

Differences in Competitive Efficiency between a Sexual Parasite and Its Host Provide Insight into the Maintenance of a Sperm-Dependent Vertebrate Species

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ABSTRACT

Theory predicts that unisexual females have a two-fold reproductive advantage over sexual species because of the benefit of not producing males. Consequently, unisexual species should competitively exclude sexual species whenever their niches overlap substantially. When the unisexual species is sperm-dependent (gynogenetic), competitive exclusion of the host sperm donor can lead to extinction of both species. Thus, persistent gynogenetic-sexual species complexes are paradoxical. Models examining competition predict that gynogenetic species will persist if the sexually reproducing species are more efficient at competing for resources than the unisexual species. We tested these models using the persistent complex of the gynogenetic *Poecilia formosa* and its parental, sexual host, *Poecilia latipinna*. We examined the effect of conspecific and heterospecific females on foraging abilities of *P. latipinna* and *P. formosa*. When foraging with a conspecific, the foraging ability was similar between the two species, whereas the presence of *P. latipinna* negatively affected the foraging ability of the gynogenetic *P. formosa*. Conversely, the presence of *P. formosa* did not have any effect on the foraging ability of its sexual host. These results are consistent with previously proposed models on the maintenance of unisexual-bisexual mating systems and provide further explanation for the maintenance of unisexual, sperm-dependent species.

INTRODUCTION

Unisexual species have a two-fold reproductive advantage over sexual species because they do not incur the cost of producing males (Maynard Smith 1968, Williams 1975). Unisexual, sperm-dependent lineages are all-female hybrid lineages that reproduce by modified parthenogenesis (Dawley and Bogart 1989). One form of this type of reproduction is gynogenesis. Gynogenesis consists of the formation of a diploid or triploid egg (Balsano et al. 1972), which is genetically identical to the mother (but see Bogart and Licht 1986, Bogart 1989, Bogart et al. 1989, Nanda et al. 2007). Gynogens require sperm from a male of a closely related species to initiate cell division but incorporate none of the male's genes into their offspring's genome (Dawley and Bogart 1989). The offspring are therefore clones of their mothers. Gynogenetic females depend on sperm donors to reproduce and be maintained over time, but since no known fitness benefits are obtained by the males when mating with these unisexual females (but see Schlupp et al. 1994), gynogenetic lineages are considered sexual parasites and the sperm donors their hosts (Hubbs 1964, Schlupp 2005). Because the host species is usually one of the two or more parental species that contributed to the hybridization event that gave rise to the unisexual vertebrate lineage (Schlupp et al. 2002, Niemeitz et al. 2002), it is predicted that the parasite and the hosts have considerable niche overlap. Consequently the two-fold reproductive advantage of the unisexual females should cause them to competitively exclude their hosts and bring about their own extinction (Moore 1975), yet gynogenetic lineages continue to persist (Beukeboom and Vrijenhoek 1998).

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Several hypotheses have been proposed to explain the maintenance of sperm-dependent unisexual lineages, and they are not all necessarily mutually exclusive because they focus on different aspects of the life history of the unisexual lineage. Vrijenhoek (1984), Schley et al. (2004), and Kokko et al. (2008) all proposed ecological mechanisms that could aid the coexistence between a sperm-dependent unisexual lineage and its host such as niche differentiation (frozen niche variation hypothesis), differential competitive abilities, or spatial structure. Additionally, Moore and McKay (1971), Kaweki (1989), Lima et al. (1996), and Heubel et al. (2009) all proposed models based on how sexual selection and the inability to properly discriminate against heterospecific females by males of the host species may affect coexistence in the long term.

Evidence supporting the frozen niche variation hypothesis has been found in the *Poeciliopsis monacha-lucida* complex (Vrijenhoek 1998), while the other ecological hypotheses and models still have not been tested. Schley et al. (2004) showed that coexistence between unisexual lineages and their hosts is possible when the sexual hosts are better competitors than the unisexual females. Similarly, Doncaster et al. (2000) proposed that coexistence between a simple parthenogen and a sexually reproducing species with high niche overlap is possible if the effect that the unisexual species has on the exploitative abilities of the sexual species is less than the effect that individuals of the sexual species have among themselves. Both models suggest that the sexually reproducing species need to be better at competing for resources than the asexually reproducing species.

