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# MATE SAMPLING IN A NATURAL POPULATION OF PECOS GAMBUSIA, *GAMBUSIA NOBILIS*

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ABSTRACT.—Much research has been conducted on the mating systems of poeciliid fish in aquaria; however, there are fewer studies that examine mate sampling of these fish in the wild. In general, male poeciliids are characterized as being unselective in their mate choices and will attempt to copulate with seemingly all available females. Females are selective, copulate infrequently, and are often pursued by "ardent" males who may force copulations. To avoid male harassment, females in aquaria will often shelter from males among other females in shoals. Here, we examined the mate-sampling behaviors of male and female Pecos gambusia *Gambusia nobilis* by following individuals swimming in an outflow pool of Diamond Y Spring in southwestern Texas. In most cases, a male approached a solitary female, followed her briefly, and then left for no apparent reason. Approaching a number of females increased the likelihood that the male would follow one, and the longer a male followed a female, the more likely he was to copulate with her. As females were larger and faster than males, they could avoid males by swimming away from them. We found no evidence of the persistent males that harass seemingly unreceptive females as seen under aquarium conditions, nor did we see females join a shoal to stop pursuit by males. However, the activity of one male following a female did appear to attract other males who would compete to follow and attempt copulation. This competition might ensure that only superior males gain reproductive opportunities.

*Key words:* Gambusia nobilis, *Pecos gambusia, promiscuity, mate sampling.*

RESUMEN.—Se han investigado extensamente los sistemas de apareamiento de pecílidos en acuario; no obstante, hay relativamente pocos estudios que examinan la elección de pareja de estos peces en su hábitat natural. Los pecílidos machos no suelen ser selectivos en su elección de pareja y parecen intentar copular con todas las hembras que estén a su alcance. Las hembras son selectivas, no copulan frecuentemente y a menudo las persiguen machos excitados que pueden copular con ellas forzadamente. Para evitar el acosamiento de los machos, en acuario las hembras a menudo se refugian de los machos entre otras hembras en bancos. Para este estudio, examinamos el comportamiento de elección de pareja de gambusias de pecos (*Gambusia nobilis*) machos y hembras al observar algunos individuos en un remanso del Diamond Y Spring en el suroeste de Texas. En la mayoría de los casos, el macho se acercaba a una hembra solitaria, la seguía brevemente y luego se alejaba sin motivo aparente. El acercarse a varias hembras aumentaba la probabilidad de que persiguiera a una de ellas, y cuanto más la seguía, más probable era que copulara con ella. Dado que las hembras son más grandes y más rápidas que los machos, podían eludirlos si no correspondían. No observamos machos persistentes que acosaran hembras aparentemente poco receptivas como se ha documentado en acuario, ni tampoco vimos hembras que se unieran a bancos para evitar la persecución de machos. Pero cuando un macho perseguía una hembra, parecía atraer otros, los cuales competían entre sí para seguirla e intentar copular con ella. Esta competencia podría garantizar que solo los machos superiores tengan oportunidades reproductivas.

Differences in secondary sex characteristics between males and females are often obvious in the family Poeciliidae, making these fish popular models for studying the evolution of sexually selected traits (e.g., Houde 1997). In general, males are smaller than females, and in many species, males demonstrate showy fin ornaments or colorful body patterns that are attractive to females (Bischoff et al. 1985, Kodric-Brown 1989, Brooks and Caithness 1995). In addition to such morphological distinctions, male and female poeciliids often differ dramatically in sexual behaviors. Although males may prefer certain females over others (Dosen and Montgomerie 2004, Hoysak and Godin 2007), males are generally characterized as unselective in their mate choices and will court (Schlupp et al. 2001), chase (Bisazza 1993), or switch between courtship and coercive chasing (Ojanguren and Magurran 2004) in attempts to copulate with seemingly all nearby females. Other, often smaller, males will rely on sneak mating to gain copulations (Plath et al. 2003).

