The significance of the male display during male-male interactions in guppies (*Poecilia reticulata*)

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Abstract

Guppies, *Poecilia reticulata*, are a model species for studies of female preference based on male courtship displays; however, males also display to each other in an aggressive context, and little attention has been paid to the role of male-male displays. The display involves a male positioning his body in front or to the side of another male, arching his body, and quivering with his dorsal fin splayed. To understand what behaviors elicit a male display, we assigned individual males a dominance status. We then examined the relationship between dominance status and the number of displays delivered and received. By knowing the status of a displaying individual, we can better understand whether the display is given more often by dominant or subordinate individuals. Our results showed no significant correlation between dominance status and display rate; however, we found a significant relationship between the number of displays received and the number of displays delivered. Additionally, we found that a display is most often followed by aggression (nips and chases) by the other male rather than aggression by the focal male. Our results suggest that the display is a subtle form of aggression that escalates agonistic interactions. It also may serve to convey information about male quality (e.g. by displaying color patterns) and aggressive intent.

Introduction

Competition among males for access to mating opportunities has been documented in many species, including fish, and has evolved via sexual selection (Darwin, 1871). Aggressive contests among males may select for male traits that indicate greater fitness to other males. One type of behavior that may indicate a male's physical condition to other males, as well as to females, is a visual display (Enquist, 1985; Maynard Smith and Harper, 2003; Stuart-Fox, 2006). Maynard Smith and Harper (2003) found a positive relationship between the sexual signal of dewlap inflation and performance ability in male Carribean *Anolis* lizards. The advantage of display signals is that males can gauge the outcome of the fight without engaging in potentially harmful and energetically demanding activities (Rohwer, 1975). Natural selection may therefore favor displays preceding or circumventing overt aggression.

Conspicuous male displays may serve to attract females (Andersson, 1991; Groothius, 1992; Borgia, 1995; Zuk et al., 1995b) or to signal resource holding potential (RHP; the ability to defend resources; Kodric-Brown, 1983, 1990; Lindstrom, 1992a) or fighting ability to other males. In some species, the same display is used for more than one function. For example, in the swordtail fish, *Xiphophorus nezahualcoyotl*, males perform a "headstand" behavior during intraspecific competition, which is characterized by males

angling their bodies 45 to 90 degrees to the ground. More aggressive males perform headstands more often to other males, suggesting the headstand is an aggressive behavior indicating RHP (Lyons and Morris, 2008). There is some evidence to suggest that the headstand display performed during male-male interactions is analogous to the headstand display performed during courtship. This may indicate that the information conveyed by the display during both contexts signals similar male characteristics. The male display is also an indicator of aggression and RHP in bowerbirds (*Ptilonorhynchus violaceus*). Male bowerbirds perform a "skrraa" call, which has been identified as an aggressive behavior that first evolved as a male-male signal but was later used as a courtship signal (Borgia and Coleman, 2000).

Guppies (*Poecilia reticulata*) are livebearing teleost fish native to Trinidad and Tobago and are a model system for studies of sexual selection (Houde, 1997). Males, which are brightly colored compared to the drab females, perform sigmoid courtship displays, during which they display their color patterns (Farr, 1976, 1980; Houde, 1997). The sigmoid display is characterized by the male positioning his body to the front or side of the female, arching his body laterally in an S-shape, and quivering (Field and Waite, 2004; Houde, 1997). Males also perform a very similar display to each other as part of their aggressive interactions, as observed in the lab (Brooks and Caithness, 1999; Kolluru and Grether, 2005) and in the field (Baerends et al., 1955; Liley, 1966; Kolluru et al., 2007). This display even occurs in the absence of females (Field and Waite, 2004); however, the function of the display in the context of male-male competition has received little attention (Kodric-Brown, 1993). The importance of the display during aggressive interactions may be a controversial topic because some researchers argue that intermale aggression is not commonly seen in guppies in the wild and may be a lab artifact (Farr, 1975, 1989; Kodric-Brown, 1992, 1993; Field and Waite, 2004). More recent studies, however, have shown that aggression among males is common (Houde, 1997; Kelly and Godin, 2001; Kolluru and Grether, 2005). Like bowerbirds and swordtails, the male display in guppies may indicate RHP to females, as well as to males. Displays may be a way to avoid spending excess energy and incurring injury during competitive interactions. Kodric-Brown (1993) found that male guppies that are more aggressive in mixed-sex social groups have more mating opportunities. This opens up the intriguing possibility that male-male display may have been co-opted from a courtship function to a male-male competition function.

