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Body Size Dependent Male Sexual Behavior in a Natural Population of Sailfin Mollies (*Poecilia latipinna*)

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ABSTRACT.—Male sailfin mollies, *Poecilia latipinna*, exhibit alternative mating strategies that are correlated with body size. Larger males court females and often prevent smaller males from accessing females, while smaller males often forcefully inseminate females. This pattern is well documented in the laboratory but has not been studied thoroughly in the field, where patterns of mating behavior are known to vary among natural populations. In an observational study of a *P. latipinna* population, we measured the proportion of time males from three size classes (small, intermediate, and large) spent exhibiting five mating behaviors: courting, thrusting, nibbling, chasing other males away, and being chased. We predicted that large males would spend more time courting females and chasing away other males, while small males would spend more time thrusting, nibbling, and being chased by other males. We also predicted that intermediate males would behave intermediately. Our findings partially supported those of previous laboratory studies: small males spent more time attempting to forcefully inseminate females but large males did not spend more time courting. Courtship displays were rare in our observations. Large males did spend more time chasing away other males however. Intermediate males behaved intermediately in some cases but also exhibited mating behavior typically characteristic of large males.

INTRODUCTION

In populations where a small number of males secure a disproportionate number of matings, sexual selection theory predicts phenotypic divergence and the evolution of alternative reproductive phenotypes (Darwin, 1871). Adaptive variation in reproductive phenotypes has been documented in numerous taxa; but there are relatively few examples of alternative reproductive strategies, which implies genetic polymorphism underlying the alternative reproductive phenotypes, with equal fitness for the alternative phenotypes (Gross, 1996). Individual males within populations are expected to exhibit different mating tactics based on their phenotypes (and underlying genotypes) for traits such as body size or color (*e.g.*, marine isopods, *Paracerceis sculpta*, Schuster and Wade, 1991; swordtail fish, *Xiphophorus nigrensis*, Ryan *et al.*, 1992; ruffs, *Philomachus pugnax*, Lank *et al.*, 1992). While theory on the evolution of alternative mating strategies has traditionally focused on interactions between males that result in a dichotomous framework of two alternative behaviors, more recent findings suggest that alternative reproductive strategies may include interactions between the sexes (Alonzo and Warner, 2000) and may expand to include more than two alternative behavioral types (Alonzo and Calsbeek, 2010). Additionally, variation in female preference (Rios-Cardenas *et al.*, 2007), sperm competition (Aspbury, 2007), sex ratio variation (Magellen and Magurran, 2007), and numerous other factors (*e.g.*, Hankison and Ptacek, 2007; Hurtado-Gonzales and Uy, 2009; Plath *et al.*, 2007; Ptacek *et al.*, 2005) have been shown to affect the maintenance and evolution of alternative mating strategies. However, the precise mechanism and maintenance of alternative mating strategies remains unclear in many systems (reviewed in Henson and Warner, 1997).

One element of uncertainty stems from the inherent variation in behavioral diversity among natural populations. Such diversity can result from variation in allele frequencies, environmental differences in behavior or environmental influences leading to phenotypic

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plasticity. Regardless of the cause, natural populations differ with regard to the distribution and prevalence of alternative mating strategies (e.g., Farr *et al.*, 1986). Additionally, quantitative studies observing alternative mating strategies in the field are far more limited than controlled laboratory experiments. While the precise controls available in the laboratory setting are often important and vital to behavioral research, it is important to validate the studies in the field. Thus, additional studies documenting condition-dependent reproductive behavior in the field are needed both to supplement and compare to extant laboratory data and to evaluate differences among natural populations.

Sailfin mollies, *Poecilia latipinna*, are one of several species of livebearing fish that exhibit male alternative reproductive strategies (reviewed in Farr, 1989). Sexual behavior in *P. latipinna* males is strongly correlated with male size. Like other poeciliids, male size is fixed at maturity (Trexler *et al.*, 1990) and likely has a genetic basis, as variation in size at maturity is hypothesized to be based primarily on a series of Y-linked alleles that control the timing of maturation and a male's final size (Travis and Woodward, 1989; Travis, 1994), as has been demonstrated in other poeciliid species (e.g., *Xiphophorus maculatus*: Kallman and Borkowski, 1978). As male body size increases, rates of courtship and defensive displays increase while rates of forced insemination attempts decrease (Farr *et al.*, 1986; Travis and Woodward, 1989). Smaller males mature earlier (30 d) than larger males (60 d) and thus can begin mating sooner (Travis, 1994). The patterns of size and behavior in *P. latipinna* highlight the species as an example of a stable continuum of reproductive strategies (Travis and Woodward, 1989).

