FEMALE-FEMALE COMPETITION IN A
UNISEXUAL/BISEXUAL COMPLEX OF
MOLLIES.—The sailfin molly, *Poecilia latipin-
na*, has a promiscuous mating system (Balsano
et al., 1989). Females produce multiply sired
broods (Travis, 1989), and males are reproduc-
tively active year-round (Monaco et al., 1981).
In *P. latipinna*, males vary greatly in body size,
which is genetically determined by the P locus
on the Y chromosome (Travis et al., 1989). *Poe-
cilia latipinna* can occur in a bisexual/unisexual
complex with the gynogenetic species *P. for-
mosa*. Gyogens are all-female species in which
inheritance is strictly maternal, but sperm is re-
quired to initiate development (Kallman, 1962).
Poecilia formosa, known as the Amazon molly, is
a gynogenetic species of hybrid origin (Hubbs
and Hubbs, 1932).

Gynogens occur in complexes with bisexual
species and must mate with males of that species
to be successful. *Poecilia formosa* will mate with
males of *P. latipinna* to reproduce. *Poecilia la-
tipinna* males, however, have been shown to mate
preferentially with conspecific females and dis-

criminate against the gynogen (Woodhead and Armstrong, 1985; M. J. Ryan and P. Batra, unpubl. data). Mating with the gynogen is thought to be a disadvantage for males because their genes will not be incorporated into the next generation. Therefore, *P. formosa* must compete with preferred *P. latipinna* females to reproduce successfully (see also Schlupp et al., 1991).

Gynogens that are successful in aquiring matings will produce twice the number of female offspring in comparison to their host species. Because females of the host species will produce male and female offspring, gynogens are capable of a higher rate of reproduction. Increasing proportions of gynogens in the population would lead to a replacement of females from the host species and an increasingly female-biased sex ratio. The rate of reproduction in the host species would fall and limit the number of males available to females of both species. Success of sperm-dependent gynogens, therefore, would result in the eventual extinction of both the species in the population (Moore, 1975).

One way to offset the higher reproductive capacity of gynogens is for females of the two species to differ in their ability to obtain sperm. Several mechanisms have been described for the maintenance of these populations through differential access to males of the host species. Males of the host species may mate preferentially with conspecific females (McKay, 1971; Woodhead and Armstrong, 1985). Experience may lead to male mate preference for conspecific females (Woodhead and Armstrong, 1985). Dominance hierarchies among males may limit subordinate males to mating with gynogens (Moore and McKay, 1971). Gynogens and females of the host species may have some niche separation in habitat that allows host females greater access to males (Kirkendall and Stenseth, 1990). The described models have all emphasized how male behavior and population dynamics could result in the maintenance of unisexual populations through preferential mating with conspecific females.

In many species, however, competition among females for mates provides a mechanism in which a female's behavior may directly affect her mating success. For example, competition among females occurs in many species that exhibit male parental care. In these systems, the quality of male parental care can vary, and females who choose better fathers can have greater reproductive success. Females have been shown to compete in polyandrous (Emlen et al., 1989), sex-role reversed (Colwell and Oring, 1988; Summers, 1989; Rosenqvist, 1990) and monog-

amous mating systems (Olsen and Olsen, 1987; Johnson, 1988; French and Inglett, 1989) in which males attend or nourish the young or provide for the female during nesting.

Female-female competition is also expected when the number of males is a limiting factor for reproduction. In complexes of gynogenetic and bisexual species, females of two species must compete for access to the same males to reproduce. These complexes may have population sex ratios that are highly female biased. Therefore, in gynogenetic/bisexual populations, males are more likely to be a limiting factor. In this study, interactions between gynogens and members of the host species were quantified to assess the level of aggressive competition for mates both among conspecific females and between *P. formosa* and *P. latipinna* females.

Methods and materials.—Fish were either directly collected from the San Marcos River near San Marcos, Texas [where *P. formosa* has been introduced from the lower Rio Grande Valley (Courtenay and Meffe, 1989)] or from a San Marcos population maintained in a breeding tank (5 m × 5 m × 8 m) at Brackenridge Field Laboratory, University of Texas, Austin. Fish were maintained in the laboratory in 4.6- and 136.4-liter aquaria on a 12:12 light cycle and fed liver paste until testing. Reproductive condition of the females was not controlled; all tested females were large enough to be reproductively active (>29 mm).