The agonistic interactions among males include behaviors such as nips and chases (Gorlick, 1976; Farr, 1980; Kodric-Brown, 1992, 1993; Bruce and White, 1995). The male-male display observed during these aggressive interactions has not yet been identified as an aggressive or submissive behavior, but it seems to play a key role in these interactions. To date, many of the studies of aggression in guppies have focused on the influence of ecological variability on aggressive behavior (Endler, 1995; Houde and Endler, 1980; Kolluru et al., 2007). For example, males in high food-availability streams tend to be more aggressive than males in low food-availability streams (Kolluru et al., 2007). By using what is known about displays in a mating context and aggression between males, we can address the role of the male-male display during agonistic interactions.

In this study, we tested the hypothesis that the male display functions as an aggressive behavior that indicates intent to fight and resource holding potential. To do this, we examined the relationship between the frequency of displays delivered and received by a given male to his level of aggression (computed as a "dominance score" using numbers of nips and chases delivered and received, which also corrected for differing densities of fish in observation tanks). We also looked at the relationship between dominance score and body size. The guppies used in this experiment were all descendents of fish from high food-availability sites, and they were fed *ad libitum* throughout the study, so variation in aggression levels is likely not due to differences in food availability. To better understand the situation during which a display occurs, we recorded the sequence of behaviors observed and the behaviors that followed a display. If our hypothesis is supported, we predict that a male display should most commonly be followed by the focal male nipping and chasing the other male, as opposed to receiving nips and chases. If the male display functions as an aggressive behavior, there should be a significant positive relationship between dominance score and display rate.

Methods

Study populations

The guppies used in this experiment were laboratory descendents within 10 generations of fish collected from three geographically isolated rivers in the Northern range of Trinidad: Marianne River (PS 858 895), Small Crayfish River (PS 965 835), and Aripo River (PS 937 803). These sites were originally chosen based on four criteria developed during surveys of various drainages in 1996 and 2000 (Grether et al., 2001). The criteria included: (1) undamaged rainforest growth; (2) similar canopy cover across all streams; (3) isolation by barriers to guppy dispersal, such as two or more waterfalls; (4) low predation, with the only predatory fish being *Rivulus hartii*. All three rivers had low forest canopy cover and high food availability (Grether et al., 1999; Grether et al., 2001). Variation in food availability has been shown to influence male behavior, including aggressive behavior (Kolluru and Grether, 2005; Kolluru et al., 2007). However, all the fish used in this experiment were descendants from high food availability sites, and all were fed *ad libitum*, so behavior is unlikely to be influenced by food availability. Similarly, although predation intensity influences male guppy behavior (Farr, 1975; Seghers, 1974; Houde, 1997), our fish are all descendants from low predation sites.

Laboratory Setting

Fish populations were originally housed in mixed-sex stock tanks for several years in the laboratory of Gregory Grether at the University of California, Los Angeles. Inbreeding was minimized because of the large tank sizes and because female guppies mate with multiple males and are able store sperm for up to eight months (Winge, 1937). Fish were transported to our laboratory at California Polytechnic State University, San Luis Obispo in 2008. Guppies from each population were housed in multiple 10-gallon stock tanks until their use in experiments. The lab temperature was maintained at $25 \pm 0.5°$ C. The

fish were exposed to 12 hours of spectrum fluorescent and incandescent light, and 12 hours of darkness per day. Guppies were fed TetraMin® Tropical flakes twice per day during the week and once per day on the weekends, and were periodically supplemented with Ocean Star International® Spirulina flakes and Hikari® frozen brine shrimp.

At the start of the experiment, approximately 20 females from each population were individually housed with one mature male each from the same population in 2-gallon tanks with net partitions that allowed fry to swim away from the adults, to minimize cannibalism. It was very likely that females were gravid by the time they were moved to the 2-gallon tanks; however, the companion male may have fathered offspring as well. Within three weeks after each female gave birth, offspring were moved to 2-gallon tanks at densities of 2 to 6 fish from no more than two litters. At approximately five to six weeks, sexes were separated. Sex was determined using pigmentation and gonopodium development in males and dark coloration around the anal fin of females (Houde, 1997). We are confident that males had no sexual experience prior to their use in observations because they were moved before complete development of the gonopodium (Houde, 1997).