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In contrast to males, females are highly selective and copulate infrequently (Brooks and Caithness 1995), and these copulations may (Schlupp et al. 2001) or may not be cooperative (Houde 1997). For example, large male sailfin mollies *Poecilia latipinna* will court females who cooperatively copulate while smaller males depend on sneak mating (Travis 1994, Plath et al. 2006). Unlike mollies, when male and female Eastern mosquitofish *Gambusia holbrooki* are placed together in small aquaria, females are often unreceptive and are relentlessly pursued by "ardent" males who may force copulations (Pilastro et al. 2003) but who also frequently switch attention from one female to another (Hoysak and Godin 2007). Under natural conditions, such male behavior is predicted to increase the female's exposure to predators (Magurran and Seghers 1994, Houde 1997) and reduce her ability to forage (Griffiths 1996, Pilastro et al. 2003).

The benefit that males derive from the persistent pursuit of unreceptive females is unclear. Possibly, males engaging in prolonged pursuits would benefit if initially unreceptive females eventually mate with them. If this were the case, however, why would males divert attention to other females? It may be that males are relentless in their pursuit of a female only when there are no alternative females that might be more receptive. Thus, when encountering a shoal of females, a male may quickly test each female to determine her degree of receptivity, and, based on this initial assessment, either pursue her to copulate or leave her to follow another female. The opportunity to select among many females helps explain why males prefer to approach larger, rather than smaller, shoals of females (Agrillo et al. 2008). Such testing behavior is the hallmark of the breeding systems of many group-living, polygynous species. However, compared to the numerous aquarium studies that emphasize mating preferences, there are few studies that examine mate-sampling behavior of poeciliid fish under natural conditions.

In a field study of a population in southwestern Texas, we examined the mate-sampling behavior of male and female Pecos gambusia *Gambusia nobilis* with 2 goals in mind. First, we were interested in comparing male behavior in the wild to that predicted from aquarium-based studies. Such studies on similar species of poeciliids report 3 stereotypical components to male reproductive behavior: a male approaches a female, he follows her, and, at various times, he attempts to copulate with her (Bisazza 1993, Pilastro et al. 2003). Males do not appear to court females (except see Houde 1997); rather, they will follow a female relentlessly, attempting copulations through gonopodial thrusting (Farr 1989, Pilastro et al. 2003). Because this pursuit is the manner in which males secure reproductive opportunities, we expected males in the wild to spend the majority of their time following prospective mates. We also predicted that the longer a male followed a female, the more likely he would be to attempt copulation. If this were the case, it would suggest that males were attempting to maximize mating opportunities by following a single female for as long as possible rather than by frequently switching between different females. However, the aquarium studies do indicate that males will often leave one female to pursue another that has swum nearby (Hoysak and Godin 2007, Agrillo et al. 2008). This suggests that males will test new females when they are immediately available and also that the males will not leave a female to search for mates elsewhere. Thus, we predicted that males would only stop following a particular female to follow another nearby female (i.e., to switch).

Second, we were interested in contrasting the behaviors of males relative to females under the framework of the aquarium-based predictions. While males were expected to show continued interest in sampling females (as described above), we predicted that the majority of female Pecos gambusia would be unreceptive to mating (as in other poeciliids; Houde 1987, Brooks and Caithness 1995). Most often, females have been observed to join shoals of other females to avoid harassment by males (Pilastro et al. 2003). Therefore, we predicted that a female being followed persistently by a male would likely move toward other nearby females. Alternatively, there is a considerable amount of "open water" in the field compared to the confines of an aquarium. Because females are considerably larger and faster than males, we anticipated that rather than sheltering among other females, a female could simply outswim and avoid her pursuers.