Some studies of competition between closely related parthenogenetic species and sexual species (Innes et al. 2000, Tagg et al. 2005) provide support for the Doncaster et al. (2000) model, but parthenogens do not depend on closely related competing species for their maintenance over time. Thus, the competitive exclusion of the sexual species will not be detrimental to the parthenogenetic species. Competitively excluding a host is, on the contrary, extremely detrimental for sperm parasites such as gynogenetic species, unless the two species follow metapopulation dynamics (Kokko et al. 2008). The focus of this study was to test the predictions of the Schley et al. (2004) model by examining if a gynogenetic species is a less efficient competitor than its sexual host.

A good system to test whether unisexual females are less competitive than their sexual hosts is the mating complex consisting of *Poecilia formosa* and *Poecilia latipinna*. Both fishes belong to the internally-fertilizing, livebearing family Poeciliidae and lack parental care. *Poecilia formosa*, the Amazon molly, is a gynogenetic female species that arose from a single hybridization event between *Poecilia mexicana* and *P. latipinna*, or an extinct ancestor of the latter about 100,000 years ago (Avisé et al. 1991, Schartl et al. 1995). The natural range of *P. formosa* spans from the Rio Tuxpan in Mexico to southern Texas (Drewry et al. 1958, Hubbs et al. 1991, Schlupp 2002). The range of *P. latipinna*, the sailfin molly, extends from the region of Tampico in Mexico to South Carolina (Miller 1983). *Poecilia latipinna* and *P. formosa* are sympatric from central Mexico to central Texas (introduced populations) and in these regions are mostly found in brackish waters along the Gulf Coast. In this unisexual-bisexual mating system, *P. formosa* and *P. latipinna* swim in mixed species shoals and probably use very similar niches (Schlupp and Ryan 1996, C. Gabor. pers. obs.). However, the finding that female *P. formosa* are larger than female *P. latipinna* when collected from the field (Gumm and Gabor 2005, Gabor and Aspbury 2008, Heubel and Schlupp 2008, Riesch et al. 2008) suggests that either the former is more efficient in transforming food into energy required for growth or that *P. formosa* does not strongly compete with its host for resources. Balsano et al. (1985) found that *P. formosa* is more abundant downstream, while the other host female (*P. mexicana*) is more abundant in headwaters, suggesting that these two species show niche differentiation. Nonetheless, Heubel and Plath (2008) found that *P. formosa* forages less when in the presence of female *P. mexicana* than with conspecifics. Schlupp

et al. (2001), on the other hand, found no significant difference in the time female *P. latipinna* forage when paired with *P. formosa* versus conspecific females, but they did not examine the foraging rates of *P. formosa* when tested with conspecifics or with *P. latipinna*.

In this study we examined foraging competition within and between female *P. formosa* and *P. latipinna* to provide insights into a potential mechanism that may contribute to the evolutionary maintenance of *P. formosa*.

METHODS AND MATERIALS

We tested female *P. formosa* and *P. latipinna* from a sympatric population in the San Marcos River near Martindale, Texas (field caught in 2008; 29°91'N, 97°74' W). Testing was conducted in March and April 2009. Fishes were maintained in large outdoor tanks (1,800 L) and moved into the laboratory at least two weeks prior to testing. Females were placed in 35-L mixed-species tanks in the laboratory. The fishes were maintained on a 14:10 h light:dark cycle using full spectrum UV lighting and at a constant temperature (25° C). They were fed Purina AquaMax 200 food twice a day, which was supplemented with live brine shrimp.

