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Male mating strategies under predation risk: do females call the shots?

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Many authors have reported that, under elevated risk of predation, male guppies (*Poecilia reticulata*) alter their behavior from courtship to forced copulation (gonopodial thrusts not preceded by sigmoid displays). This shift is presumed to benefit the brightly colored male, whose intense courting activity might otherwise increase his risk of detection and attack by predators. However, there is some evidence that females engaged in reproductive activity with males may be even more vulnerable to predators than the males themselves, which suggests an alternative hypothesis: females in high-risk situations are less receptive to male courtship, and this leads males to change their behavior. We tested this hypothesis by providing either males and females separately, or both sexes concurrently, with information about elevated predation risk from a cichlid (*Crenicichla* sp.). We found that when only females were provided with information about increased risk, males performed fewer courtship displays and fewer thrusts. They did not perform more forced copulations in any treatment group. Nonetheless, our results suggest that the female's perception of predation risk can be at least as important as the male's in changing male mating behavior. *Key words:* courtship, guppies, mating behavior, *Poecilia reticulata,* predation. *[Behav Ecol 10:452–461 (1999)]*

Brightly colored males occur in many species of animals, where their conspicuous coloration can be advantageous in attracting potential mates (Andersson, 1994). Although bright colors may entice females of the same species, they can also attract predators, thereby elevating the male's risk of predation (Lima and Dill, 1990; Magnhagen, 1991). Female choice for bright males and an enhanced risk of predation for bright males have both been well documented (e.g., Endler, 1980; Hill, 1990; Houde, 1987; Kodric-Brown, 1985; Moodie, 1972; Semler, 1971).

Less attention has been focused on the risk of predation for females that are attracted to bright males. Inconspicuous females mating with colorful males may also be vulnerable, because predators that are attracted to males can detect females once they approach the pair. Few studies have investigated the costs for females of associating with conspicuous males in order to mate (but see Gibson and Bachman, 1992; Pocklington and Dill, 1995). Nonetheless, evidence suggests that females are sensitive to predation risk and change their mating decisions with levels of risk. In the cricket *Gryllus integer,* for example, females choose males with less preferred calls in safe locations rather than males with more preferred calls in dangerous locations (Hedrick and Dill, 1993). Female sand gobies (*Pomatoschistus minutus*) also become less selective in mate choice when predation risk increases (Forsgren, 1992). In the guppy (*Poecilia reticulata*), a small, Trinidadian fish, females under predation risk associate with less colorful males when given a choice between these and the more conspicuous males they would otherwise prefer (Godin and Briggs, 1996; Gong and Gibson, 1996).

Male guppies also respond to predation risk by altering their mating behavior (see below), making guppies a good species in which to compare the relative sensitivity of males versus females to predation risk during mating activities. Here, we examine the differential effects of male versus female exposure to predation risk on courtship and mating behavior of males within pairs of guppies.

Study species

Male guppies bear a series of orange, yellow, iridescent blue, and black spots, whereas females are drab (Endler, 1987). Males offer no resources other than sperm to their mates. Females are receptive only as virgins and for a short period following parturition. Because few females are receptive at any one time (Kodric-Brown, 1993), receptive females often can choose among several males vying for their attention (Kodric-Brown, 1985). Before mating, males commonly perform courtship displays (sigmoid displays) in which they curve their bodies into an arc or S-shape and quiver in front of the female. Females can either accept or reject males following these displays (Luyten and Liley, 1985). Fertilization is internal via the male's gonopodium, which he inserts into the female's genital pore using gonopodial thrusts (Luyten and Liley, 1985). Although female mate choice is based on multiple criteria (Kodric-Brown, 1993), many studies have shown that females generally prefer more colorful males as mates (e.g., Houde, 1987; Kodric-Brown, 1985; Long and Houde, 1989). Thus, female choice presumably selects for brighter male colors in this species.

However, bright male coloration in guppies also increases predation risk. Males from streams with high levels of predation are less colorful than males from streams with low predation (Endler, 1995), and selection experiments have shown that high predation selects for cryptically colored males, whereas female choice (and low predation) selects for brighter males (Endler, 1980). Predation affects many other life-history characteristics in the guppy, including clutch size (reviewed in Endler, 1995). Additionally, male coloration (specifically, orange spots) and female preferences for orange males are often genetically correlated (Houde and Endler, 1990; Stoner and Breden, 1988). Therefore, male coloration in guppies is thought to result from a balance between female choice favoring brighter colors, versus predation selecting for less conspicuous colors (Endler, 1980; Houde, 1987).

Predation risk affects male mating behavior as well as male coloration. Male guppies under predation risk often switch

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from their normal courtship sequence, which begins with the conspicuous sigmoid display, to a ''sneaky'' mating tactic, in which they perform gonopodial thrusts without displaying first (Endler, 1987; Godin, 1995; Luyten and Liley, 1985; Magurran and Seghers, 1990; Reynolds et al., 1993). Although this strategy entails a lower probability of successful insemination (Liley, 1966), it is probably less conspicuous to predators than sigmoid displays (Endler, 1987). Therefore, the behavioral shift has been interpreted as an adaptive response by the male to his own perception of danger (Endler, 1987; Magurran and Seghers, 1990).

Males also switch to the alternative, sneaky strategy, however, when females are unreceptive to sigmoid displays (Luyten and Liley, 1985). Moreover, females are also exposed to predation risk during mating activities and sometimes respond to risk by moving away from males (Godin and Briggs, 1996; Gong and Gibson, 1996). This suggests an alternative interpretation for the switch in male behavior: perhaps males adopt the sneaky strategy because females change their behavior when they perceive predation risk, becoming less receptive to male courtship.

Female guppies may be even more vulnerable to predation than males. Natural guppy predators are differentially attracted to females (Pocklington and Dill, 1995), and females are generally larger than males, making them especially profitable prey items (Pocklington and Dill, 1995). Females must survive to parturition to achieve reproductive success after mating, whereas mated males do not. Furthermore, females seem particularly sensitive to predation risk. Females exposed to predators are more likely than males to school (Magurran and Nowak, 1991) and to ''inspect'' the predator by approaching it closely. By inspecting, they often subject themselves to forced copulations by males (Magurran and Nowak, 1991). Inspection may also provide females with additional information about predation risk (Magurran, 1990), which could affect their mating behavior. Females exposed to predation risk spend less time near males and are less attracted to colorful males, instead associating with inconspicuous males when given a choice (Godin and Briggs, 1996; Gong and Gibson, 1996). These observations suggest that females may become less receptive to male courtship when they perceive that predators are present nearby. If so, males may respond by trying to sneak a mating. Alternatively, males may respond by depressing their own mating activity. Depression of mating activity occurs as a response to predation risk in many species (Magnhagen, 1991).