To quantify the competition among females, the frequencies of four activities were recorded. Blocking was defined as a female swimming between another female and the male. One female forcefully pushing laterally against another was considered butting. Biting and chasing were also recorded. In addition, in tests with males, the number of gonopodial thrusts directed at each female was recorded. These activities were recorded in six types of tests. Each test differed in species composition of females and/or presence or absence of a male.

Competition between females of the two species for mates was examined by pairing female *P. latipinna* and *P. formosa* and testing them both with and without a *P. latipinna* male present in two tests. Intraspecific competition was determined by testing a pair of female *P. latipinna* or *P. formosa* with and without a male present and recording their behavior in four tests. All females were measured, matched for size within 1 mm, and placed at the ends of a 90-liter aquarium divided into three sections by Plexiglas barriers. For tests involving *P. latipinna* males, males were also premeasured and placed in the center

section. The fish remained separated for two days, when the barriers were removed, and then observed for 15 min.

Results.—Blocking usually occurred only in the presence of a male and thus appears to function in increasing a female's access to the male. The number of blocks significantly increased with the presence of the male in both *P. latipinna* (without male: median = 0.00, n = 20 and with male: median = 3.00, n = 26; Mann-Whitney U = 501, $P < 0.001$) and *P. formosa* (without male: median = 0.00, n = 20; and with male: median = 1.50, n = 20, Mann-Whitney U = 37, $P < 0.001$). In addition, blocking was positively correlated with the number of gonopodial thrusts directed toward each female (Pearson r = 0.526, n = 46, $P < 0.001$).

Competition for mates between *P. formosa* and *P. latipinna* was greater than competition between two *P. formosa*. In tests with heterospecific females, *P. formosa* performed significantly more blocks than in tests with other *P. formosa* (with heterospecific females: median = 3.00, n = 13 and with conspecifics: median = 1.50, n = 20; Mann-Whitney U = 55.5, $P < 0.005$). *Poecilia latipinna* females also tended to increase blocking behavior in heterospecific tests although the change was not significant (with heterospecific females: median = 5.00, n = 13 and with conspecifics: median = 1.00, median = 3.00, n = 26; Mann-Whitney U = 118, $P < 0.124$).

In tests with *P. latipinna* females and *P. formosa*, *P. latipinna* males tended to mate preferentially with conspecific females although the discrimination was not significant (with *P. latipinna* females: median = 3.00, n = 13 and with *P. formosa*: median = 1.00, n = 13; Mann-Whitney U = 115, $P < 0.107$). However, gynogens received significantly more gonopodial thrusts in tests with *P. latipinna* females than in tests with conspecifics (with heterospecific females: median = 1.00, n = 13 and with conspecifics: median = 0.00, n = 20; Mann-Whitney U = 78, $P < 0.018$). In addition, the number of blocks performed by *P. formosa* was positively correlated with gonopodial thrusts in tests with heterospecific females (Pearson r = 0.847, n = 13, $P < 0.001$). These results are summarized in Figure 1.

Biting, butting, and chasing generally occurred together and were performed by the same female; therefore, they were analyzed collectively as aggressive acts. Both *P. latipinna* females and *P. formosa* were significantly more aggressive in the absence of a male (*P. latipinna* females without male: median = 8.50, n = 20 and with male: median = 0.00, n = 26; Mann-

Whitney U = 96, $P < 0.001$; *P. formosa* without male: median = 15.00, n = 20 and with male: median 0.00, n = 20; Mann-Whitney U = 37, $P < 0.001$). *Poecilia latipinna* females were more aggressive in the presence of a male than *P. formosa* in tests with heterospecifics (*P. latipinna*: median = 2.00, n = 13 and *P. formosa*: median = 0.00, n = 13; Mann-Whitney U = 133, $P = 0.008$). These results are summarized in Figure 2.

Discussion.—Models for the coexistence of unisexual and bisexual species generally incorporate the assumption that males vary in quality or availability and, therefore, are a limiting resource for reproduction. If males are limiting, competitive females would have a reproductive advantage, and the frequency of competitive females would be expected to increase through sexual selection.

Studies of competition among females for mates have mainly been limited to species showing male parental care. Competition for mates among sex-role reversed species includes infanticide in wattled jacanas (Emlen et al., 1989), fighting and defensive posturing in Wilson's phalarope (Colwell and Oring, 1988), and bouts of fighting in green poison-dart frogs (Summers, 1989). Monogamous species such as lion tamarins (French and Inglett, 1989) and raptors (Olsen and Olsen, 1987) also have high male parental investments, and resident females aggressively repel other females. In monogamous pinyon jays, a species in which males are involved in care of the offspring (Johnson, 1988), females establish dominance hierarchies to determine access to mates.