## METHODS

We studied the reproductive behavior of 166 individual Pecos gambusia in an outflow pool of the Diamond Y Spring, located 20 km north of Fort Stockton, Texas (30.9°N, 102.9°W). The pool is approximately 20 m in diameter, with a center depth of just over 1 m. The gambusia were easily observed from the shoreline, as they spent the majority of their time swimming near the surface of the shallow water where they fed primarily on small insects that fell into the pool. Typical of other gambusia species (McPeek 1992), the sexes of Pecos gambusia differ in size, with the female being larger than the male; in this population, females were approximately 4–5 cm in total length, while males were 3–4 cm. There are no obvious differences in coloration between the sexes, and the male does not have the fin ornaments seen in other poeciliids (Farr 1989, Pocklington and Dill 1995).

Our observations consisted of arbitrarily selecting any solitary male or female among the many within view and following its movements for as long as the fish remained visible. All behaviors witnessed were dictated onto audiotape for later transcription, allowing the observer to maintain a constant view of the subject. Because some individuals ranged widely and others moved less, observation times ranged between several seconds and 300 seconds. Because our primary interest was to record interactions between individuals, we did not consider any observations that were shorter than 25 seconds ($n$ = 129). An interval of at least 10 seconds was used to transition to a new fish after the previous fish was lost from view.

From the audio tapes, we recorded the following activities: (a) total time—the total amount of time that a focal fish was followed; (b) percent of time alone—the proportion of total time that any focal fish spent swimming without another fish in close proximity (>25 cm away); (c) male approach—this behavior was recorded when a focal male swam toward a female and moved to within 10 cm of that female or when a focal female was approached to within 10 cm by a male; (d) approach rate—the amount of time between when a focal male left a female and when he approached a different female, or the amount of time between when a male left a focal female and when she was approached by another male; (e) male follows—the number of females that the focal male followed after approaching, or the number of different males that followed a focal female; (f) time following—the amount of time that the focal male followed a given female, or the amount of time that the focal female was followed by a male; (g) multiple male following—the amount of time that a focal male joined or was joined by other males in following a female, or the amount of time that more than one male simultaneously followed a focal female; (h) thrust (copulation attempt)—a thrust occurred when a male that was following a female increased his swimming speed to advance on the female, appearing to copulate with her. For animals involved in copulation attempts, we considered that a focal male could perform one thrust toward one female, one thrust toward each of more than one female, or multiple thrusts toward a single female. We considered that a focal female could be involved in one thrust by one male, one thrust by each of more than one male, or multiple thrusts by each of one or more males.

On 8 separate occasions on different observation days at different times of day, we counted the number of males and females visible within a 2-m radius (or to the shoreline) of a focal animal immediately after the focal observation had concluded. From these censuses, we calculated the sex ratio of the population of fish with which the focal individuals were likely to interact. In addition, we independently video recorded 150 circumstances of a single male pursuing a single female. We followed the pair until they parted and recorded the immediate subsequent behavior (as described above) of both the male and the female.

For both focal males and females, we compared relationships among the recorded behaviors using Spearman rank correlation. We used Mann–Whitney $U$ tests to compare data for males relative to females.

## RESULTS

The population of fish studied had equal numbers of males and females (50.66% male, SE = 0.03%). We analyzed the behavior of 78 females and 51 males. Males (94 seconds, SE = 10) and females (101 seconds, SE = 8) were observed for similar periods of time ($U$ = 1844.00, $P$ = 0.49; Table 1), and both sexes spent similar proportions of their time swimming alone ($U$ = 1648.50, $P$ = 0.10; Table 1). There was a significant correlation between the amount of time a male was observed and the number of females he approached ($r_S$ = 0.58, $P$ < 0.01). The amount of time that a female was observed was also significantly correlated with

TABLE 1. Contrasts in the behaviors recorded for focal males versus focal females (means are given with standard errors in parentheses).