Hypothesis and predictions

We hypothesized that changes in male mating behavior with predation risk are due more to the female's perception of predation risk (and her response to it) than the male's. This hypothesis explicitly addresses changes in male behavior, and therefore we focused on male behavior here. Our study examined male courtship and mating behavior in guppy pairs when (1) the male alone sees a predator, (2) the female alone sees a predator, (3) both sexes see a predator, and (4) neither sex sees a predator, in a short period immediately before being allowed access to one another. Because predator inspection apparently affected our results, we also examined whether and how predator inspection influences the outcome of mating trials. Predator inspection is common in guppies, particularly females (Magurran and Nowak, 1991), may be performed by inherently ''bold'' individuals (Wilson et al., 1994), and is thought to provide inspectors with additional information on predation risk which affects their subsequent behavior (Magurran, 1990).

Specifically, we tested the predictions that:

1. When both sexes are exposed to predation risk, mating activity of males will change to less conspicuous strategies relative to the control situation. Potentially, thrusts will become relatively more common and sigmoid displays relatively less common than when neither sex is exposed. Alternatively, all male mating activity may be depressed relative to controls.
2. When only the female is exposed, male mating activity will again either be depressed or will change to less conspicuous strategies, relative to the control situation.
3. When only the male is exposed, changes in male behavior will be significantly less marked than in either the ''both exposed'' or ''female exposed'' situations, relative to controls.
4. Predator inspection by one or both of the guppies before the courtship trial will moderate the effect of predation risk on male mating activity. Specifically, if inspection decreases the perception of risk, and/or if inspectors are inherently more ''bold'' than other fish, then inspection by one or both guppies will be associated with diminished effects of predation risk on mating activity. Alternatively, if inspection increases the perception of risk, then inspection by one or both guppies will be associated with increased effects of predation risk on mating activity.

METHODS

Guppies and predators

Guppies were descended (approximately five to eight generations) from individuals collected from a single site on the Quare River, Trinidad, as described in Reynolds and Gross (1992). Natural predators present at this location include the pike cichlid *Crenicichla frenata* (Ploeg, 1991). We divided approximately 100 fish (50:50 sex ratio) among 5 breeding tanks, with spawning mops and rocks as refuges for breeding females and young. A breeding population of at least 100 individuals was maintained throughout the study. We removed young from these breeding tanks before their gender became identifiable and placed them into another tank. This tank was scanned daily to pick out sexually maturing fish. As soon as fish began showing signs of sexual development (in fin shape, body coloration, or ovary or gonopodium growth), they were transferred to holding tanks and reared in same-sex groups until they were used in the experiment. This ensured that all males and females used in the experiment were virgins. Test fish ranged from 20–25 mm total body length (mean±SD, females: 23.38±1.53 mm; males: 21.87±1.03 mm), and each fish was tested only once.

Guppies were raised on ground Tetramin flakes and live brine shrimp nauplii; adults were also fed live adult brine shrimp. Lighting was from fluorescent tubes on a 12 h:12 h light/dark cycle, and the room temperature was 30±2° C.

The two predators we used were a male and a female *Crenicichla,* species affinity *saxatilis,* both measuring 150–160 mm total body length. These were from the same species complex (*saxatilis*) as the natural predators, and resembled them in morphology and behavior (W. Leibel, personal communication). Predators were fed a diet of live juvenile guppies during the data collection period.

Experimental setup

The experimental setup consisted of a clear plexiglass courting tank (35 cm×22 cm×16 cm deep), divided in half by a removable opaque panel (Figure 1). This panel was connected by monofilament to a pulley, which allowed it to be lifted

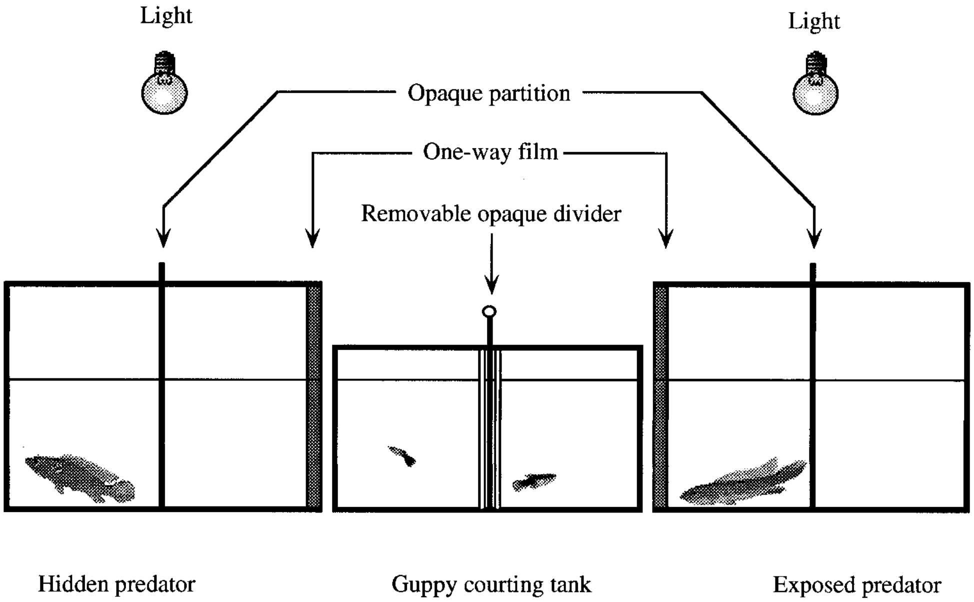

Figure 1
The experimental setup. One male and one female guppy were placed on either side of the courting tank in the center, and both guppies, neither guppy, or one of the guppies was allowed to see a predator before the beginning of the subsequent courtship trial.