After sexing, fish were held in single-sex 2-gallon tanks at densities of 2 to 4 males per 2-gallon tank. Males and females did not have visible contact with each other after this point, to minimize the influence of visual contact between the sexes on male competitive interactions (Hibler and Houde, 2006).

Focal Behavior Observations

Male color patterns were sketched for individual identification, and each male was assigned a unique number-letter combination (with the number indicating the tank and the letter, W, X, Y, or Z, indicating the male within the tank). Observations were performed from March to December, 2009. On the observation day, a tank was chosen at random (determined using the Excel random number generator), and a male within that tank was also randomly selected for observation. Cardboard was placed on either side of the tank so that the males were not distracted by fish in surrounding tanks. Data were collected in 5-minute focal observations at three times of day. The first observation was made between 9:00am and 11:00am, the second observation was made between 2:00pm and 4:00pm, and the third observation was made between 6:00pm and 9:00pm. Employing three observation sessions spaced apart in this way allowed us to capture diurnal variation in behavior patterns (Endler, 1987; Reynolds et al., 1993).

Before each observation, each tank was fed a small pinch of the flake food as described above. After approximately five minutes, the fish were acclimated to the presence of the observer by the observer standing relatively motionless 12 inches in front of the tank for two minutes. After the acclimation period, the focal male was observed for five minutes, during which time the observer recorded the sequence of behaviors exhibited by the focal male and the other male(s) in the tank. The behaviors recorded included chases, nips, and displays by both the focal male and the other male(s). A "display" to another male was very similar to the characteristic sigmoid courtship display performed by male guppies to

females and is characterized by a male positioning himself in front of another male, arching his back into a sigmoid shape, and quivering (Rodd and Solowski, 1995; Field and Waite, 2004). Displays can occur with the fins closed or open (Farr, 1976). "Nips" involved one male approaching another male from the posterior end and quickly biting the base of the other male's gonopodium (Kodric-Brown, 1993) or dorsal surface. "Chases" involved one male pursing another male that was actively swimming away. Additionally, we recorded "face-offs", involving both males pointing their mouths towards each other while separated by a distance of a few centimeters or less. Males sometimes remained in this position for an extended period of time, and as one male moved, the other male sometimes simultaneously mirrored the movement.

Following the third focal observation of the day, the focal male was anesthetized using tricaine methane sulfanate (MS-222, Finquel®, Argent Chemical Laboratories) and weighed using an electronic balance to the nearest 0.001 g. Standard length (the distance from the tip of the mouth to the caudal peduncle) was measured using electronic calipers to the nearest 0.1 mm under a dissecting microscope at 15X.

Data Analysis

Using the statistical software JMP 7.0, pair-wise correlations were performed between dominance score (defined below), displays received, displays given, and standard length for all 108 males used in the experiment. Dominance scores were determined using the following equation, developed by Oliveria and Almada (1996a): (total number of nips and chases delivered by the focal male) / (total number of nips and chases received and delivered by the focal male). We used another equation, also developed by Oliveria and Almada (1996a): (total number of nips and chases delivered by the focal male) – (the number of nips and chases received by the focal male). This second equation had no substantial effects on our results, so we only present the results employing the first equation. For those males that were in tanks with a density of 2 males per tank (N=27), we used Excel to generate bar graphs of the behaviors that occurred after a focal display using our sequence-of-behavior data. This analysis was incorporated only for paired males because it made it easier to understand what behavior followed a display without questioning which male the behavior was directed towards. We also performed a binomial test comparing the number of displays received by a dominant focal male to the number of displays received by a subordinate focal male following a focal display.

Results

We found a significant positive relationship between dominance score and standard length (Table 1). This suggests that the larger a male is, the more aggressive he is towards other male(s). There was also a significant positive relationship between displays received and displays delivered by the focal male (Table 1). This suggests that males who deliver more displays receive more displays in return. There was no significant relationship between dominance score and either displays delivered or received by the focal male (Table 1). This suggests that more aggressive males do not display significantly more to other males and do not receive more displays from other males.

Table 1. Outcome of pair-wise correlations.

Variable 1	Variable 2	r	P
Displays delivered by focal	Standard length (mm)	-0.111	0.3091
Displays received by focal	Standard length (mm)	0.0205	0.8517
Displays received by focal	Displays delivered by focal	0.3119	0.0035*
Dominance score	Standard length (mm)	0.2823	0.0085*
Dominance score	Displays delivered by focal	0.0257	0.8144
Dominance score	Displays received by focal	0.0416	0.7035

*significant at the $\alpha = 0.05$ level.