Poecilia latipinna is an excellent system for examining male mating strategies because they exhibit phenomenal variation in size, both within and among populations (Farr *et al.*, 1986). However, some genetic control of behavior in *P. latipinna* may be independent of genetic variation for size (Travis, 1994), thus suggesting more nuanced mechanisms controlling size and behavioral rates among *P. latipinna* populations. Although size-dependent mating behavior has been well documented in the lab, studies in the field are lacking but are important for establishing this pattern in natural populations and better understanding the precise mechanisms that control it.

Poecilia latipinna is a widely distributed and geographically adaptable species, native to brackish waters along the southeastern coastline of North America but capable of tolerating a wide range of water conditions, and has been introduced to locations around the world (Al-Akel *et al.*, 2010). We investigated size-dependent male reproductive strategies in *P. latipinna* by testing the laboratory results of Travis and Woodward (1989) using a population occurring in Hays Co. Spring Lake, Texas (29.893°N, 97.931°W). We tested the following predictions: (1) large males will spend more time courting, (2) small males will spend more time thrusting, (3) intermediate males will behave intermediately, and (4) large males will chase other males more often than intermediate or small males.

METHODS

SEXUAL BEHAVIOR IN POECILIA LATIPINNA

Mature male sailfin mollies have a modified anal fin called a gonopodium, which they insert into the gonopore of a female during a mating attempt. A successful mating attempt results in the transfer of packets of sperm (spermatozeugmata) (Travis, 1989). Three characteristic sexual behaviors occur in males of *Poecilia latipinna*, the first of which is a courtship display. During courtship, a male raises his dorsal fin and orients toward the female, making a marked display. Females signal receptivity and thus gain attention from males in the form of courtship displays (Farr and Travis, 1986). The second behavior is

gonopodial thrusting, which is a clear attempt at insemination of the female. The third characteristic behavior, gonoporal nibbling, is not as clearly understood but may be related to male assessment of female reproductive state (Travis and Woodward, 1989). Male *P. latipinna* also defend females and frequently chase away other males. We made observations of males engaged in five behaviors related to mating (courtship, thrusting, nibbling, chase away, and being chased) in a natural population.

FIELD OBSERVATIONS

Field observations were made from 27 Jun. to 11 Jul. 2001, in Spring Lake at the headwaters of the San Marcos River. Spring Lake is a constant-temperature spring in southern temperate North America. *Poecilia latipinna* was introduced to Spring Lake during the 1930s (Brown, 1953). These waters are constant in flow, with stable nutrient availability and chemical properties (Groeger *et al.*, 1997). All observations were made between 0900 and 1400 h.

We observed focal males from the shore, switching observations of small, intermediate, and large males throughout the day. We did not mark males so, therefore, we assumed that by moving to a new location, we were observing different males. This method follows closely with the protocols established by Morris *et al.* (1992). Focal observations were made on 22 small, 16 intermediate, and 15 large males.

To establish body size ranges within the Spring Lake population, we first measured 28 male fish from the same population using digital calipers in the lab. The mean standard length (SL) of measured males was $29.53 \text{ mm} \pm 7.60 \text{ sd}$. Therefore, we categorized males at or above 1 sd above the mean as large, males within 1 sd of the mean as intermediate, and males at or below 1 sd below the mean as small. A similar size distribution has been confirmed in a subsequent study using a much larger sample of males with ready sperm collected from the same population during the mating season ($n = 142$; mean SL: $27.77 \text{ mm} \pm 5.90 \text{ sd}$; Robinson *et al.*, 2011). Male sizes in the field were visually estimated based on predetermined size ranges as measured in the lab.

Before behavioral observations commenced, specific observational sites were established. Ten sites of known *Poecilia latipinna* occurrence were selected. Care was taken to ensure minimal disturbance to fish during observations. An observational site was defined as an area that could be visually separated from another area using specific landmarks (*e.g.*, trees, water fountains, aquatic plants, piers).