out of the tank from a remote location. Outer surfaces of the tank were white except for the two end walls facing the predators, which were clear. The courting tank was filled with 7 l of water (8 cm deep) and placed at the center of the experimental stage. We placed predator tanks (27 cm×25 cm×24 cm deep) on either side of the courting tank, leaving gaps of <3 mm between each. Predator tanks had opaque plexiglass on three sides, and a glass front facing the courting tank. The outer surface of the glass front was covered by one-way tinting film. We kept predator tank water at the same depth (8 cm) as the courting tank. A light above each predator tank was shielded from the courting tank by a white wooden partition. When the light above the predator tank was on, the guppies could see the predator, but not vice versa. When the light was off, the film on the glass prevented viewing in either direction. A divider in each predator tank cut each tank in half during trials; depending on the experimental treatment, the predator was positioned on one side or the other. This allowed us to expose one, both, or neither predator to the guppies in the courting tank, while always displaying one lit half of each predator tank. Airstones in the predator tanks were positioned behind the divider so as not to influence predator visibility.

Tanks were positioned on a shelf approximately 1 m from the floor and surrounded on all sides except the top by white sheets that allowed some light through. Incident light levels within the experimental setup were 80–100 lux. A video camera was mounted 25 cm directly above the courting tank, providing a view of that tank and the front quarter of both predator tanks. The camera was connected to a VHS tape deck with which we recorded guppy activity, along with a time track. Predator exposure lights, the camera, monitor, and VHS deck were all operated from outside the experimental setup.

Table 1
Modification of a randomized Latin square design for the sequence of treatments

Trial	Treatment	Male's position	Female's position	Predator exposed
1	Control	L	R	Neither
2	Male	R	L	R
3	Female	R	L	L
4	Both	L	R	Both
5	Control	R	L	Neither
6	Male	L	R	L
7	Female	L	R	R
8	Both	R	L	Both

The sequence was repeated 12.5 times. L indicates the left chamber of the guppy courting tank and R the right chamber. For the predator, R and L indicate the side(s) on which the guppies were exposed to the predator.

Experimental procedure

The day preceding a trial, we randomly selected one female and one male guppy and placed them into opposite sides of the courting tank, with the opaque door in place. Positioning of each fish was determined by a preset order (see below). White cardboard screens were present between the courting tank and the two predator tanks. Lids were placed over each half to keep fish from jumping out, and the fish were held in the courting tank until the next morning (approximately 23 h).

We started all trials between 0830 and 0930 h. Just before the trial, lids were removed. Dividers were placed in the middle of each predator tank and predators positioned on the appropriate side of their divider wall, as determined by the experimental treatment. Next, the cardboard screens between the predator and courting tanks were removed. Four minutes later, VCR recording began.

One minute after starting the recording, we turned on both lights, exposing one, both, or neither predator to the male and female guppies. The treatment period lasted for 10 min. During this time, the video recorded the activity of the guppies and also any activity of the predator(s) near the front glass. After 10 min, the lights were switched off and the cardboard screens gently replaced between the tanks. One minute later we raised the divider in the courting tank and the courting trial began. The trial was 20 min long.

After 20 min, the video was stopped and the test guppies were captured and measured (total body length, mm) before placing them into the breeding tanks (i.e., no guppy was tested more than once). Courting tank water was removed and tank walls were scrubbed before adding fresh, conditioned water. Dividers were removed from the predator tanks, and predators were fed and their tanks cleaned if necessary. The

Table 2
Scoring behavior

Behavior	Definition
Sigmoid display	Sigmoid displays were recorded when a male moved near the female, arched his body in an arc or S-shape, and quivered, as described by Baerands et al. (1955) and Liley (1966). A new and separate display was recorded when the male stopped displaying, bent the body in the opposite direction, and then continued to display.
Time to first sigmoid	The total amount of time elapsed in the trial (to the nearest second) before the male began his first sigmoid display.
Total sigmoid time	The total amount of time (to the nearest second) during a trial that the male spent in sigmoid displays.
Thrust	A mating attempt in which the male turned towards the female, aligned his body with the female's and moved so as to insert his gonopodium into the female's genital pore. Thrusts were sometimes, but not always, preceded by a sigmoid display, and were either attempted thrusts (no contact made) or complete thrusts, in which insemination could have occurred (see below).
Attempted thrusts	A thrust in which no physical contact was made between the male and female.
Complete (successful) thrusts	Thrusts in which the male made very close physical contact with the female such that insemination could have occurred. (Actual insemination could not be discerned from videotapes.) Complete thrusts usually included paired swimming, during which the male's and female's bodies were in close proximity.
Total thrusts	Attempted plus complete thrusts.
Time to first thrust	The total time elapsed in the trial before the male made his first thrust.
Indices of sneaky mating	
Total thrusts/total sigmoids	The total number of thrusts divided by the total number of sigmoid displays during the trial. This ratio should increase with an increase in sneaky mating attempts, because these involve thrusts unaccompanied by sigmoids.
Thrusts preceded by sigmoids/ total thrusts	The proportion of all thrusts which were immediately preceded by a sigmoid display. We posed this as an alternative index of sneaking. It is expected to decrease with an increase in sneaky mating attempts.
Complete thrusts/total sigmoid time	The number of complete thrusts divided by the total time spent in sigmoid displays. This was used as a plausible measure of the amount of courtship time required for a potentially successful mating.

courting tank divider was replaced and new guppies were selected and placed into the tank for the following day's trial.

We conducted four treatments in a modified Latin square design (Table 1; Sokal and Rohlf, 1981). The treatments consisted of control trials (in which neither sex of guppy was exposed to a predator before the courting trial); male-exposed trials (in which only the male saw the predator); female-exposed trials (only the female saw the predator); and trials in which both guppies were exposed to a predator before the courting trial. Two trials in each of these four treatments were completed before a new cycle of trials began. In each cycle of trials, we balanced the position of males and females to eliminate any possible bias due to differences between the two predators or other differences between the two sides of the courting tank.

Video and data analysis

We analyzed videotapes at the end of each block of eight trials, and behaviors were scored as described in Table 2 for each

Table 3
Frequencies of behaviors observed in each of the four treatment groups

	Control	Both exposed	Male exposed	Female exposed	χ^2 (df = 3)
Sigmoid display	672	600	540	370	91.30***
All thrusts	209	147	175	107	35.13***
Complete thrusts[a]	83	47	50	36	22.77***

[a] Complete thrusts are a subset of all thrusts.

