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Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*

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SUMMARY

The risk of predation and cost or benefit of a mating attempt are rarely the same for both sexes. An excellent example is provided by the guppy, *Poecilia reticulata*, a species that has a promiscuous mating system in which female choice plays an important role. Males engage almost continuously in courtship behaviour but, as females are sexually receptive for short periods only, most male displays are ignored and sneaky mating attempts avoided. Experiments on guppies from wild Trinidad populations reveal that females appear to perceive themselves to be at a greater risk of predation and devote more time to anti-predator behaviour, for example, schooling when threatened. Inspections of the predator are also mainly initiated and led by female guppies. Males exploit this behavioural switch by increasing their sneaky mating attempts. A game theoretical analysis is used to explore the sexual asymmetry in mating cost and predation risk. Together these approaches show that there is no intersexual cooperation during predator inspection behaviour in this species, and may explain the paradoxical increase in mating activity by male guppies under threat.

1. INTRODUCTION

As even the best anti-predator tactic is ultimately counterproductive if it prevents an individual allocating time or energy to other fitness-related activities, behavioural flexibility is a particularly important weapon in the arms race between prey and their predators (Dawkins & Krebs 1979). This flexibility allows animals to modify their behaviour on the basis of the prevailing threat of predation and to balance risk against other conflicting demands (Dill 1987). Many trade-offs between foraging behaviour and predator avoidance have now been documented (Lima & Dill 1990) and there is good evidence that individuals are able to make subtle and adaptive behavioural decisions. Foraging animals rarely try to draw attention to themselves (but see Godin & Smith 1988). By contrast, courtship involves elaborate displays that seem as likely to catch the eye of a potential predator as a potential mate. Surprisingly, little is known about risk assessment during courtship, and there have been few attempts (either empirical or theoretical) to determine whether courting animals trade-off the threat of predation against an opportunity to mate (Lima & Dill 1990; Magnhagen 1991; Sih 1987).

Those studies that have examined the influence of risk on reproductive activity have generally concluded that predators inhibit or reduce mating behaviour. Sih *et al.* (1990), for example, found that both mating

duration and mating frequency in water striders, *Gerris remigis*, decreased in the presence of a predatory green sunfish, *Lepomis cyanellus*, and Tuttle & Ryan (1982) and Ryan (1985) showed that exposure to model predators led male tree frogs, *Smilica sila*, and male Tungara frogs, *Physalaemus pustulosus*, to reduce their calling activity. Magnhagen (1990) discovered that young black goby, *Gobius niger*, males ceased spawning when confronted with a cod, *Gadus morhua*.

The dilemma faced by reproductively active animals is, however, more complex than it may initially appear. The risk of predation and cost or benefit of a mating attempt are rarely the same for both sexes. Differences in behaviour, body size or conspicuousness can make one sex more vulnerable to capture than the other. For example, egg-carrying female copepods (*Cyclops vicinus* and *Eurytemora hirundoides*) suffer increased predation by fish (Winfield & Townsend 1983; Vuorinen *et al.* 1983), and male ducks with bright plumage are significantly more likely to be shot by hunters than males from species in which the sexes are similar in appearance (Metz & Ankney 1991). Differences in mating cost are brought about by asymmetries in gamete production, parental care and intrasexual competition. As mating is usually less costly for males it is in a female's interest to choose a good quality partner (Parker 1983). Adaptive female choice, which reflects this need, occurs widely in fish and other groups of animals (Kodric-Brown 1990). Sneaky mating attempts however provide males with a means of circumventing female choice. Atlantic salmon, *Salmo salar*, (Jones 1959) and bluegill sunfish, *Lepomis*

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macrochirus, (Dominey 1981; Gross 1982, 1984) are but two of many species of fish in which some males adopt this tactic.

In this paper we investigate the effect of predation risk on the behavioural interactions of male and female guppies, *Poecilia reticulata*. We intend to determine whether both sexes respond equally to threat by reducing their reproductive activity or whether there is a sexual asymmetry in the trade-off of mating behaviour against danger. To do this we employ two complementary approaches. First, we quantify anti-predator behaviour and male–female interactions under experimentally varied predation risk. We then use a game theoretical analysis to explore the conflict between mating behaviour and predator avoidance.

