and see Brown and Laland 2001).

In conclusion, we provide evidence that male guppies alter their mating tactics under predation risk as a result of changes in female behaviour. Our results therefore lend support to the hypothesis that males alternate between mating strategies to increase their reproductive success, rather than to reduce their vulnerability to predators. The identification of the behavioural cues used by males, as well as the potential reproductive fitness benefits associated with switching mating tactics, await further investigation.

References

Baerends GP, Brouwer R, Waterbolk HT (1955) Ethological studies on *Lebistes reticulatus* (Peters), I. An analysis of the male courtship pattern. Behaviour 8:249–334

Brown C, Laland K (2001) Social learning and life skills training for hatchery reared fish. J Fish Biol 59:471–493

Candolin U (1997) Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behav Ecol Sociobiol 41:81–87

Candolin U (1998) Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. Proc R Soc Lond B 265:1171–1175

Chivers DP, Wisenden BP, Smith JF (1995) Predation risk influences reproductive behaviour of Iowa darters, *Etheostoma exile* (Osteichthyes, Percidae). Ethology 99:278–285

Cooper WE (1999) Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. Behav Ecol Sociobiol 47:54–59

Crowley PH, Travers SE, Linton MC, Cohn SL, Sih A, Sargent RC (1991) Mate density, predation risk, and the seasonal sequence of mate choices: A dynamic dame. Am Nat 137:567–596

Dill LM, Hedrick AV, Fraser A (1999) Male mating strategies under predation risk: do females call the shots? Behav Ecol 10:452–461

Endler JA (1987) Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim Behav 35:1376–1385

Endler JA (1995) Multiple-trait coevolution and environmental gradients in guppies. Trends Ecol Evol 10:22–29

Forsgren E, Magnhagen C (1993) Conflicting demands in sand gobies: predators influence reproductive behaviour. Behaviour 126:125–135

Godin J-G (1995) Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224–229

Godin JGJ, Briggs SE (1996) Female mate choice under predation risk in the guppy. Anim Behav 51:117–130

Gong A (1997) The effects of predator exposure on the female choice of guppies (*Poecilia reticulata*) from a high predation population. Behaviour 134:373–389

Gong A, Gibson RM (1996) Reversal of a female preference after visual exposure to a predator in the guppy, *Poecilia reticulata*. Anim Behav 52:1007–1015

Hazlett BA, Rittschof D (2000) Predation-reproduction conflict resolution in the hermit crab, *Clibanarius vittatus*. Ethology 106:811–818

Houde AE (1997) Sex, color, and mate choice in guppies. Princeton University Press, Princeton, N.J.

Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–327

Koga T, Blackwell PRY, Jennions MD, Christy JH (1998) Elevated predation risk changes mating behaviour and courtship in a fiddler crab. Proc R Soc Lond B 265:1385–1390

Kroodsma DE, Byers BE, Goodale E, Johnson S, Lui WC (2001) Pseudoreplication in playback experiments, revisited a decade later. Anim Behav 61:1029–1033

Liley NR (1966) Ethological isolating mechanisms in four sympatric species of poeciliid fishes. Behaviour (Suppl XIII) 13:1–197

Liley NR, Seghers BH (1975) Factors affecting the morphology and behaviour of guppies in Trinidad. In: Baerends G, Beer C, Manning A (eds) Function and evolution in behaviour. Clarendon Press, Oxford, pp 92–118

Lima SL, Dill LM (1990) Behavioral decision made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Magnhagen C (1991) Predation risk as a cost of reproduction. Trends Ecol Evol 6:183–186

Magurran AE (1990) The adaptive significance of schooling as an anti-predator defence in fish. Ann Zool Fenn 27:51–66

Magurran AE, Nowak MA (1991) Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. Proc R Soc Lond B 246:31–38

Magurran AE, Seghers BH (1990) Risk sensitive courtship in the guppy (*Poecilia reticulata*). Behaviour 112:194–201.

Magurran AE, Seghers BH (1994a) Predator inspection behaviour covaries with schooling tendency amongst wild guppy populations. Behaviour 128:121–134

Magurran AE, Seghers BH (1994b) Sexual conflict as a consequence of ecology: evidence from guppy, *Poecilia reticulata*, populations in Trinidad. Proc R Soc Lond B 255:31–36

Magurran AE, Seghers BH, Shaw PW, Carvalho GR (1994) Schooling preferences for familiar fish in the guppy, *Poecilia reticulata*. J Fish Biol 45:401–406

Matthews IM, Magurran AE (2000) Evidence for sperm transfer during sneaky mating in wild Trinidadian guppies. J Fish Biol 56:1381–1386

Pilastro A, Bisazza A (1999) Insemination efficiency of two alternative male mating tactics in the guppy (*Poecilia reticulata*). Proc R Soc Lond B 266:1887–1891

Pocklington R, Dill LM (1995) Predation on females or males: who pays for bright male traits? Anim Behav 49:1122–1124

Reynolds JD, Gross MR, Coombs MJ (1993) Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. Anim Behav 45:145–152

Rodd FH, Sokolowski MB (1995) Complex origins of variation in the sexual behaviour of male Trinidadian guppies, *Poecilia reticulata*: interactions between social environment, heredity, body size and age. Anim Behav 49:1139–1159

Rodd FH, Reznick DN, Sokolowski MB (1997) Phenotypic plasticity in the life history traits of guppies: response to social environment. Ecology 78:419–433

Ryan MJ (1985) The Tungara frog: a study in sexual selection and communication. University of Chicago Press, Chicago, Ill.

Seghers BH (1973) An analysis of geographic variation in the antipredator adaptations of the guppy, *Poecilia reticulata*. University of British Columbia, Vancouver, Canada

Sih A (1988) The effects of predators on habitat use, activity and mating behaviour in a semi-aquatic bug. Anim Behav 36: 1846–1848

Sih A (1994) Predation risk and the evolutionary ecology of reproductive behaviour. J Fish Biol 45:111–130

Warner RR, Dill LM (2000) Courtship displays and coloration as indicators of safety rather than of male quality: the safety assurance hypothesis. Behav Ecol 11:444–451