Observations began when a male with secondary sexual characteristics was seen in the area or when a small male either thrust or nibbled at a female (small males do not possess colorful fins and thus are difficult to sex). We observed each male for up to 3 min, during which time most focal males exhibited some kind of interaction with other males and/or females. We recorded the proportion of time each focal male spent engaging in each of 5 behavioral categories: courting, thrusting, nibbling, chasing another male away, and being chased away. We then ranked for each male the frequency of time spent in each behavior. We examined if there was variation across male size classes in the ranks of the proportion of time that males spent in each behavior using nominal logistic regression (Warton and Hui, 2011). We then compared the frequency of each of the five behaviors between size classes using the Dunn method (non-parametric comparison of all pairs).

RESULTS

There was a significant interaction between male size class and the behavior category (nominal logistic regression: behavior * size class $F = 49.26$, $df = 32$, $P = 0.026$). Post-hoc

TABLE 1.—Results of non-parametric comparisons (Dunn Method for Joint Ranking) for all pairs of male size classes (small, intermediate, and large) in proportion of time spent engaging in each of the five behavioral categories. Significant P-values are in italics

Behavior	Comparison	Z	P
Chase Away	Small-Intermediate	3.65	<i>0.000</i>
	Small-Large	3.74	<i>0.000</i>
	Intermediate-Large	0.14	1.000
Chased	Small-Intermediate	0.64	1.000
	Small-Large	0.94	1.000
	Intermediate-Large	0.27	1.000
Courting	Small-Intermediate	1.59	0.333
	Small-Large	1.98	0.142
	Intermediate-Large	0.38	1.000
Nibbling	Small-Intermediate	1.91	0.169
	Small-Large	2.55	<i>0.032</i>
	Intermediate-Large	0.62	1.000
Thrusting	Small-Intermediate	1.91	0.169
	Small-Large	2.55	<i>0.032</i>
	Intermediate-Large	0.62	1.000

comparisons of each behavior between size classes revealed that large and intermediate males chased away other males more than small males (Table 1; Fig. 1) but that there was no difference between the male size classes in the proportion of time males were chased (Table 1, Fig. 1). Small males also thrust more than larger males, but intermediate males did not differ from small or large males in thrusting (Table 1, Fig. 1). There was no difference in the proportion of time spent courting across the male size classes (Table 1, Fig. 1). Small males also nibbled more than larger males, but intermediate males did not differ from small or large males in nibbling (Table 1, Fig. 1).

DISCUSSION

This study sought to evaluate the pattern of body size dependent male alternative mating strategies in the Spring Lake, Texas population of *Poecilia latipinna*, and to compare these results to those of Travis and Woodward (1989) from laboratory tested animals from a population in Florida. Overall, our results were consistent with previous laboratory results, indicating that alternative mating strategies are present within this population of *P. latipinna*. Our first prediction, that larger males would spend more time courting, was not supported however. Although intermediate and large males spent more time courting females on average than did small males, these differences were not significant, which is a departure from the findings of previous studies (e.g., Travis and Woodward, 1989). Although we did not examine why there are differences between the results of our field study and the lab study of Travis and Woodward (1989), there are several non-mutually exclusive hypotheses that could explain the differences. First, there may be fewer receptive females in a natural population at any time thus limiting the amount of time males spent courting. We did not quantify the receptive state of females in this observational study; however, in this population, 67%–69% of all females sampled during the mating season were fecund (Robinson *et al.*, 2011).

A second possible explanation for the differences in display rate variation between these studies is that there is wide variation in body size distributions among populations (e.g.,