In contrast, competition for mates in *P. latipinna* occurs in the absence of any parental investment. *Poecilia latipinna* and *P. formosa* aggressively compete for mates with conspecific and heterospecific females in a laboratory setting. A female's access to potential mates was increased through blocking which was the most common competitive behavior. The competitive behavior of *P. formosa* and *P. latipinna* in the laboratory suggests that males may be limiting in this population. Field studies involving another *P. formosa* complex indicate that sperm is not a limiting factor for reproduction (Monaco et al., 1981). It has not been determined whether *P. latipinna* males are scarce in this population.

Interspecific female competition for access to mates may also occur in other gynogenetic species. Dawley and Dawley (1986) have demonstrated that males in a bisexual/gynogenetic complex of salamanders discriminate against
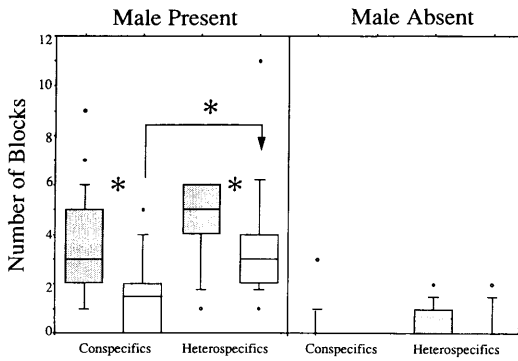
Fig. 1. The median number of blocks performed by *Poecilia latipinna* females □ and *P. formosa* □ in tests with conspecific females and with heterospecific females. Blocking is significantly less frequent in the absence of a male in all cases. Significant differences ($P < 0.05$) in the number of blocks between other groups is indicated by an asterisk. The box represents the median 50 percentile of the values; the center line is the median. The whiskers show the values that fall between the 10th and 90th percentiles. Outlying values are indicated by points.
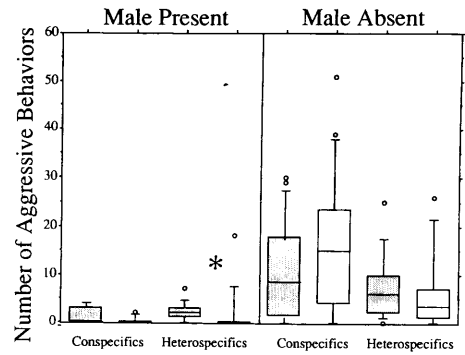

Fig. 2. The median number of aggressive acts, including biting, butting, and chasing, performed by *Poecilia latipinna* females □ and *P. formosa* □ in tests with conspecifics and heterospecifics. There are significantly more aggressive acts performed by females in tests without males except in the case of *P. latipinna* females in tests with heterospecifics. A significant difference in the level of aggression between *P. formosa* and *P. latipinna* females in tests with heterospecifics is indicated with an asterisk. The box represents the median 50 percentile of the values; the center line is the median. The whiskers show the values that fall between the 10th and 90th percentiles. Outlying values are indicated by points.

gynogens in laboratory tests. If males in this complex are scarce or vary in quality or desirability, females with a competitive advantage may increase in frequency.

Models for the existence of gynogenetic complexes have emphasized the role of male behavior in the maintenance of these populations. For example, male mating preference and social interactions may influence the relative mating success of conspecifics and gynogens. Our results suggest female behavior may also affect mating success. The presence of heterospecific females is associated with an increase in the amount of blocking by the gynogen and the number of gonopodial thrusts the male directs at the gynogen. Blocking may allow the gynogens to receive more matings by positioning themselves between a heterospecific female and a courting male. Females can block the access of the male to another female by actively swimming between a male and the female that he is approaching or swimming beside. Schlupp et al. (1991) have described this behavior as a female interrupting mating and also discussed the potential adaptive significance of this behavior.

Poecilia latipinna males tended to mate preferentially with conspecific females; however, *P. formosa* received more gonopodial thrusts in tests with *P. latipinna* females. Males in the presence of a preferred conspecific mate may be less discriminating than in tests where only gynogens were present. The correlation between blocking and gonopodial thrusts may be a result of

an increase in the male's mating behavior that would provide more opportunities for females to block. Thus, the gynogen may benefit from the presence of the *P. latipinna* females despite the ability of *P. latipinna* males to discriminate against them.

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