Predation as a Potential Mechanism Allowing Asexual Mollies to Invade Sexual Mollies

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Predation is one important factor structuring natural freshwater communities, but do predators play an important role in the ongoing coexistence of *Poecilia formosa* (*P. formosa*) and *Poecilia latipinna* (*P. latipinna*)? *Poecilia. formosa* is a gynogenetic fish that arose in a single hybridization event of *Poecilia mexicana* (*P. mexicana*) and *P. latipinna* about 100.000 years ago. *Poecilia formosa* requires sperm to trigger embryogenesis, and consequently has to coexist with at least one sperm-donor. In Texas, *P. latipinna* is the host species. It is not clear so far what stabilizes the coexistence of gynogenetic species and their hosts. In the present study we investigated whether predators might play a role in stabilizing this system by consuming more *P. formosa* than *P. latipinna*.

Adult females of both species were confronted with *Micropterus salmoides* (*M. salmoides*), *Lepomis cyanellus* (*L. cyanellus*), *Cichlasoma cyanoguttatum* (*C. cyanoguttatum*) and *Oreochromis aureus* (*O. aureus*) as potential predators. Out of these species, only *M. salmoides* was an effective predator and caught significantly more *P. latipinna* than *P. formosa*. Given the estimated age of their coexistence this disadvantage seems not to hinder their coexistence. But it might be speculated that this is one ecological factor which allowed *P. formosa* to invade into populations of its hosts in the first place. Other factors, however, must balance the reproductive advantage of *P. formosa*. © 2007 *Oklahoma Academy of Science.*

INTRODUCTION

Predation is one of the most important factors to structure natural freshwater communities (Jackson et al., 2001) through two main effects. Mortality is its direct effect, but predation acts also indirectly as potential prey fishes try to reduce predation risks. The most important aspect of the indirect effect is probably the conflict of energy gain and predation risk (Houston et al., 1993; Brown, 1999). Higher predation risk induces shifts in habitat usage (Schlosser, 1987; Chick & Mcivor, 1997) or hinders movement to some degree (Fraser et al., 1995; Fraser et al., 2006). Even feeding habits like night feeding are prevented (Fraser et al., 2004). In addition, predation has also considerable influence on mate decisions by selecting less conspicuous males under predation risk (Godin & Briggs, 1996). Furthermore, mating behavior as male-male interactions (Kelly & Godin, 2001) and courting (Evans et al., 2004) are reduced under high predation regimes as shown for guppies. There are also indications that predation can change the life history of fishes by altering the age and/or size when individuals mature (Rodd and Reznick 1997; Johansson et al. 2004).

In the present study we address the direct effects of mortality in an unusual mating system. In this particular system the *Poecilia formosa* (*P. formosa*) is an all female, gynogenetic species, which originated from a single hybridization event of a *Poecilia mexicana* (*P. mexicana*) like female and a *Poecilia latipinna* (*P. latipinna*) like male ancestor between 10,000 and 100,000 years ago (Avise et al., 1991; Schartl et al., 1995; Tiedemann et al., 2005). As a member of the Poeciliidae, *P. formosa* depend on internal fertilization (e.g., it needs intimate contact with a sperm donor), from *P. latipinna*, *P. mexicana* (Schlupp et al., 2002; Schlupp, 2005) or *P. latipunctata* (Niemeitz et al., 2002). Although *P. formosa* and *P. latipinna* look relatively similar to the human eye, males are able to discriminate between both species (Schlupp et al., 1998; Dries, 2003; Gabor et al., 2005). This raises two questions: 1) Are predators able to distinguish between both species? 2) Do predators prefer one species over the other?

One of the unsolved questions in this and other asexual / sexual mating systems is how the two different types of females can coexist. The asexual species has a two-fold advantage – assuming that everything else is equal – over the sexual species, because they do not produce male offspring (Maynard Smith, 1978). Asexual species should replace the sexual species after a few generations, which would eliminate the sperm donor for them. This situation would not be stable in the long run and there could be mechanisms in place that selectively reduce the fitness of *P. formosa*. A potential mechanism contributing to stability would be if *P. formosa* would be taken more often by predators. This could be either because of predator preferences or because of inferior anti-predator behavior. To test if differential mortality occurs, mixed shoals of adult females of both species were confronted with one individual of four different potential fish predators in wadding pools. Survivors were counted after 24 hours and 72 hours.