Guppies occur in northeast South America and the adjacent islands. The small poeciliid fish have a promiscuous mating system in which female choice has a major role (Houde 1987; Houde & Endler 1990). Male guppies engage almost continuously in courtship behaviour and employ two methods of obtaining a mating (Baerends *et al.* 1955; Luyten & Liley 1985; Endler 1987). They may either perform a sigmoid display in which the fins are extended and the body is arched in an S-shaped posture (Baerends *et al.* 1955; Liley 1966) or use gonopodial thrusting in an attempt to achieve a sneaky mating (Baerends *et al.* 1955; Endler 1983; Farr 1980; Luyten & Liley 1985). As females are receptive to male displays only as virgins or for short periods following the birth of a brood (Liley 1966; Houde 1988) most sigmoid displays are ignored (Endler 1987). However, male mating success is related to degree of female preference during the receptive period (Houde 1988; Houde & Endler 1990) and it appears that a standard copulation following a sigmoid display is more likely to lead to insemination than gonopodial thrusting alone. The relative success of sneaky mating is unknown but the frequent occurrence of gonopodial thrusting provides strong circumstantial evidence that it is an important reproductive tactic. Luyten & Liley (1985), who made field observations of the courtship behaviour of four wild populations of guppies in Trinidad, observed rates of between 0.5 and 3 gonopodial thrusts and 1.5 and 5.5 sigmoid displays per male over 3 min. Individual males use both tactics although there are individual differences in their preference for one or the other (Magurran & Seghers 1990). Guppies continue to court throughout the day but are particularly active when light levels are reduced (Endler 1987).

The high intensity of reproductive activity means that males are constantly vigilant for females to whom they can display or with whom they can attempt to copulate. Most females that the males encounter will not be in their receptive period and are consequently uninterested in sexual activity. Furthermore, given the importance of female choice during reproduction (Houde 1988; Houde & Endler 1990) it is in a female's interest to avoid a forced copulation.

Many populations of guppies are exposed to considerable levels of predation from a range of predators including the pike cichlid, *Crenicichla alta*, and the blue acara, *Aequidens pulcher* (Liley & Seghers 1975; Endler

1978, 1980, 1983). These predators act as a strong selective force influencing such traits as life history tactics (Reznick & Endler 1982; Reznick *et al.* 1990), male colour (Endler 1983), schooling tendency (Seghers 1974), body size (Liley & Seghers 1975), feeding tenacity (Fraser & Gilliam 1987) and the risk-sensitivity of courtship behaviour (Endler 1987; Magurran & Seghers 1990). Both sexes must reconcile their investment of time and energy in obtaining copulations, or avoiding them, with anti-predator behaviour.

2. EMPIRICAL ANALYSIS OF THE EFFECT OF RISK ON GUPPY MATING BEHAVIOUR

(a) *Methods*

The following experiment was designed to examine the effect of risk on male and female behaviour. Laboratory-bred guppies descended (for two to three generations) from individuals collected from the Oropuche River in Trinidad, were used (mean \pm s.d. total lengths, male = 21.4 ± 1.66 mm; female = 29.7 ± 5.55 mm). In the wild this population is subject to predation from cichlids (*C. alta* and *A. pulcher*) and characins (Magurran & Seghers 1992). In each trial, five male and five female guppies were placed together in an aquarium (90 \times 25 \times 32 cm, with water 20 cm deep). The aquarium otherwise contained only a small filter and a clump of Java moss, *Vesicularia dubyana*. The guppies were allowed 24 h to settle before their behaviour was observed. Males were individually distinguishable by their unique colour patterns. Females could also be individually recognized because of small size differences.

Each trial was divided into two sections. In the first part the behaviour of the guppies was observed in undisturbed circumstances. During this time each fish was monitored for 5 min. The number of sigmoid displays and gonopodial thrusts delivered by a male was recorded along with the length of time (in seconds) he spent schooling (defined as being within five body lengths of another fish, but not involved in courtship or aggressive behaviour). Female schooling behaviour was also measured using the same criteria. In addition, the number of occasions on which a female avoided a male (swam or darted away from a courtship attempt) and received a thrust (when the male's gonopodium appeared to make contact with her genital pore) was noted.