| Behavior | Focal female | Focal male | *U* statistic | *P* value |
|---|---|---|---|---|
| a. Total time | 101.0 (8) | 94.0 ± 10 | 1844.00 | 0.49 |
| b. % Time alone | 63.6 (4.2) | 57.1 ± 4.3 | 1648.50 | 0.10 |
| c. Male approach | 3.5 (0.4) | 5.4 ± 0.7 | 1437.50 | 0.01 |
| d. Approach rate | 36.0 (3.7) | 11.6 ± 1.6 | 890.50 | 0.0001 |
| e. Male follows | 2.9 (0.3) | 3.6 ± 0.5 | 1677.00 | 0.13 |
| f. Time following | 23.8 (3.7) | 31.8 ± 4.4 | 1525.50 | 0.03 |
| g. Multiple male following | 10.6 (2.7) | 4.1 ± 1.3 | 1503.50 | 0.02 |
| h. Thrust | 1.4 (0.3) | 1.7 ± 0.3 | 1635.00 | 0.09 |

the number of males that approached her ($r_s$ = 0.73, $P < 0.01$).

Irrespective of observation time, most males (50 of 51) approached at least one solitary female, and of these males, 68% (34 of 50) made at least one copulation attempt (thrust). Males did not approach groups of females. Of the 34 males who attempted copulation, 12 performed one thrust directed toward one female. The remaining males performed multiple thrusts toward one female ($n$ = 13) or a single thrust toward each of multiple females ($n$ = 9). Similarly, most females (70 of 78) were approached by at least one male, and of these females, 50% (35 of 70) were involved in a copulation attempt (Table 1). Of these females, 14 were involved in one copulation attempt by one male, 15 were involved in multiple attempts by the same male, and 6 were involved in one copulation attempt by each of more than one male. Because of the low sample size for each of these subcategories, we considered thrusts equally in statistical analyses.

Focal males approached more females more often than focal females were approached by males, but focal males followed a similar number of females relative to the number of males that focal females allowed to follow them. This similarity notwithstanding, focal males spent more time following prospective mates than focal females were pursued by males. That is, focal males approached many females and followed a number of them, while focal females were followed by a similar number of males but for less time. Despite this difference, males and females performed or experienced similar numbers of copulation attempts.

Because focal males approached more females than they followed, and because it appeared that following, more than approaching, was related to copulation attempts by the males, we used Spearman rank correlations to consider the relationships among the number of approaches (c), the number of females followed (e), the amount of time that females were followed by a single male (f) and by multiple males (g), and the number of copulation attempts (h) (Table 2). Males appeared to approach and then follow as many females as possible. As a result, the number of females approached was significantly correlated with the number of females followed, but neither of these variables was correlated with the amount of time that the male followed females (Table 2). That is, males approached and followed many females rather than spending a substantial portion of their time following any one female. This result is particularly interesting as the duration in which a male followed females was the only variable that was significantly correlated with the number of copulation attempts the male made. In addition, males appeared likely to approach females that were already being pursued by other males, but multiple males following did not relate to an individual male's copulation attempts.

From the perspective of focal females (Table 2), it was not surprising that the number of males that approached a female would be correlated with the number of males that followed her. Essentially, each female was approached by many males, and many of these males tried to follow her; however, the number of males that approached and followed was not correlated with the total duration that a female was followed. That is, the duration a female was followed was not simply a sum of the number of males that approached and followed her. Whether or not a male approached and followed a female was correlated with other males already following her. The number of times that males attempted copulations with the female was correlated with the total number of males that had approached

TABLE 2. Spearman rank correlations describing the interrelationships of several observed behaviors (asterisks indicate the significant correlations).

| Behavior | e. Male follows | f. Time following | g. Multiple male following | h. Thrust |
|---|---|---|---|---|
| FOCAL MALES | | | | |
| c. Male approach | 0.72* | 0.03 | –0.32* | –0.12 |
| e. Male follows | | 0.22 | –0.22 | –0.05 |
| f. Time following | | | 0.14 | 0.60* |
| g. Multiple male following | | | | 0.21 |
| FOCAL FEMALES | | | | |
| c. Male approach | 0.97* | 0.23 | 0.70* | 0.33* |
| e. Male follows | | 0.28 | 0.75* | 0.37* |
| f. Time following | | | 0.11 | 0.41* |
| g. Multiple male following | | | | 0.47* |

her as well as the total time that she was followed either by a single male or by multiple males. Thus, increasing activity directed at a female by one or more males in pursuit was related to whether or not males attempted to copulate with her.