MATERIALS AND METHODS

a) Fishes

For the experiment, four individuals of each supposed predatory species, namely *Micropterus salmoides* (*M. salmoides*) (SL (mean ± SD): 135±6mm), *Lepomis cyanellus* (*L. cyanellus*) (SL (mean ± SD): 148±10mm), *Cichlasoma cyanoguttatum* (*C. cyanoguttatum*) (SL (mean ± SD): 90±9 mm) and *Oreochromis aureus* (*O. aureus*) (SL (mean ± SD): 100±6 mm) were used. All four species can be found together with *P. formosa* and *P. latipinna* at the collection sites in Texas. Not all predators used were collected from these collection sites because not all individual predators met the size requirements. Hence, fish from several other sites were used. They were housed in large tanks in fish holding facilities of the University of Oklahoma and were fed once a week with other fish including *Gambusia* spec, *Jordanella floridae*, *Heterandia formosa* and few *P. latipinna*.

b) Experimental Setup

Sixteen wading pools (109cm diameter, 10cm deep) were set up in a greenhouse at the Aquatic Research Facility of the University of Oklahoma, Norman Oklahoma. Each pool was set up with cover consisting of 2cm thick fine sand underground, two bricks with bores of a rather small diameter (roughly 4cm), four plastic-tubes (diameter 7cm, length 20-25cm) and algae (a patch with a diameter of roughly 25cm) were used as test arenas for individual predatory fishes. The cover was arranged in a quadrate with an edge length of roughly 45cm, whereas the same parts were arranged diagonal to each other, with two plastic-tubes lying crossed over each other. To prevent the fishes from jumping out of the pool, while allowing them to use jumps as escape behavior (Witte & Schlupp, 2002), the water level was maintained at 2cm below the rim and the pools were covered with a net.

For each predatory individual, five *P. latipinna* and five *P. formosa* were used as potential prey. These fishes were caught at four different collection sites in 2006 and 2007. Most *P. latipinna* and *P. formosa* were collected in a lake, which is part of the oxbow lake system of the Rio Grande, near Brownsville, South Texas. The other *P. formosa* were caught in a side branch of the

San Marcos River near Martindale, Central Texas. And the rest of *P. latipinna* originated a few kilometers downstream of the spring at County Road 101 near Martindale in the San Marcos River or from the springhead of the Comal River near New Braunfels, both sites are located in Central Texas. The five conspecific individuals of the ten potential prey fishes in each pool originated from the same collection site.

After measuring their standard length, potential prey-fish were allowed to habituate to the pools for two days before introducing the supposed predators. After this habituation phase, one predatory fish was haphazardly added to each pool. The predatory fish were not fed for the two days prior to the experiment.

After 24 hours survivors were counted and measured for the first time to be sure that all predatory fish had the opportunity to eat in their preferred light intensity (McMahon & Holanov, 1995). After this first measurement the experiment was run for another 48 hours before it was terminated.

c) Data analysis

For all statistical analysis SPSS version 12 was used. First it was evaluated if each tested predatory species had a preference for either of the two *Poecilia* species using paired T-tests. At this point it should be noted, that every consumed individual changes the ratio of the remaining fish. If one of the two species is preferred by the predator, or inferior in escaping, it should still be preyed upon despite the fact that the other species is more frequent. Additionally, a univariate ANOVA for each predatory species was run to determine if there is a preference to for larger individuals of both *Poecilia* species using standard length (SL) as response variable and consumed (yes or no) and species as fixed factors. Finally, a univariate ANOVA using SOP-values (strength of preference: (number of eaten *P. latipinna* – number of eaten *P. formosa*) / total eaten fish) should be conducted to test if differences between the predatory fish according to the preferences of either *P. latipinna* or *P. formosa* were present, while the p-values were Bonferroni (α'=0,05/2) corrected.

RESULTS

Since no fish were preyed upon by *O. aureus* or *C. cyanoguttatum* and only one *P. formosa* was consumed by one *L. cyanellus* after 24 hours no preferences for either *Poecilia*-species could be found for these species. Furthermore, this renders a comparison of differences between the used predatory species unnecessary.