Fishes were tested under the following treatments (N = 13 pairs/treatment): 1) two female *P. latipinna*- intraspecific competition, 2) two female *P. formosa* - intraspecific competition, and 3) one female *P. latipinna* and one female *P. formosa* - interspecific competition. We used size-matched females (± 2 mm), and each fish was tested only once in any paired treatment. Four treatments were randomly assigned each testing day. The standard length of each fish was recorded prior to testing, and there was no significant difference in size between females of the two species across all treatments ($t_{38} = -1.29$, $P = 0.200$). The test system consisted of three parallel abutting 21-L aquaria filled with approximately 17 L of dechlorinated tap water and lined with a gravel substrate. The central tank was continually occupied by four *P. latipinna* of mixed sex (at least one male), as Padur et al. (2009) showed that fish spend more time feeding in the presence of an "audience" of conspecifics. By using the same audience species each time, any differences could be attributed to the treatment and not to the audience. Each lateral tank was a separate testing unit, but they shared the same central tank fish. Subject females were placed in either of the lateral testing aquaria. Subject females were only able to interact visually with the four *P. latipinna* in the central tank. A white curtain with holes for viewing was erected between the fish and the observer to reduce observation effects. Water was changed between testing sessions.

Two subject females were moved into each test aquarium 24 h before testing to acclimate to the new environment. Fishes were not fed during the acclimation period. To begin testing, a small amount of Purina AquaMax 200 pellet food was dropped into the central tank by hand. The food naturally spread uniformly over the surface of the water and then slowly fell through the water column. Within 2 min of feeding the central tank, the subject fish in one of the outer testing tanks were fed the same amount of pellet food. After the first piece of food was consumed by one of the subject females, the number of foraging events (pecking at food pellets) and nips (aggressive displays) was recorded using Jwatcher (Version 0.9 D. Blumstein, UCLA) for each subject fish separately during a 10-min trial. Next, food was dropped into the other outer testing tank, and foraging and nips were recorded for 10 min for this set of subject females. Both *P. formosa* and *P. latipinna* made conspicuous lunges during foraging events, which facilitated the tallying process.

Statistical analyses

We first tested whether *P. latipinna* and *P. formosa* differed in overall foraging rates when paired with conspecific females. We averaged foraging events for each pair of

females and then compared mean foraging events between *P. latipinna* and *P. formosa* in intraspecific treatments (1 and 2) using a Mann-Whitney *U* test. We next tested whether foraging rates of each species differed based on being paired with a conspecific vs. heterospecific female. We randomly chose one female from each intraspecific pair (treatments 1 and 2) and compared mean foraging attempts between intraspecific and interspecific (treatment 3) pair treatments within each species using a Mann-Whitney *U* test. We also performed a Wilcoxon sign rank test to compare the means of *P. latipinna* and *P. formosa* when tested in the interspecific treatment (treatment 3). We chose not to use corrections for multiple comparisons (e.g., Bonferroni) because in the field of behavioral ecology statistical power is already low and the correction would greatly increase the probability of Type II errors (Nakagawa 2004). We used non-parametric analyses because the variances of the datasets were not equal.

RESULTS

Not enough aggressive displays (nips), either aimed at conspecific or heterospecific female, were recorded for these data to be analyzed. There was no significant difference in the mean number of foraging events between *P. latipinna* and *P. formosa* in intraspecific pairing treatments (1 and 2) (Mann-Whitney *U* test; $Z_{25} = -1.795$, $P = 0.073$; Fig. 1a). There was no significant difference in the mean number of foraging events of female *P. latipinna* when tested in the intraspecific treatment 1 versus in the interspecific treatment 3 (Wilcoxon sign rank test; $Z_{25} = 0.026$, $P = 0.979$; Fig. 1b). For *P. formosa*, the number of foraging events was significantly lower in the interspecific pairing treatment 3 than in the intraspecific pairing treatment 2 (Wilcoxon sign rank test; $Z_{25} = 2.796$; $P = 0.005$; Fig. 1c). No significant differences were found between the two species when foraging with heterospecific females only in treatment 3 (Mann-Whitney *U* test; $Z_{25} = 1.720$; $P = 0.085$; *P. formosa* (mean \pm s.e.) = 20.30 ± 5.78 and *P. latipinna* = 39.07 ± 8.28).