Using video recordings, we determined how likely it was for a male that was following a female to switch to a different female and for a female to seek shelter within a shoal of other females. We followed the pair until they parted; then we followed each to determine his or her next behavior. Of these observations, 129 of the males left the female they had been following without approaching another nearby female. Often, these males would swim alone or apparently leave the female to feed. In the remaining 21 cases, the male quickly approached another female after leaving the initial female. In all the video and the audio records, we never observed a male to leave and then immediately return to the same female after the two had parted. We never observed a female to approach a male, and we never witnessed a female that was being followed by a male to swim closer to another solitary female or to join a shoal of females.

## DISCUSSION

Male Pecos gambusia did not attempt to copulate with every female they approached. In most cases, males approached a female, followed her briefly, and then left. Because focal males approached females more times than focal females were approached by males, despite the 50:50 sex ratio, it appears as though approaching may have provided males with an initial assessment of female quality or receptivity. Males never approached the same female immediately after leaving, but they may have returned after foraging or assessing other females. This suggests that while males are promiscuous, females vary in a quality that is quickly assessed on approach (Liley 1983).

For the vast majority of females approached and followed, we found no evidence of the persistent males that harass seemingly unreceptive females as seen under aquarium conditions (e.g., Pilastro et al. 2003). Indeed, because females are larger and faster than males, and were not confined in aquaria, it is likely that unreceptive females swam away from approaching males while only receptive females allowed males to follow them. This would explain why females were followed for different periods of time and why the period of time that a male spent following a female, rather than the number of females he approached, related to copulation attempts. Females followed for the longest amount of time were, or were perceived to be, more receptive or of a higher quality to the male.

For a male, approaching multiple females increased the likelihood that he would follow one; and the longer he followed, the more likely he was to mate. Despite this, males often left females for no apparent reason with or without having copulated. Males may both incur benefits and suffer costs in following females. The benefit is that a solitary male following a female is likely to copulate; the cost is that the activity of the male following a female appears to attract other males (Bisazza and Marin 1995). In our study, multiple males following a female was not correlated with thrusts by the focal male, but focal females that did copulate often mated one or more times with each of more than one male. Likewise, in mosquitofish interacting in aquaria (Pilastro et al. 2003), multiple males following a female reduced the number of mating attempts that each male made. In both cases, the reduced copulation attempts by a particular male were likely due to infighting among the males as each vied for access to the female.

For females, the number of approaches, the number of males that followed, and the duration that single and multiple males followed were all significantly correlated to the number of mating attempts. Given that females could easily swim away from males, we suspect that receptive females were attractive to males and allowed these males to follow. The activity of one male appeared to attract others, and the resulting competition among these males benefited the female, as only the most dominant among them was likely to secure copulations (sensu Bisazza et al. 1995).

As in other poeciliids, male Pecos gambusia gained copulations by following, rather than courting, females. Although it was clear that females could resist copulation attempts by fleeing from the males, we found no evidence that females swam into shoals of other females to shelter from approaching males. In aquarium studies of mosquitofish, females in shoals suffered from less harassment and could spend more time foraging compared to solitary females (Pilastro et al. 2003), and males would join shoals to search for mates (Agrillo et al. 2008).

Shoaling benefits females in a number of ways, including providing protection from predators (Tobler and Schlupp 2008) and increased opportunity to forage (Pilastro et al. 2003), but we suggest that shoaling is not directly reproductively beneficial to female Pecos gambusia. That is, in our study, males did not appear to search for shoals of females to join, and single females were often approached by a number of different males, with many of these males following and performing thrusts. This activity attracted more males, who attempted copulations. In a group, unreceptive females suffer from less male "harassment." In contrast, solitary, receptive females attract a number of males, and the competition among males likely serves as an indirect manner in which females ensure that competitively superior males gain copulations.

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