For unknown reasons two *P. latipinna* died in two different pools with *C. cyanoguttatum*. Furthermore, in one pool with *O. aureus* one *P. formosa* as well as one *P. latipinna* died. All these individuals were found dead after 24 hours. However, they all showed no obvious injuries and therefore, their death may or may not have been caused by the presence of the predatory fish and will not be considered further. Additionally, some pools accidental *Poecillia*-offspring could be found. Two of the pools with *C. cyanoguttatum* contained *Poecillia*-offspring after 24 hours. After another 48 hours they were all eaten. After 24 hours fry were also found in two pools with *O. aureus* and in one pool with *L. cyanellus*, and at least some of them were still alive at the end of the experiment.

M. salmoides consumed more fish. The data suggest a symmetrical distribution with no outliers, thus a paired T-test is appropriate. After 24 hours only 0, 0, 0, 1 *P. formosa*, but 0, 1, 3 and 3 *P. latipinna* were devoured in the four pools respectively. However, this is not statistically significant (paired T-test, t=-2.324, n=4, p=0.103). After an additional 48 hours 1, 2, 1 and 2 *P. formosa* and 2, 4, 2 and 4 *P. latipinna* were preyed upon, resulting in a significant preference for *P. latipinna* (paired T-test, t=-5.196, n=4, p=0.014). This is accompanied by an increase of taken *P. formosa* if less *P. latipinna* are left (paired sample correlation, correlation=1, n=4, p<0.0005).

The assumptions of normality and homogeneity of variances for the ANOVA testing for preferences of smaller or larger individuals by *M. salmoides* were met. *M. salmoides* preyed upon significantly larger individuals of *P. formosa* (SL (mean ± SD) *P. formosa* consumed: 37±3mm and SL (mean ± SD) not taken: 32±4mm) as it was also the case for *P. latipinna* (SL (mean ± SD) *P. latipinna* consumed: 32±5mm and SL (mean ± SD) not taken 29±4mm; ANOVA, $F(1)=9.039$, $n=40$, $p=0.005$). The difference in standard length of taken and not taken individuals of both prey species is mostly caused by the significant difference of 3mm between the mean standard length of *P. latipinna* (SL (mean ± SD) 31±4mm) and *P. formosa* (SL (mean ± SD) 34±4mm) tested with *M. salmoides* (T-test, $t=-3.073$, $n=40$, $p=0.045$).

DISCUSSION

Only *M. salmoides* (not *O. aureus*, *C. cyanoguttatum* or *L. cyanellus*), was an effective predator on adult mollies. All four tested individuals consumed more *P. latipinna* than *P. formosa*, although *M. salmoides* preferred generally larger individuals and the *P. formosa* tested were slightly larger than *P. latipinna*. Therefore, *M. salmoides* did not only choose larger individuals as previously shown for herons preying on *P. latipinna* (Trexler et al., 1994) and for pike cichlid (*Crenicichla saxatilis*) preying on guppies (*Poecilia reticulata*) (Johansson et al., 2004), but for some reason caught more *P. latipinna* despite its smaller size in our experiment. Thus, the association of *P. latipinna* individuals with larger individuals could reflect predator avoidance (Gabor, 1999). Most interestingly, the outcome of our experiment did not reveal the predicted advantage for the sexual species, but indicated the opposite, namely an advantage for the asexual *P. formosa*. This may explain the correlation of relative higher numbers of predators with an increased proportion of *P. formosa* found in several populations in Texas (Heubel, 2004).

Unfortunately the mechanism leading to our unexpected result is not clear because we did not directly observe the interactions. The following types of behavior of prey to prevent capture by predators are frequently mentioned. Predator inspection is used in order to assess the actual risk of the present predator (Fishman, 1999) including predator attack motivation and size (Smith & Belk, 2001). Fast start performance is important for the escape of a predator attack (Law & Blake, 1996; Cameron et al., 2004; Langerhans et al., 2004; Langerhans et al., 2005; Walker et al., 2005). Shoaling can aid in detection of predators and can reduce the chance of single individuals becoming the target of an attack (Weetman et al., 1998, Weetman et al., 1999, Doucette et al., 2004). Furthermore, the positioning of prey fish in the water column as well as jumping out of the sight of the predators can influence the outcome of an attack (Christensen, 1996).