After 24 h, an 11.5 cm *A. pulcher* was gently introduced to the test tank for the second, 'risky' phase of the trial. This predator swam slowly from end to end of the tank, pausing occasionally under the filter. Although it did not attack the guppies, the acara elicited strong anti-predator behaviour including rapid darts, surface jumps (Seghers 1973), flash expansions and fountain effects (Magurran & Pitcher 1987). Inspection behaviour, which takes place when one or more fish approach a predator to monitor its behaviour or confirm its identity (Licht 1989; Magurran 1986; Magurran & Girling 1986; Magurran & Pitcher 1987; Magurran 1990) was also observed.

For this experiment, inspection was defined as a steady approach by one or more fish towards the acara. Such an approach was followed by either a rapid dart (or skitter: Magurran & Pitcher 1987) or avoidance drift (Seghers 1973) during which the guppy turned laterally to the predator and swam in an arc-like trajectory along the predator's body, before retreating. The number of times each individual approached the predator during the 5 min period was recorded. All other behaviour was scored as before. Guppies were fed 2 h before each recording session. The order in which individuals were observed was randomized.

The trials were replicated four times using different fish, thus providing information on the behaviour of 20 male and 20 female guppies.

In pilot work it rapidly became apparent that sexual asymmetry in behaviour under threat extended to participation in inspection. This observation was quantified in a separate experiment as follows. As before, groups of five male and five female guppies were placed together in the test aquarium and allowed to settle overnight. Next day, 2 h after feeding, the blue acara was added to the aquarium. (The predator was the same individual used in the previous work but no guppies participated in both experiments). The number and sex of guppies in each inspection was recorded using an audio tape along with fish order (the position of males and females from the front to the back of the inspecting group) and the presence of either gonopodial thrusting or sigmoid displays. The experiment was repeated using both wild-caught (collected in Trinidad in March 1990) and laboratory-bred guppies. Three populations were compared (wild: Guanapo, Turure and Oropuche; lab: Oropuche) and all fish were derived from sites where guppies occur sympatrically with predators including *C. alta* and *A. pulcher* (Magurran & Seghers 1992). There were four replicates of each category of guppy. Each replicate used different fish (sizes of fish tested were as follows: Guanapo (mean \pm s.d. total length), males = 20.8 ± 1.44 mm, females = 24.9 ± 2.75 mm; Turure, males = 20.4 ± 1.47 mm, females = 25.3 ± 2.64 mm; Oropuche wild, males = 20.4 ± 1.69 mm, females = 26.5 ± 2.09 mm; Oropuche lab, males = 21.6 ± 1.51 mm, females = 28.9 ± 4.01). After 15 min the predator was removed from the tank and the trial terminated.

(b) Results

Both sexes responded to the presence of the predator by a significant increase in schooling behaviour ($F_{1,64} = 93.9$, $p < 0.001$) although a greater behavioural shift occurred in female than in male guppies (significant sex \times risk interaction in a 3 way ANOVA of log transformed data, $F_{1,64} = 4.95$, $p < 0.05$; Sokal & Rohlf 1981) (figure 1a). The third factor in the ANOVA, test group, was non-significant ($F_{3,64} = 0.70$, $p > 0.5$) suggesting that guppy behaviour was consistent across the four replicate trials. Females inspected the predator significantly more often than males (female mean \pm s.e. = 5.6 ± 0.56 ; male = 3.7 ± 0.54 ; $F_{1,32} = 6.04$, $p < 0.05$). Again there was no effect of test group ($F_{3,32} = 1.70$, $p > 0.05$).