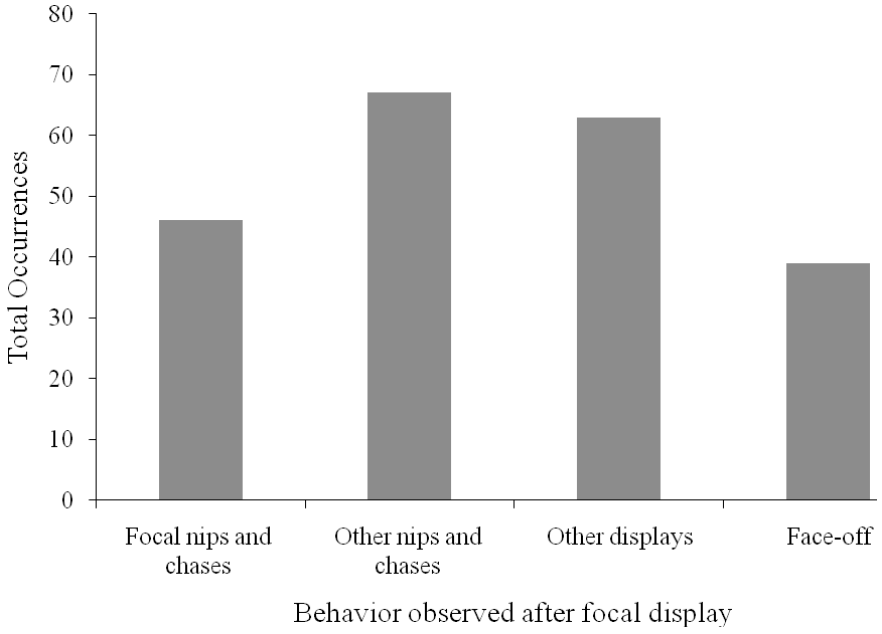

Figure 1. The total occurrences of behaviors observed immediately following a focal display for all males in tanks with a density of 2 males per 2-gallon tank (N=27). Focal nips and focal chases, as well as other nips and other chases, were each grouped together because nips and chases both represent aggressive behaviors.

A display by the focal male was most often followed by a nip or chase by the other male (Figure 1). The next most common response to a display by the focal male was a display by the other male. The third most common response to a display was a nip and chase by the focal male. The least common behavior observed was a face-off.

Additionally, we compared the number of times a dominant male's display was met by a display to the number of times a subordinate male's display was met by a display and found this ratio to be 37:27. A binomial test was performed on these values ($P = 0.046$). This indicates that the observed values were significantly different from chance and that dominant males were more likely to receive displays in response to their displays than were subordinate males.

Discussion

Our data suggest that larger males tend to be more dominant than smaller males, which means that larger males deliver more nips and chases than smaller males. This is interesting because males were often very close in size to their tank mates because they were usually from the same brood and were raised together. Therefore, even such subtle differences in body size translated into substantial differences in aggression. Larger males may be more aggressive because they have more energy to invest into behaviors such as nipping and chasing. Smaller males may allocate more energy to foraging and other behaviors that directly increase their fitness. Additionally, we found a significant relationship between the number of displays delivered and the number of displays received between males. This suggests that as a male displays more, he receives more displays in return. Thus, the display may serve as a mild form of aggression that then escalates to more costly chases and nips. As observed in our sequence-of-behavior data, a display by either a dominant or subordinate male was most often followed by nips and chases by the other male. It seems likely that the display is a subtle indicator of aggressive intent, whereas nips and chases are a more overt aggressive behavior. In response to displays by dominant and subordinate focal males, the data suggest that dominant males receive more displays than do subordinate males. Houde (1997) suggested that males in tanks with one to two other individuals establish dominance hierarchies based on nips and chases. If males are able to gauge each other's dominance status, it follows that dominant males should receive more displays. Subordinate males responding to dominant males may be less likely to be overtly aggressive because they can gauge the outcome of the fight. Subordinate males, therefore, should respond with a subtle form of aggression like the display because nipping and chasing incur costs (Lahti et al, 2002; Fawcett and Johnstone, 2003; Kolluru and Grether, 2005).