*** $p < .001$.

20-min trial. After all 100 trials were completed, we conducted statistical analyses. Data did not conform to a normal distribution, and we therefore used nonparametric statistical analyses (Mann-Whitney *U* tests). Ratios with 0 in the denominator were considered undefined and dropped from the analysis.

Predator inspection

The 10-min predator treatment period was also monitored and data were recorded on the activity of the guppies while exposed to the predator(s). Sometimes the treated guppy moved to the glass to "inspect" the predator. This was an obvious behavior: the guppy moved to a point close to the glass in front of the predator and oriented directly toward it. Guppies who moved to the glass (0.5 mm or less from the glass), oriented toward the predator, and remained there for even a short period ($\geq$ 1 s) during the treatment were classified as inspectors. We then analyzed inspector and noninspector trials separately to look for effects of inspection on responses of mating behavior to predator exposure.

RESULTS

All fish

We conducted a total of 100 trials, 25 for each test condition (controls, both fish exposed to the predator, female-only exposed, and male-only exposed). A grand total of 2,182 sigmoid displays, 638 thrusts, and 216 complete thrusts (probable matings) were observed. Courtship and mating did occur under the threat of predation, but occurred less often when only the female had seen the predator (Table 3) than in any other test condition (controls, both fish exposed, and male exposed).

Surprisingly, predator exposure had no effect on either the ratio of thrusts to sigmoids or on our alternative index of sneaky matings, the proportion of all thrusts preceded by a sigmoid. Both measures were largely unaffected by predation risk (Figure 2). Similarly, examination of complete (potentially successful) thrusts per time spent in sigmoid displays, a plausible measure of mating success as a function of courtship investment, revealed no significant changes relative to controls for male-exposed, female-exposed or both-exposed trials (Figure 2C). Thus, sneaky matings (thrusts without sigmoid displays) were not more frequent when fish were exposed to predators.

Other measures of mating activity were more affected by predator exposure, and these effects were most marked when only the female was exposed. For example, both the total number of sigmoid displays (Figure 3A) and the total time spent in sigmoid displays (Figure 3B) were significantly lower than controls when only the female was exposed to predation risk, but not when only the male was exposed. Time to the first thrust was significantly longer compared to controls when only females were exposed, but not when only males were exposed (control: 268.5±262.0 s, n = 25; males: 327.2±304.0 s, n = 25, ns; females: 550.0±478.3 s, n = 25, Mann-Whitney *U* test, p = .045). Total thrusts were also influenced by predation risk. Exposure of the female alone resulted in a significant drop in the number of thrusts (Figure 3C) compared to controls; this effect was significantly greater than when only males were exposed. The total number of thrusts was also significantly affected when both sexes were exposed to the predator. However, the number of thrusts that were complete (possibly successful) did not change significantly with predator exposure (Figure 3D).

Comparisons of the results from male-exposed versus female-exposed trials demonstrated significant differences between the sexes in the effects of predation risk on total sig-

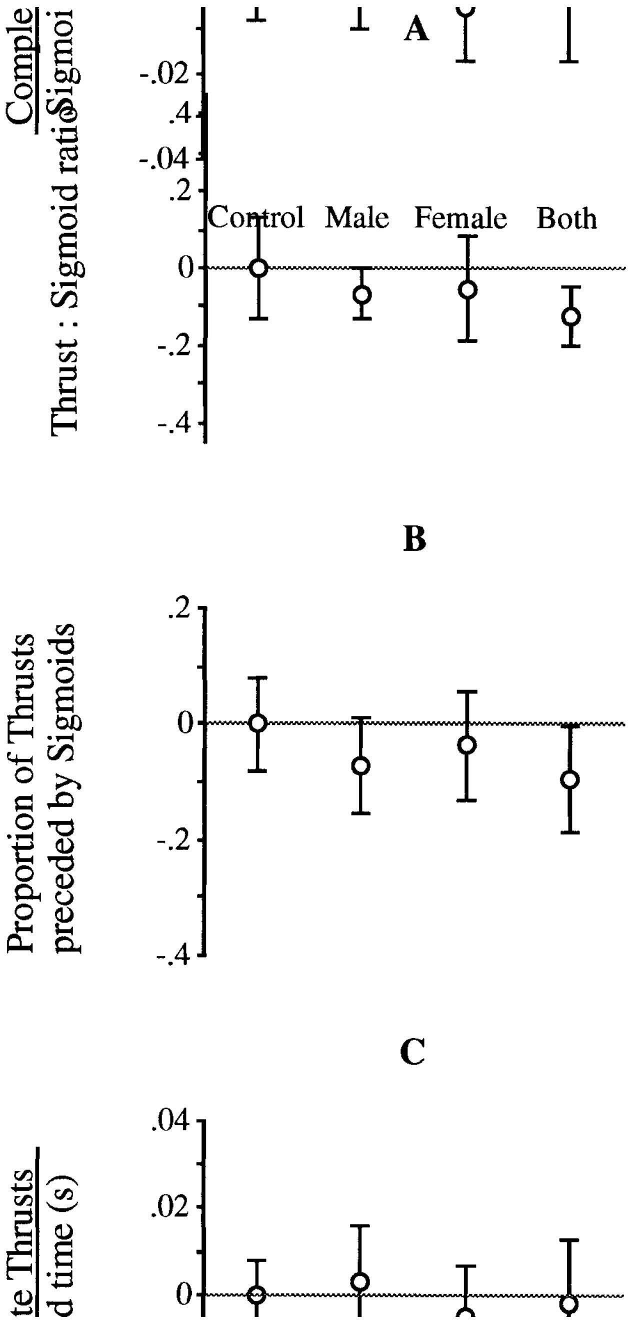

Figure 2
(A) Number of thrusts/number of sigmoids, (B) proportion of all thrusts preceded by sigmoids, and (C) complete thrusts per time (s) spent in sigmoids. Values represent the proportion by which treatment values differed from control values (in control trials, neither guppy saw a predator), and bars represent standard errors. No treatment values were significantly different from controls.