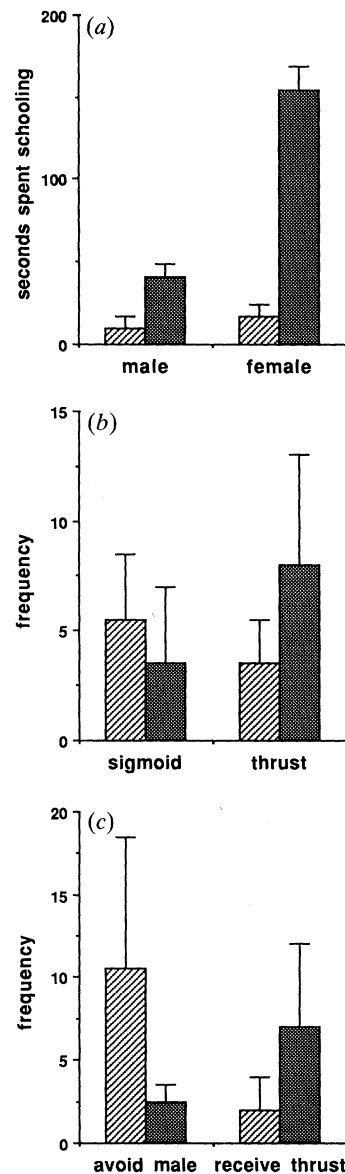
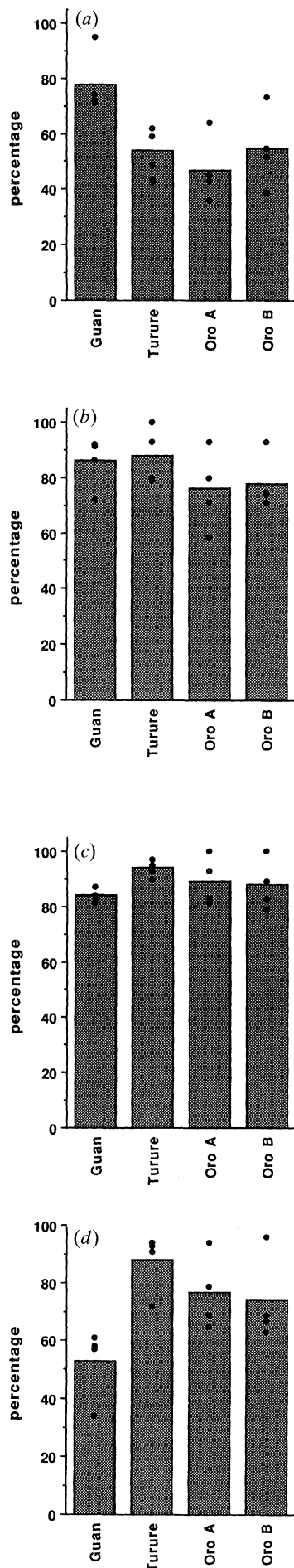


Figure 1. (a) The mean ($n = 20$) \pm s.e. time spent schooling by male and female Oropuche guppies in the absence (stripes) and presence (stippled) of the predator; (b) median frequency ($n = 20$) and upper quartile range of sigmoid displays and gonopodial thrusts (sneaky mating attempts) by male Oropuche guppies in the absence and presence of the predator; (c) median number ($n = 20$) and upper quartile range of occasions when female guppies successfully avoided thrusting males or received thrusts (when gonopodium appeared to contact the genital pore) in relation to the absence or presence of the predator. Quartile ranges reflect overall variation, statistical analyses (see text) were based on a paired design.

Male courtship behaviour varied in response to risk. Although males reduced their number of courtship displays (Wilcoxon signed-ranks test, $z = 2.02$, $p < 0.05$), the frequency of sneaky mating attempts increased in the presence of the predator ($z = 3.25$, $p < 0.01$) (figure 1b). Females, by contrast, made fewer attempts to avoid the attentions of the males when under threat ($z = 3.60$, $p < 0.001$), and received more gonopodial thrusts as a consequence ($z = 3.26$, $p < 0.01$, all probabilities two-tailed) (figure 1c).