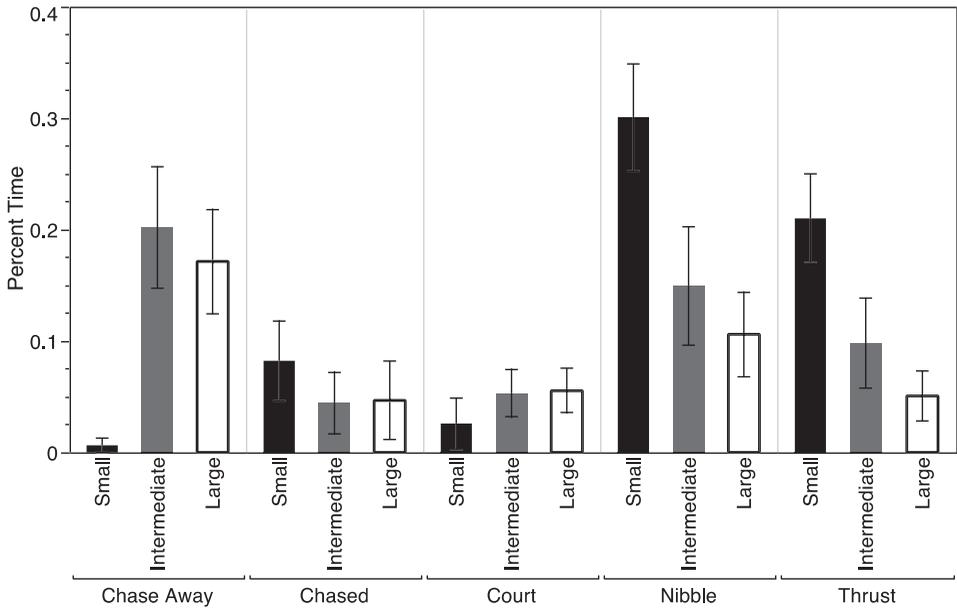


FIG. 1.—Mean (± 1 SE) proportion of time male *Poecilia latipinna* from each of three size class spent engaged in each of five behaviors (Chase Away, Chased, Courting, Nibbling, and Thrusting) during focal periods lasting up to 3 min. Small males indicated by black bars, Intermediate males indicated by grey bars, and Large males indicated by open bars

mean SL ranges from 21.9–44 mm across four Florida populations; Snelson, 1985). Travis and Woodward (1989) selected small and large males from the extreme ends of the size distributions, whereas we designated males based on the total size distribution of our population. Based on measurements of males during the mating season, this population has a relatively small average body size (Robinson *et al.*, 2011). For the current study, large males were those greater than 37.13 mm SL. Travis and Woodard (1989) defined large males as those 51–59 mm SL and small males as 20–31 mm SL for their population. Smaller average male body size in the Spring Lake population could provide an explanation for an additional pattern observed in our data as well. Intermediate males behaved intermediately in most cases in keeping with our third prediction, but their behavior was far more reflective of large males than of small ones. In some cases, they were almost indistinguishable from large males in behavior. Intermediate males are known to vary their behavior according the respective presence of large or small males, and in the case of our study, the lack of relatively large males may have caused them to adopt behavioral traits characteristic of larger males in a population.

The precise reasons for male body size variation among populations are still not fully understood but may be primarily due to differences in genotype frequencies as opposed to environmental factors (Trexler and Travis, 1990). Although the distribution and frequency of male size classes varies widely among populations, there is one key similarity: large males are always the least frequent phenotype (*e.g.*, Snelson, 1985; Farr *et al.*, 1986; Travis and Woodward, 1989). In a population where large males are rare, courtship displays may be infrequent and courting behavior was indeed rare in our study. Intermediate and large males did spend more time courting females than small males on average, but courtship

displays were atypical for all size classes. Large males, who spent the most time courting females, only courted for approximately 6% of the time observed.

Findings regarding our second prediction, that small males would spend more time thrusting at females, supported the patterns documented in previous research (e.g., Travis and Woodward, 1989). Small males spent a significantly greater proportion of time thrusting at females than did intermediate or large males (Table 1). Intermediate males did behave quite intermediately regarding gonopodial thrusting, unlike other behaviors in which they closely match large males (Fig. 1). Thus there was not a significant difference in time spent thrusting between intermediate males and any other size class but only between small and large males.

Results from this study also supported our fourth and final prediction; that large males would attempt to prevent smaller males from gaining access to females. However, both intermediate and large males spent significantly more time chasing away other males than did small males. This trend further supports the conclusion that intermediate males adopt mating behavior characteristic of large males in the Spring Lake population.

In conclusion, we found that small males spent more time thrusting at females, that intermediate males behaved intermediately in some cases, and that large males attempted to block access to females by smaller males. We did not find support for our prediction that large males would spend more time courting females. It would be interesting to determine if large males from this population also court less in the lab. Additionally, comparison among field populations in the lab and field would provide further insights into variation in male alternative reproductive strategies.

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