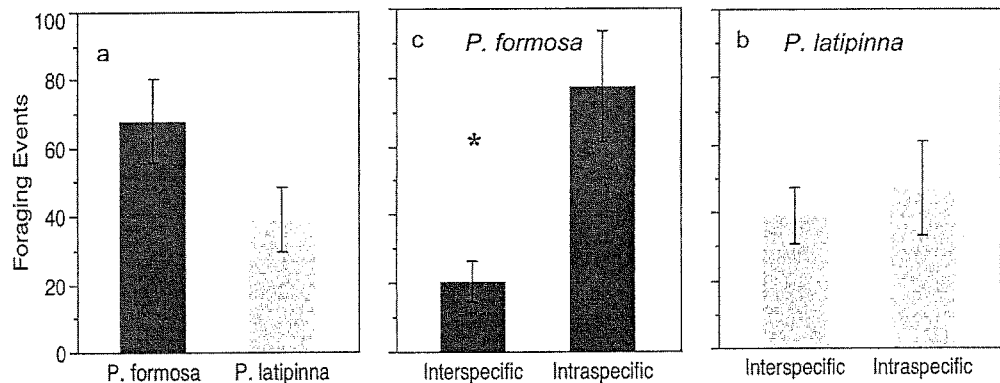


Figure 1. Mean number of foraging events \pm SE for: (a) treatment 1 and 2 when *P. latipinna* and *P. formosa* only experienced intraspecific competition, (b) treatment 1 and 3 for *P. latipinna* when they experienced intra- versus inter-specific competition, and (c) treatment 2 and 3 for *P. formosa* when they experienced intra- versus inter-specific competition. Note that to obtain the means of graph (a) we averaged foraging events for each pair of females in treatments 1 and 2 and then compared mean foraging events; therefore, each replicate was used as a data point. To obtain the averages for the intraspecific treatments in (b) and (c), we randomly selected one female from each replicate in treatment 1 and 2 to compare to the 13 females of each species tested in treatment 3. Hence in this case one female per replicate in treatments 1 and 2 was randomly selected as a data point.

DISCUSSION

We found that the unisexual *P. formosa* decreased foraging in the presence of female *P. latipinna* but not in the presence of conspecific females. Furthermore, the foraging activity of *P. latipinna* was not affected by the presence of the gynogenetic species. This provides evidence that the presence of the sexual host negatively affects the foraging ability of the unisexual species, suggesting that the host is a better competitor than the gynogen when found in mixed shoals but perhaps not overall. This statement is further supported by the observation that *P. formosa* did not forage less than *P. latipinna* when the two were tested with only conspecifics.

Schlupp et al. (2001) found that female *P. latipinna* spent more time feeding in the presence of *P. formosa* or conspecific females than with conspecific males. Our study examined the rate *P. formosa* foraged with conspecifics and found that it foraged at a higher rate with conspecifics than with *P. latipinna*. Heubel and Plath (2008) found that *P. formosa* spent less time feeding when with conspecifics than did female *P. mexicana* and that the presence of males resulted in females of both species feeding less and starting to feed later. It is difficult, however, to compare feeding times between their experiment and ours as the mean time *P. formosa* spent foraging was not presented in Heubel and Plath (2008). It is possible that *P. mexicana* forages at a higher rate than both *P. latipinna* and *P. formosa* and that the rate *P. formosa* fed was comparable to that in our study.

Our results provide some empirical support for the Schley et al. (2004) and Doncaster et al. (2000) models. However, it is important to recognize that the theoretical two-fold reproductive advantage of *P. formosa* may be limited by a combination of factors that play in concert. For example, male *P. latipinna* prefer to associate and mate with conspecific females over female *P. formosa* and prime fewer sperm for *P. formosa*, which limits the reproductive output of the gynogen (Gabor and Ryan 2001, Aspbury and Gabor 2004, Riesch et al. 2008). Some evidence suggests that *P. formosa* does not have a higher reproductive output than its host species. Hubbs (1964) found that *P. formosa* carried a higher proportion of unfertilized eggs than sexual *P. latipinna*, and *P. formosa* and *P. latipinna* appear to have equal fecundities when sperm is not limiting (Heubel 2009). Additionally, field collections and embryo counts show that *P. formosa* and *P. mexicana* (the other main sperm host species) have equal reproductive outputs (Balsano et al. 1985).

Tobler and Schlupp (2010) found that *P. formosa* had lower tolerance to stressful food conditions than *P. latipinna*. We found that *P. formosa* has a lower foraging rate than one of the host species. These results combined suggest that food limitation and the superior exploitative ability of the host may act together to keep the reproductive rate of the gynogenetic species low enough to allow for coexistence.

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