The male exploitation of female inspection was dramatically revealed in the second experiment. Typically, about half to three quarters of inspections comprised more than one fish (figure 2*a*). In 15 out of 16 trials (figure 2*b*), most of these grouped inspections contained both sexes (frequency of inspections containing both males and females significantly greater than 50%: $p < 0.01$ in all cases, G test (Sokal & Rohlf 1981)). Females led between 79% and 100% of the mixed-sex inspections (frequency of female lead significantly greater than 50% in all cases, $p < 0.01$, G test, figure 2*c*). Sneaky mating attempts during mixed-sex inspection occurred in all 16 trials (figure 2*d*). The incidence of sneaky mating ranged from 34% to 96%. With the exception of the Guanapo population, which had fewer single fish inspections ($F_{3,12} = 5.34$, $p < 0.05$, 1 way ANOVA with arcsin transformation of proportions) and a reduced level of sneaky mating attempts during mixed-sex inspections ($F_{3,1} = 4.09$, $p < 0.05$), there were no significant behavioural differences among categories of fish (ANOVAs on proportion of inspections with more than one sex, $F_{3,12} = 1.10$, $p > 0.05$, proportion with female leading $F_{3,12} = 0.75$, $p > 0.05$).

Unlike gonopodial thrusts, sigmoid displays occurred only rarely during inspection (mean per trial 2.81, s.e. = 0.64). There were no significant differences in display rate amongst categories of fish ($F_{3,12} = 0.99$, $p > 0.05$).

3. DISCUSSION

The female guppies in the experiments showed an immediate and adaptive behavioural response in the presence of a predator. Not only did they inspect the predator more often, but they also increased their level of schooling behaviour. Schooling confers a number of important anti-predator advantages including increased vigilance and more effective evasion tactics (see Magurran (1990) for a review). This heightened female perception of danger could reflect a genuine disparity in risk. Female guppies are substantially larger than males (unlike males they continue to grow after sexual maturity (Constanz 1989)) and may represent more profitable targets for size-selective predators. The pike cichlid (*C. alta*) is less proficient at handling small prey and, like the predatory characin *Hoplias malabaricus*, tends to select larger guppies in laboratory tests (Liley & Seghers 1975). During

Figure 2. (a) Percentage of inspections in which more than one fish participated. Bars give the population (or category) mean, points give the values for the individual trials. Total numbers of inspections for the 15 min recording period were as follows: Guanapo (Guan: 53, 82, 103, 50), Turure (63, 112, 68, 44), Oropuche lab-reared (Oro A: 32, 66, 51, 64), Oropuche wild-caught (Oro B: 48, 74, 44, 65); (b) percentage of grouped inspections (that is those in which two or more fish participated) with both males and females present; (c) percentage of mixed-sex inspections in which a female led the inspecting school and approached the predator most closely; (d) percentage of mixed-sex inspections in which females received one or more gonopodial thrusts from males.

inspection, Lower Aripo females stay significantly further away from the attack cone (i.e. the dangerous mouth region) of a fish predator than Lower Aripo males (Magurran & Seghers 1990). Female guppies (from five Trinidad populations) also respond more vigorously when threatened by a model predator (Seghers 1973). Males, however, could either be less vulnerable to predators (because of their smaller size) or choose to disregard risk in favour of increased opportunities for sneaky mating attempts. It is likely that both factors operate. In Trinidad, male guppies are smaller in sites with high predation pressure (Liley & Seghers 1975) and transplant experiments confirm that male size increases when guppies are exposed to less severe predation regimes (Reznick *et al.* 1990). Furthermore, many wild Trinidad populations show a female bias in the sex ratio despite the fact that both sexes are equally represented when guppies from the same populations are bred and raised in the laboratory (Seghers 1973). Interestingly, Seghers (1973) found that female guppies were approached and attacked more often by Hart's rivulus, *Rivulus hartii*, but were actually killed less frequently than males.

(a) Another battle of the sexes: a game for guppies

We can illustrate the conflict between mating behaviour and predator avoidance by an imaginary game. Let us suppose that males and females can opt for one of two strategies: mating behaviour (S) or predator-avoidance behaviour (A). For simplicity we focus on the situation where males attempt to obtain sneaky matings. In this case, by playing S, a male incurs an increased investment of time and energy in gonopodial thrusting. We further assume that females are sexually non-receptive (the actual state of the majority of mature females in the wild). For a female, therefore, strategy S means the avoidance of sneaky mating attempts. In both sexes strategy A stands for a number of anti-predator tactics, including inspection behaviour. We can now define the following parameters: P and p denote the relative costs (for males and females respectively) of the risk of predation in the absence of anti-predator behaviour. The parameters M and m describe the benefit (for males) and cost (for females) of a sneaky mating. (Note that we use capital letters to denote pay-off to males and lower case letters for pay-off to females.) These assumptions lead to the pay-off matrix in table 1.