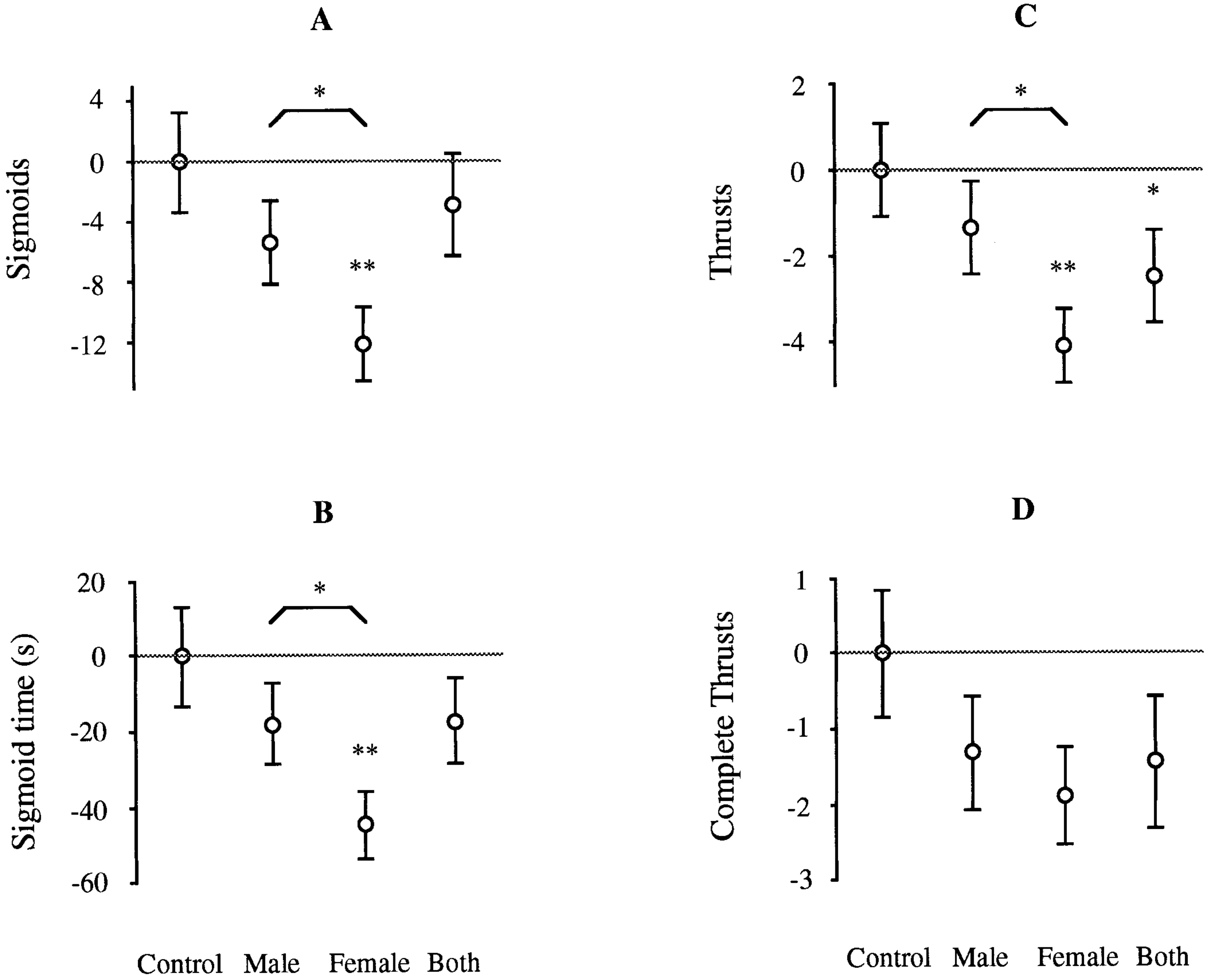

Figure 3
(A) Total number of sigmoid displays, (B) total time spent in sigmoid displays, (C) total number of thrusts, and (D) total number of complete thrusts. Values represent the proportion by which treatment values differed from control values (in control trials, neither guppy saw a predator), and bars represent standard errors. Asterisks without brackets indicate that the treatment values were significantly different from controls ($p < .05$); asterisks over brackets indicate significant differences ($p < .05$) between male-exposed and female-exposed treatments.

moids (Figure 3A), total sigmoid time (Figure 3B), and total thrusts (Figure 3C). All three measures declined significantly more when only the female had been exposed to the predator than when only the male had been exposed.

Inspectors versus noninspectors

Inspection behavior, in which the guppies closely approached the glass in front of the predator and oriented to it during some part of the exposure period, was strongly correlated with levels of mating activity. When one or both sexes inspected the predator, predator exposure had few effects on mating activity. In contrast, when either the male or female (or both) was exposed to the predator, but neither fish inspected, mating activity was depressed relative to controls.

For example, noninspecting fish performed significantly fewer sigmoid displays than controls when either the male or female was exposed. However, inspectors showed no significant change in this measure (Figure 4). Sigmoid time declined significantly for noninspectors in male-treated trials and female-treated trials, yet in inspector trials this measure never deviated significantly from controls (Figure 4). In noninspectors the number of thrusts was significantly lower than controls for female-treated trials, but inspectors showed change in this measure only when both fish were treated (Figure 5). Also, time to the first thrust was significantly greater than controls when males or females were exposed to the predator and did not inspect (control: 268.5±262, $n = 25$; males: 410.9±314.0, $n = 11$, $p = .0462$; females: 688.5±486.1, $n = 15$, $p = .0066$), but not when inspection occurred.

Again, we found no consistent evidence for a switch to a sneaky strategy. Ratios of thrusts/sigmoids for noninspectors and inspectors did not differ significantly from controls (Figure 5), and neither inspectors nor noninspectors differed significantly from controls in the proportion of thrusts preceded by a sigmoid display (not shown).