Since *P. latipinna* and *P. formosa* form shoals together (Schlupp & Ryan, 1996), *P. formosa* could leave risky tasks like predator inspection to *P. latipinna*, but this is theoretically no stable situation (Milinski, 1993). In our experiment the dimensions of the pools itself could prevent either species from effective shoaling, and if *P. latipinna* relies more strongly on this, it could be a disadvantage for them. But this limitation is not present in the field where a correlation of reduced proportions of *P. latipinna* and higher relative numbers of predators was found (Heubel, 2004). As jumps were allowed in this experiment and the wading pools were not deep, the positioning of prey fish and jumps should not play a role. The last anti-predator type of behavior mentioned above is the possibility of different fast start performances. This seems possible given the hybrid origin of *P. formosa* and the slight differences between both parental species. *P. formosa* and *P. mexicana* appear to be a little less high bodied and relatively elongated, which was connected to higher fast start performance in *G. affinis* (Langerhans et al., 2005). Furthermore, it was shown for pregnant guppies that pregnancy, partly through the wider body but also through higher weight, reduces fast start performances (Cameron et al., 2004) and *P. latipinna* often look wider if viewed from above. Future analysis is needed to show if there is a difference in fast-start performances between *P. formosa* and *P. latipinna*.

Apart from this, some components could also influence the behavior of the predators. *M. salmoides* was only familiar with *P. latipinna* as prey, even though this was only the minority of the diet offered prior to the experiment. Studies showed that predators handle familiar prey better (Croy & Hughes, 1991a; Croy & Hughes, 1991b). This was more effective if only pure diets were used, which was not the case in this study. Another study referred to search images which should select for example in guppies the most frequent phenotype, but this should favor the sexual species because of a greater variance of phenotypes (Punzalan et al., 2005). Furthermore, predators could exhibit an innate aversion towards unfamiliar prey as it was shown for example in birds (Marples et al., 1998), but it seems unlikely that the difference between *P. formosa* and *P. latipinna* is large enough for that.

Interestingly, only *M. salmoides* caught adult mollies despite small sample sizes underscoring their potential ecological importance. However, additional offspring occurred accidentally, but unfortunately fry could remain undetected if already devoured before inspection after 24 hours and 72 hours. Maybe some of the tested predators prefer fry and thus did not prey upon adults, but this can only remain speculative.

Fish usually shift their diets during their growth, as they are at first strongly gape limited (Wootton, 1998). Different piscivorous and omnivorous fish, that seldom consume fish, start at different points during their ontogeny to eat fish (Christensen & Moore, 2007). This is usually correlated with body length. Omnivorous fish could start consuming fish very late, like yellow perch, which can switch as late as up to 3 years of age (Graeb et al., 2005). For largemouth bass the switch in the diet, measured as behavioral reaction on familiar alarm pheromones, is reported to happen around 50mm SL and for green sunfish at a size above 90mm SL (Golub & Brown, 2003). Therefore, individuals of both species used in this study should be able to consume fish. But the individuals of *C. cyanoguttatum* might be too small to eat adult mollies as it might be true for the used *O. aureus*.

It is unclear if the diet of *O. aureus* also includes fish (Gu et al., 1997). It seems more likely that *O. aureus* could have an impact on mollies due to their influence on the habitat: like higher turbidity and lower structuring (Noble, 1989). Furthermore, morphology predicts that *M. salmoides* is best suited for catching elusive prey like fish (Nyberg, 1971; Norton & Brainerd, 1993; Carroll et al., 2004), but to some point behavior might compensate this (Norton, 1991). Therefore, it was expected that *M. salmoides* would be the most effective predatory species tested.

Another problem might be that the predatory fish were fed 2 days before the experiment, but at least for *M. salmoides* studies showed that these are opportunistic feeders (Essington et al., 2000; Sass & Motta, 2002).

Information on predation on juveniles and the testing of other predators, including avian predators and snakes, are needed in order to fully understand the role of predation in this mating system, but this study showed that at least adult *P. latipinna* females have a disadvantage regarding predation. This might be one ecological factor allowing the gynogens to invade populations of the sexual species. Clearly our present study is only a starting point for future investigations.

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