This game can be classified into three generic situations, depending on the prevailing risk.

1. In very threatening circumstances both sexes perform anti-predator behaviour. The state (A, A) is then called a strict Nash solution. This happens if $P > M$ (regardless of whether $p > m$ or $p < m$). Biologically, this means that when risk of predation is high, both sexes should optimize their pay-offs by opting for predator avoidance behaviour (the strategy A). Both male and female guppies do indeed employ a range of anti-predator responses when under direct attack from a predator (Seghers 1973).

2. Under less severe but still considerable danger of predation, i.e. if $P < M$ but $p > m$, the state (S, A) is

Table 1 The pay-off matrix for the guppies' battle of the sexes

(The 'guppy game' describes the asymmetric interaction between males and females engaged in sneaky mating activity (S) and anti-predator behaviour (A). Mating activity means sneaky mating attempts for male guppies and male avoidance behaviour for females. The parameters, P, p, M, m , describe, respectively, the cost of predation risk for males and females and the benefit or cost of sneaky matings to males and females. When both sexes are engaged in mating behaviour – the state (S, S) – then the pay-off consists of the enhanced risk of predation ($-P$ for males and $-p$ for females). In this simplest version of the game we assume that thrusting is not successful if the female plays S. If males are sexually active while females avoid the predator – the state (S, A) – then a mating can be forced leading to a payoff $M - P$ for males (who run the risk of predation) and the cost, $-m$, for females. Alternatively, if males avoid the predator while females avoid males – the state (A, S) – then no mating activity results and zero pay-off is obtained by males. Females get $-p$. Finally, should both sexes employ anti-predator behaviour – the state (A, A) – nothing happens in our game; both sexes obtain the zero pay-off (which can be considered as an arbitrary level of scaling). For moderate predation risk ($P < M$ and $p < m$) the game has a cyclic structure and none of the four states (A, A), (A, S), (S, A) and (S, S) is a Nash solution.)

		female	
		S	A
male	S	$-P/-p$	$M-P/-m$
	A	$0/-p$	$0/0$

the stable outcome. This means that if the risk of predation is sufficiently high for females to engage in anti-predator behaviour at the expense of receiving sneaky matings, then the males optimize their pay-off by thrusting (playing S).

3. Most interesting is the case of moderate risk, i.e. $P < M$ and $p < m$. This was in essence the behavioural outcome of the experiment in which the fish were exposed to a threatening, but non-attacking, predator. Here there is no strict Nash solution, but rather cyclic domination. We can see this by looking at a situation where the game starts in state (A, A), i.e. where both sexes are engaged in anti-predator behaviour. In this case the males would increase their pay-off by changing to (S, A) because $M > P$. Females, however, could then increase their pay-off by switching to male avoidance (S, S). Now the males would do better by reverting to anti-predator behaviour, i.e. to state (A, S). At this point the females should switch too, and we end up at the initial state (A, A) again.

Our moderate risk game appears to be an oscillatory system. Its dynamical behaviour can be understood in the context of an appropriate differential equation. Let us define the quantities x and y , which denote the

fraction of time invested in mating activity by males and females respectively. A male playing the mixed strategy x devotes a fraction x of his time to sexual activity and $1-x$ to anti-predator behaviour. His pay-off against a female playing the mixed strategy y is given by

$$G(x, y) = x(M - P - My). \quad (1)$$

The female's pay-off is obtained as

$$H(x, y) = -mx(1-y) - py. \quad (2)$$

Suppose males and females continuously adjust their strategies, x and y , to maximize their pay-offs. This means that the rate of change of x and y follows the gradient of the functions G and H .