In both noninspectors and inspectors, depression of mating activity was again greatest when females alone were exposed to the predator. For example, in noninspectors, decreases in the number of thrusts (Figure 5) were significantly greater for

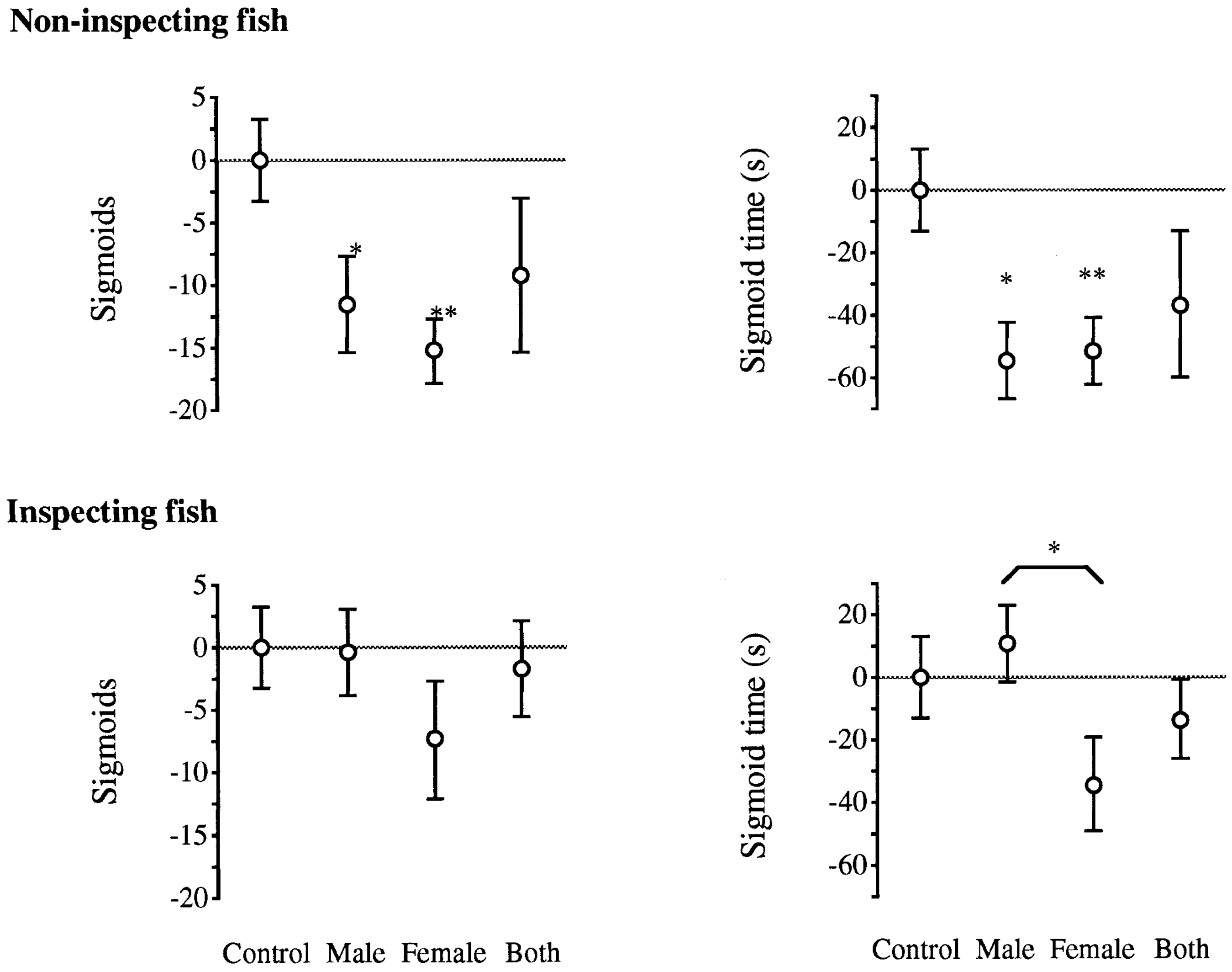

Figure 4
Inspectors versus noninspectors: total number of sigmoids, and total sigmoid time. Values represent the proportion by which treatment values differed from control values (in control trials, neither guppy saw a predator), and bars represent standard errors. Asterisks without brackets indicate that the treatment values were significantly different from controls ($p < .05$); asterisks over brackets indicate significant differences ($p < .05$) between male-exposed and female-exposed treatments. Control trials for inspectors and noninspectors were identical.

female-treated trials ($n = 15$) than male-treated ($n = 11$) trials ($p < .05$). In inspector trials, the sexes also differed in the time spent in sigmoid displays (Figure 4), with female exposure yielding a larger negative effect on sigmoid time than male exposure ($p = .0202$; $n = 10$ females and 14 males).

Finally, within the noninspectors, exposure of females seemed to have longer lasting effects on some measures of mating activity than exposure of males. When only males were exposed to the predator, decreases in the number of thrusts occurred in the first 10 min of the trial, but disappeared in the second 10 min. When only females were exposed, the effect on thrusts not only began early in the trial, but persisted over the entire 20-min period (Figure 6). In contrast, decreases in sigmoids persisted over the entire trial when either sex was exposed to the predator.

DISCUSSION

Our results demonstrate that mating activity in general is depressed by exposure to a predator. Guppies showed a lower frequency of courtship and mating behaviors (sigmoid displays and thrusts) after predator exposure. Our results also show that in guppies, the effect of predator exposure is strongest when the female sees the predator. When only the male was exposed, frequencies of sigmoid displays and thrusts were diminished relative to controls. However, when only the female was exposed to the predator, sigmoid displays and thrusts were diminished even more. Additionally, effects of predator exposure on thrusts were longer lasting when females were treated, compared to the duration of effects when males were treated. Although sigmoid displays and thrusts are behaviors whose rates of performance have been attributed solely to decisions of the male guppy, our results show them to be strongly affected by the female's perception of risk. These results suggest that in this species, females may be more sensitive to predation risk than males are.