Several authors have described a behavior between male guppies termed a "lateral" display, which they distinguish from a "sigmoid display" to a female (Farr, 1976; Houde, 1997; Liley, 1966). According to Houde (1997), a lateral display involves a male positioning himself in parallel with another male and splaying his caudal fin. We observed lateral displays in our study, and in another set of observations including males and females. However, the behavior we describe in our study is a distinct display, clearly directed from one male to another, that is more similar to a sigmoid courtship display than to a lateral display. This lateral display was observed very rarely during our observations; therefore, it was not included in the analysis.

Previous studies of male displays in guppies and related species lead us to believe that the display may convey information about a male's fitness or RHP. Female guppies have shown a preference for more brightly colored males who display more frequently (Kodric-Brown, 1989), most likely because the area of orange spots on a male convey information about immune system strength and overall fitness (Grether et al., 2005). Kodric-Brown (1989) also found that males who display more to females have higher reproductive success, thus suggesting there has been strong sexual selection on male coloration and intensity of display during courtship. Likewise, if males who use this display during agonistic interactions can gauge the status and fighting ability of a rival

male and reduce their risk of injury and death, natural selection will act to maintain this trait through evolutionary time.

Although we have concluded that the male display seems to be a subtle form of aggression that conveys a message about male status and fitness, Field and Waite (2004) described this display as a homosexual behavior that occurs when males are deprived of contact with females during development. Field and Waite (2004) observed that when males from both single-sex tanks and mixed-sex tanks were placed with one stimulus male, the males from single-sex tanks had a higher display rate towards the stimulus male than did the males from mixed-sex groups. They suggested that "male-directed courtship displays", which they described as homosexual behaviors, were learned behaviors influenced by social context. Our experimental design was similar to the female-absent scenario described by Field and Waite (2004), in that the males we used did not see females after becoming sexually mature. However, in both their experiment and ours, male-male interactions may reflect dominance interactions rather than aberrant homosexual behavior. Since guppies raised in groups of two establish dominance hierarchies more readily than do males in larger groups (Houde, 1997), the males raised in single-sex tanks in Field and Waite's (2004) study could have formed dominance relationships as well. The heightened aggressive interactions experienced by these males may have caused the males to be more likely to initiate aggression with a new male. In contrast, in Field and Waite's (2004) study, the males raised in mixed-sex tanks may not have formed such stable dominance relationships. Those males may therefore not have been as likely to instigate aggression when faced with courtship opportunities instead. Overall, the results of our observations would be consistent with Field and Waite (2004) if they had suggested an adaptive aggressive context for male-male displays.

Our results are consistent with other studies of aggression, including studies of swordtail fish, *Xiphophorus nezahualcoyotl* (Lyons and Morris, 2008) and widowbirds, *Euplectes ardens* (Pryke et al., 2001). In *Xiphophorus nezahualcoyotl*, the aggressive headstand display provides information regarding the motivation to continue fighting other males, indicating RHP. Lyons and Morris (2008) additionally suggest that this display is a less aggressive behavior than nipping and chasing, which supports our finding as well. While our study interprets the guppy display to be a milder form of aggression than chases and nips, instead of as an indicator of motivation to continue fighting, we believe that it might provide information about RHP as well. Because signaling is energetically costly (Zahavi, 1975; Grafen, 1990; Lyons and Morris, 2008), a male who can afford to display more may have higher RHP. Likewise, it has been shown in *Euplectes ardens* that males with brighter coloration are more dominant (Pryke, 2001). The color displays are used as agonistic signals that honestly indicate a male's health and fighting ability, suggesting that they also have higher RHP. Studies such as these further support the role of the display as an aggressive behavior in guppies.

Although we examined a few different measures of aggression in guppies, it would be useful for future studies to include additional measures of "submission" such as backing away from a dominant male during a fight. If the display is in fact an aggressive behavior, then subordinate males should retreat more often from dominant males after

being displayed to. This would provide further support for our argument that the display is an aggressive behavior indicating relevant information about the displayer. Additionally, it would be interesting to explore the relationship between coloration and dominance as well as coloration and frequency of displays delivered to males. Since males with larger orange spots are suggested to be of higher quality (Grether et al., 2005) and are more dominant (Kodric-Brown, 1993), we predict that males with larger, brighter orange spots will display more frequently. This would suggest that higher quality males are more dominant, can afford to display more than subordinate individuals, and indicate dominance status via the display.

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