$$dx/dt = a(\partial G/\partial x) = a(M - P - My), \quad (3)$$

$$dy/dt = b(\partial H/\partial y) = b(mx - p). \quad (4)$$

Here a and b denote some rate constants; the time derivative is proportional to the partial derivative. For the case of moderate predation pressure ($P < M$ and $p < m$) this system of differential equations has an interior fixed point given by

$$\hat{x} = p/m, \quad \hat{y} = 1 - P/M \quad (5)$$

which represents a Nash solution of the game. A stability analysis reveals that this fixed point is a centre surrounded by neutral oscillations. We find an invariant of motion given by

$$I(x, y) = ay[M - P - My/2] + bx[p - mx/2]. \quad (6)$$

It can be shown that the fixed point values, (\hat{x}, \hat{y}) , represent the average fractions of time spent playing each of the two strategies (averaged over the oscillating cycle). The dynamical properties of the guppy game are similar to Hofbauer & Sigmund's (1988) analysis of Dawkins' (1976) 'Battle of the sexes'.

The mathematical analysis helps us to understand the observed guppy behaviour. Let us assume that the risks of predation for males and females are related to each other via the parameter s , which denotes predation risk. To keep things simple, we consider the situation $P = p = s$. Figure 3 shows the average time devoted to sneaky mating behaviour by males and its avoidance by females as a function of predation risk. There are interesting transitions as this risk increases beyond the threshold values m and M . At moderate risk, $s < m$, sneaky mating activity increases for males (the time average of the oscillations is given by $x = s/m$) and avoidance of males by females decreases (time average $y = 1 - s/M$). For $M > s > m$ the state (S, A) becomes the stable equilibrium. For still greater predation risk, $s > M$, mating activity ceases completely. The three generic outcomes of the game are adopted depending on relative risk of predation and it will be interesting in future work to pinpoint the behavioural transitions arising through changes in risk. We can, however, already find evidence that our game is played across, as well as within, populations of guppies. In Trinidad, male guppies from rivers with high predation pressure (i.e. greater numbers of predators) perform more gonopodial thrusts and fewer

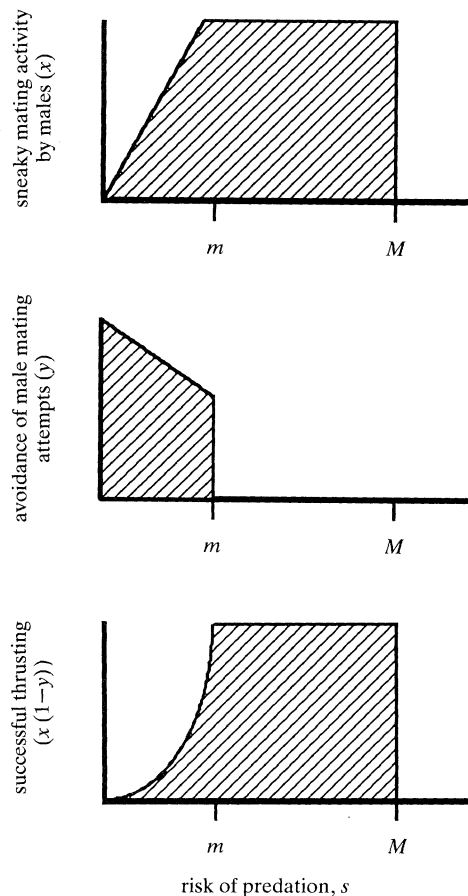


Figure 3. Mating activity as a function of predation pressure according to the game theoretical analysis of the guppies' battle of the sexes (see text). Mating behaviour entails sneaky mating attempts by males and male avoidance behaviour by females. The parameters M and m specify respectively the benefit for males and cost for females of sneaky matings. The parameters x and y denote the fraction of time devoted to mating behaviour by males and females respectively. The amount of successful thrusting is proportional to the product $x(1-y)$ which denotes the fraction of time when males are engaged in mating behaviour, but females are not. As the risk of predation, s , increases, mating behaviour becomes more rewarding for males and less rewarding for females ($s < m$). This results in a state where females optimize their pay-off by devoting all their resources to anti-predator behaviour while males continue to attempt sneaky matings ($m < s < M$). Here the risk of predation is larger than the cost of receiving a sneaky mating for females but smaller than the benefit of gaining a sneaky mating for males. Under high predation risk ($s > M$), mating behaviour ceases completely.

sigmoids than males from less dangerous habitats (Luyten & Liley 1985), even when no predators are in the vicinity. If predators are present, males from high predation regimes show a proportional increase in sneaky mating attempts (Magurran & Seghers 1990). Figure 3 also shows the probability of a successful sneaky mating as a function of the risk of predation, s . This quantity is proportional to $x(1-y)$ which denotes the probability that males play S while females play A.