Depression of mating activity in response to predator exposure has been found in other animals, including gobies, pipefish, salamanders, water striders, and voles (Fuller and Berglund, 1996; Magnhagen, 1991; Ronkainen and Ylonen, 1994; Sih, 1988; Uzendoski et al., 1993). Moreover, other studies have hinted that female guppies may be more sensitive

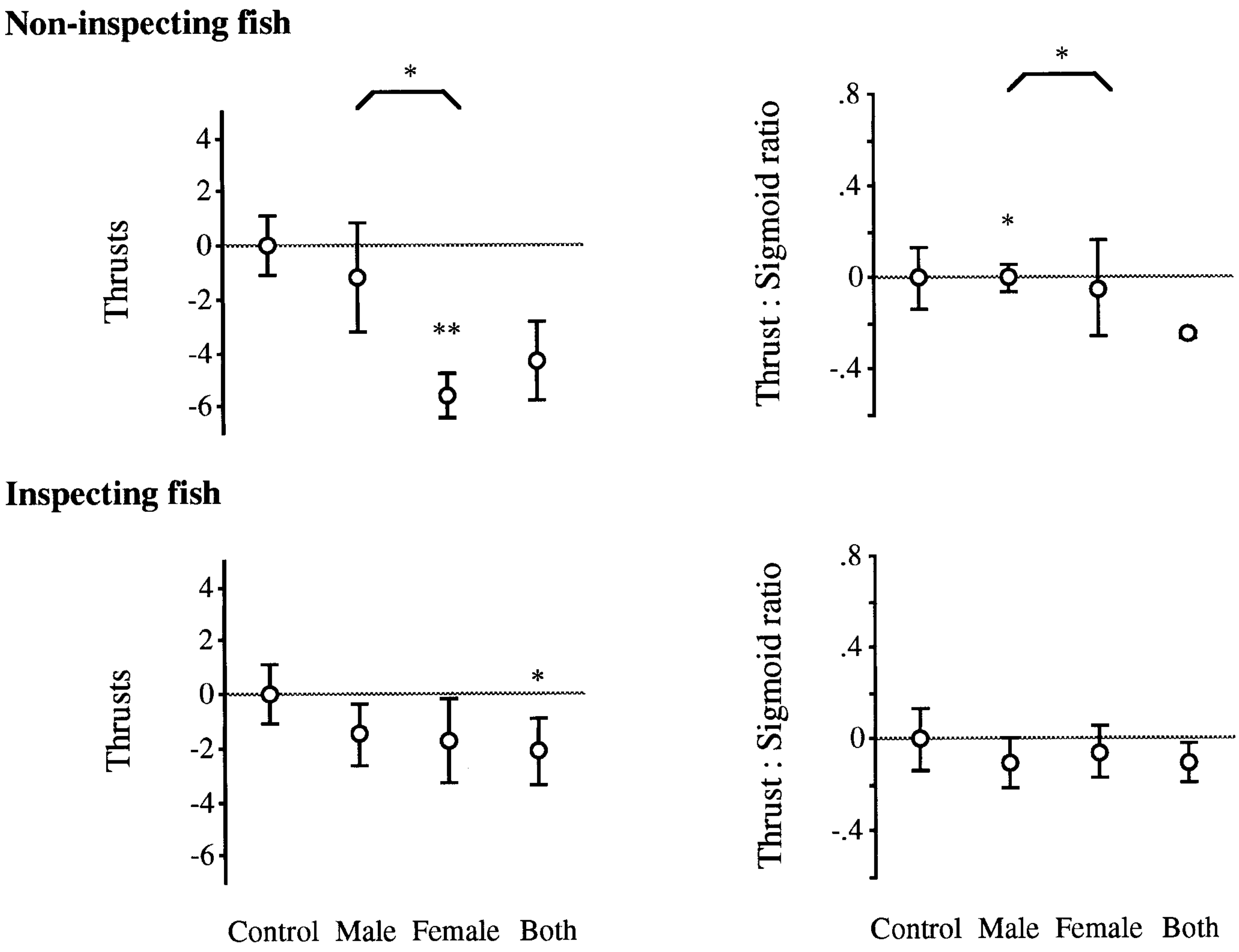

Figure 5

Inspectors versus noninspectors: total number of thrusts and number of thrusts/number of sigmoids. Values represent the proportion by which treatment values differed from control values (in control trials, neither guppy saw a predator), and bars represent standard errors. Asterisks without brackets indicate that the treatment values were significantly different from controls ($p < .05$); asterisks over brackets indicate significant differences ($p < .05$) between male-exposed and female-exposed treatments. Control trials for inspectors and noninspectors were identical. The thrust/sigmoid ratio for noninspecting male-treated trials was slightly greater than that of the controls.

than males to predation risk. Magurran and Nowak (1991) reported that female guppies school more than males in the presence of risk and that females also engage in more predator inspection behavior than males, and Andreev (1993) reported that females are less active than males in unfamiliar environments, where higher activity might be expected to increase vulnerability to predation.

Female behavior after predator exposure

How exactly do female guppies react to predator exposure, and how does this affect the expression of sigmoids and thrusts by males? Although we did not specifically study female behavior, one possibility is that females become less active in general after predator exposure, and therefore less available to males for courtship. For example, females in our experiments sometimes responded to predator exposure by hugging a wall or corner of the courtship tank and reducing their rates of movement. Presumably, such inactivity would make a female less conspicuous to a predator, but it also could reduce her ability to respond to males. In nature, a female might reduce her vulnerability to predators by moving to a sheltered spot and remaining inactive there.

Alternatively, females might actively avoid males after predator exposure, even fleeing from the male's vicinity. This behavior has been described for female guppies trying to avoid harassment by persistently courting males (Magurran and Seghers, 1994), but it has not been related specifically to predation risk. Finally, females might be distracted by predators, especially when they are inspecting them, and so become less receptive toward male courtship. This can then lead males to attempt sneaky matings with them (Magurran and Nowak, 1991). Our data on females are not sufficiently detailed to allow us to evaluate these various alternatives. However, in our experiments, predator inspection before male–female interaction was not associated with a higher frequency of sneaky matings. Also, in a laboratory study of the same guppy population that we used (Quare River), Godin and Briggs (1996) found that females usually moved away from males after seeing a predator. This suggests that active avoidance of the male by the female may have been responsible for the changes in male behavior that oc-