Simple though it is, our model suggests that an interesting range of behaviour can arise in systems of this kind, depending on the relative strengths of male or female costs or benefits. In particular, the model

provides a functional explanation for the unexpected observation that predation risk can lead to an increase in sneaky mating activity.

(b) *Conflict or cooperation during predator inspection?*

To maximize information, and avoid any unexpected attacks, inspecting fish must constantly monitor the predator. Close observation of the predator clearly conflicts with a female's ability to avoid the attentions of the thrusting males. By following females during an inspection, males potentially maximize information gain while minimizing risk, and have an opportunity of getting a sneaky mating into the bargain. Such male exploitation of female inspection can be observed in the wild as well as in the laboratory (AEM & B. H. Seghers, Tacarigua River, Trinidad, March 1991, personal observation; J.-G. Godin, Quare River, Trinidad, March 1991, personal communication).

In the past few years, predator inspection has been viewed as a possible example of cooperative behaviour amongst non-relatives. Milinski (1987) argued that small inspecting groups are caught in a prisoner's dilemma (Axelrod & Hamilton 1981). Approaching a predator inevitably entails some risk (Magurran 1990). Defection from (or non-participation in) an inspection would therefore appear to be the best strategy, particularly as non-inspecting individuals can obtain information on the predator by observing the behaviour of their inspecting school-mates (Magurran & Higham 1988). However, by forming cooperative alliances based on the Tit for Tat strategy, pairs of fish can reduce individual risk while increasing information gain. This idea was first tested by Milinski (1987) in an experiment in which solitary sticklebacks (*Gasterosteus aculeatus*) were confronted by a predator. The sticklebacks approached the predator more closely when accompanied by cooperating, as opposed to a defecting, mirror image. Dugatkin (1988) repeated the experiment with guppies and obtained the same result. This interpretation of predator inspection behaviour has been challenged by Lazarus & Metcalfe (1990) and others, who argue that the apparent cooperation may simply arise as a safety in numbers effect allied to schooling behaviour. Nevertheless, experiments have shown that both sticklebacks (Milinski *et al.* 1990*a, b*) and guppies (Dugatkin & Alferi 1991) recognize better cooperators (those that approach a predator more closely) and preferentially associate with them in subsequent tests. Sticklebacks have a limited breeding period and spend considerable portions of their life in non-reproductive schools (Wootton 1984). Adult guppies, by contrast, are constantly engaged in reproductive activity. Although Dugatkin & Alferi (1991) observed no courtship in any inspection trials in which both males and females were present, we argue that cooperation between male and female guppies during inspection is incompatible with the male exploitation of female anti-predator behaviour. Both our experimental observations and model illustrate how male mating behaviour is carefully tuned to the female response to the prevailing risk of predation. Consequently, the concepts of 'niceness', 'retaliation'

and 'forgiveness', used to characterize the Tit for Tat strategy (Axelrod & Hamilton 1981) are clearly not applicable to situations where males are using female inspection behaviour to obtain sneaky matings. In the wild, male guppies will have many opportunities to exploit female inspection, as observations of guppy behaviour in a number of rivers in Trinidad reveal that natural schools contain both sexes (Seghers 1974; Magurran & Seghers 1992). Our work does not rule out the possibility that cooperation may be observed in laboratory tests of inspection behaviour in guppies, particularly those that concentrate on single-sex groups. It does, however, diminish the likelihood of cooperation during inspection in the natural world. Such cooperation that does occur may well be centred on female alliances whose members share a common perception of danger and are able to remain together and interact with one another despite the unwanted attentions of their male colleagues. Alternatively, as suggested by Milinski (personal communication), females might even, contrary to our interpretation, be choosing the males willing to risk a mating in the presence of a predator for their 'good genes'. The subject is clearly ripe for further research.

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