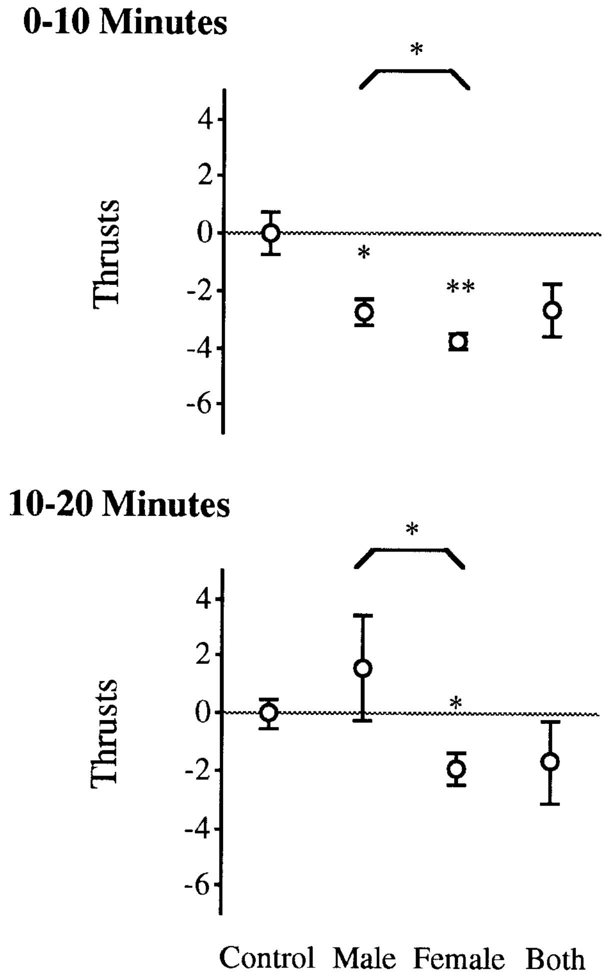

Figure 6
Noninspectors: total number of thrusts in the first 10 min and second 10 min of the trial. Values represent the proportion by which treatment values differed from control values (in control trials, neither guppy saw a predator), and bars represent standard errors. Asterisks without brackets indicate that the treatment values were significantly different from controls ($p < .05$); asterisks over brackets indicate significant differences ($p < .05$) between male-exposed and female-exposed treatments.

curred in our experiments. Additional data on female behavior are needed to assess this possibility.

Male behavior after predator exposure

Contrary to expectation, males in our experiment did not switch to a "sneaky" strategy (thrusts without displays) when they were exposed to predation risk. Rather, the frequencies of both sigmoid displays and thrusts declined. There are several possible reasons for this finding, which differs from the results of previous studies (e.g., Endler, 1987; Magurran and Nowak, 1991; Magurran and Seghers, 1990). First, in our experiments the predator was not present during courtship trials. Guppies that were exposed to the predator before trials had to remember it later. If males have shorter memories than females, then they could be less affected than females by prior exposure to the predator. This could lead to fewer sneaky matings in the male-exposed trials, although it does not explain why both thrusts and sigmoids declined relative to controls, nor why sigmoids remained depressed. Second, the virgin females that we used in courtship trials are especially attractive to male guppies (Crow and Liley, 1979). Perhaps males perceived the risk of predation, but largely disregarded it, and performed sigmoid displays (albeit at a lower rate than in control trials) to ensure successful mating with virgins. Note that thrusts preceded by sigmoid displays more often result in insemination than do sneaky matings (Luyten and Liley, 1985). Third, the virgin males that we used in our trials may have been very highly motivated to mate, leading them to partly disregard danger and perform sigmoid displays (again, at a lower rate than in control trials) to ensure successful mating. Finally, our predator stimulus was presented behind glass, and might have been too weak to trigger sneaky mating: the predator could be seen by the guppies, but this perception was not reinforced by other senses. Data in Godin and Briggs (1996), collected on the same population of guppies, also show little effect of a predator behind glass on the thrust/sigmoid ratio, although this point is not mentioned by the authors.

Both sexes exposed to the predator

The previous literature (e.g., Endler, 1987; Luyten and Liley, 1985; Magurran and Seghers, 1990; Reynolds et al., 1993) had led us to believe that effects of predation risk on mating behavior would be most apparent when both sexes experienced predation risk, yet our data did not show this pattern. Predator inspection behavior might account for this discrepancy between our results and those of previous studies. Although we conducted 25 trials in which both fish were exposed to the predator, in 21 of these trials at least one fish inspected the predator. Because inspectors and their mating partners both showed diminished effects of predator exposure compared to noninspectors (see below), most of the both-exposed trials were biased (by the guppies' own behavior) against finding significant effects.

Effects of predator inspection

Interestingly, predator inspection behavior was strongly tied to the mating response to predator exposure. Fish that had inspected the predator (or whose partner had inspected it) were much less likely to depress their mating activity than fish that had not inspected. We did not have sufficient sample sizes and statistical power to test effectively for the differential effects of female inspection, male inspection, or inspection by both fish. Nonetheless, the strong link we found between predator inspection and subsequent mating behavior suggests several possible interpretations. First, fish that inspect may be bolder individuals (sensu Wilson et al., 1994; but see Budaev, 1997) than those that do not inspect. Bolder fish may be more inclined to approach the predator and also less inclined to depress their mating activity in response to predation risk. Moreover, if females prefer bold males, as reported by Godin and Dugatkin (1996), then bold males may enjoy greater mating success because of female mating preferences.

Second, fish that inspect the predator may gain information during inspection that makes them feel safer. This could make them less inclined to change their mating activity to avoid danger. These two possible explanations for the effects of predator inspection on mating behavior merit further investigation. Because guppy pairs with only one inspector showed as little depression of mating activity as those with two inspectors, our results leave open the intriguing possibility that inspectors may in some way pass information about the predator or the level of predation risk to their mating partner.

Conclusion

Guppies have been considered a classic example showing the evolutionary effects of predation risk on the color, morphology, and behavior of males, and on many other life-history characters (reviewed in Endler, 1995). Our study demonstrates that at least some effects on male behavior with predator exposure are indirect results of the responses of females to danger. Thus, females mediate the effects of predation risk on male mating behavior in this species. This suggests that females warrant more attention in this and other mating systems where conspicuous males show variable mating strategies in the presence of predation risk. Our work also suggests that direct effects of predation risk on females may be important factors in constructing genetic models for the evolution of male mating traits. Recent evolutionary models that incorporate direct effects on females (e.g., Kirkpatrick, 1996; Pomiankowski, 1987; Pomiankowski et al., 1991) show that these can substantially alter evolutionary outcomes. Finally, our study shows that predator inspection by male guppies or their partners significantly diminishes the effects of predation exposure on male courtship and mating behavior. The mechanisms by which all of these processes occur await further study.

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