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Male-Male Competition and Access to Females in the Swordtail *Xiphophorus nigrensis*

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Xiphophorus nigrensis **males exhibit three size classes (small, intermediate, and large) that are primarily derived from allelic variation at the Y-linked pituitary (P) locus. Previous studies of *X. nigrensis* demonstrated that large males have greater reproductive success than small males and suggest that female choice should provide large and intermediate courting males an advantage over small noncourting males. In this study, field and laboratory observations suggest that male-male competition, in addition to female choice, contributes to the greater reproductive success of large males over small males. In the field, large males had greater access to females than did small males, and large males excluded access of other males to females more often than did small males. In the laboratory, the larger male of a pair blocked access to the female more than the smaller male, irrespective of size class. Laboratory results suggest that the pattern of size-biased mating success due to male-male competition should be different than the pattern predicted by female choice.**

SEXUAL selection, as proposed by Darwin (1871), consists of two modes: usually male-male competition and female choice. In many systems, male-male competition and female choice both operate (Bradbury and Andersson, 1987), yet studies often focus on one mode or the other, without considering the effects of both modes or their interactions (but, see Moore, 1990). Within a species, females choice and male-male competition might favor different characters (Arnold, 1983; Moore, 1990) or select for the same character in different ways (Moore, 1990). Additionally, the roles of these two modes can vary depending on factors such as density (Gwynne, 1984) or operational sex ratio (OSR; Kodric-Brown, 1988; Krupa, 1989). Therefore, to determine the evolutionary consequences of sexual selection, it is useful to distinguish the results of the two modes. In this study, we examine sexual selection on male size through male-male competition in the swordtail fish, *Xiphophorus nigrensis.* We then compare our results to previous studies of female choice and male reproductive success in this species.

Male body size in *Xiphophorus nigrensis* is controlled by genetic variation at the Y-linked pituitary (P) locus, with males possessing one of three alleles (*s*, *I*, *L*) at this locus (Kallman, 1984, 1989). Males drastically reduce growth at sexual maturity, hence the genetic polymorphism at the P locus underlies much of the variation in male body size. Narrow sense heritability for body size in males is 91% (Ryan and Wagner, 1987; Kallman, 1989). Males with the Y-*L* allele are large (>31 mm), mature later than the other two size classes (Morris and Ryan, 1990), and court females (Ryan and Causey, 1989). The Y-*I* males are intermediate in size (25–32 mm) and in the time it takes males to reach sexual maturity. Within the intermediate size class, the larger males use courtship behavior exclusively, whereas the smaller intermediate males use sneak-chase mating behavior (Ryan and Causey, 1989). Males with Y-*s* allele are small (<26 mm), mature earlier, and only use sneak-chase mating behavior. Thus, not only are size and age at sexual maturity tightly linked with genotype, but also mating behavior is correlated with the Y-*L* and Y-*s* genotypes.

Ryan et al. (1990) demonstrated a significant difference in reproductive success between the Y-*L* and Y-*I* males relative to Y-*s* males in the field. They did not, however, detect a difference in reproductive success between Y-*L* and Y-*I* males. Their laboratory experiments suggested that the reproductive advantage Y-*L* and Y-*I* males have over Y-*s* males could be due, in part, to female preference for courting males; females did not discriminate between males of different body size if both males courted. In the present study, we examined the relationship between male size and access to females in the field to determine whether male-male competition might also contribute to the large male mating advantage. We quantified male behavior and access to females in nature and used laboratory experiments for a more detailed analysis of the effects of male size on male-male competition. Territoriality, mating behavior, and female preference have been described for various species of *Xiphophorus* from laboratory studies; however, there are no descriptions of these behaviors in nature.

Methods

Field observations.—Field observations were made in April 1989, in headwaters of the Rio Choy near Ciudad Valles, San Luis Potosi, Mexico, with SCUBA and snorkel. All observations were made between 0900 and 1400 h.

Focal observations were made on 12 small and 26 large males in order to compare both male-male interactions and access to females between these two size classes. There is some overlap in phenotypes between the Y-*s* and Y-*I* as well as the Y-*I* and Y-*L* males, which causes some ambiguity when inferring the genotype from body size for some individuals. This ambiguity would have been increased in our field observations, because male size was visually estimated; therefore, we did not collect data on intermediate males to reduce our error in determining genotypes. The males we classified as small were either Y-*s* or possibly small Y-*I* individuals, and the males we classified as large were either Y-*L* or possibly large Y-*I* individuals.

Before behavioral observations commenced, the numbers of females, large males, and small males within 1 m^2 of the focal male were counted. A rope marked with tape every meter was tied across the bottom of the river to delimit sampling quadrats. Depths of the quadrats ranged from 0.3–4.0 m. The census of conspecifics was not made for one small focal male, and therefore these data are only available for 37 quadrats (11 small and 26 large).

Two divers made observations on different focals at approximately the same time. As often as possible, divers observed small and large males alternately so that both size classes were being observed throughout the day. Males were not marked, and therefore we made the assumption that when we moved to a new area we were observing different males.

Each male was observed for 10 minutes. This period was long enough that most males interacted several times with both females and other males, but not so long that it was impossible to track unmarked individuals. Twenty of the 26 large focal males and 10 of the 12 small focal males were observed for the full duration of a focal observation. Males observed less than 10 min were lost when they moved off the quadrat and out of view. All fish left the quadrat for a short time when large *Cichlasoma labridens* or *Gobiomorus dormitor*, both likely predators, moved into the area. In three such cases, the focal male was lost. Of all males observed, large males were as likely to move off the quadrat and be lost from view (five out of 20), as were the small males (two out of 10). These data suggest that we should have been no more likely to duplicate observations of a large male than a small male.

Focal observations were made for a total of 336 min. During focal observations we recorded the number of times each male displayed (glided back and forth either to the side or in front of the female; Ryan and Causey, 1989) or exhibited sneak-chase behavior. We also recorded the number of times each male chased or was chased by another male. The relative size of the other male involved in the chase was noted when possible.

We examined the relationships between the rate of male interaction with females and number of large males on a quadrat, number of females on a quadrat, number of small males on a quadrat, and time of day, using partial correlation coefficients. This analysis allowed us to test the influence of a variable on male behavior while holding other correlated variables constant.

Laboratory experiments.—We staged laboratory interactions between two males and a female so that we could determine with better size resolution the relative competitive abilities of male size classes. Males were wild-caught fish, whereas females were either wild-caught or virgins raised in the laboratory from wild-caught females. Before testing, males were kept in a stock tank with other males and females.

Two males were measured (standard length) and placed in a 10-gallon tank for two days prior to testing. Males were classified as Y-*L* if ≥32 mm, Y-*I* if 26–31 mm, and Y-*s* if ≤25 mm. We tested 30 pairs of males, comparing four to six pairs from each of six different combinations of size classes. A female was placed inside an opaque plastic cylinder (diameter 6 cm) in the tank and allowed to acclimate for two h. After the acclimation period, the cylinder was removed, and the behaviors of the two males were recorded for 30 minutes. Behaviors recorded are described below (see also Ryan and Causey, 1989):

Display: male raised his dorsal crest to its fullest extent or curved his body into a "C" shape in front of the female.

Block: one male blocked vision or access of the other male to the female by positioning his body between that of the competitor and the female. Block was also recorded when both males were within 10 cm of the female and a chase was initiated by one male toward the other.

Sneak-chase: when a male initiated a high speed chase of the female. The female's response to a sneak-chase was always a fast retreat.

Each pair of males was tested with three different females over a period of a week. The rates of behaviors for each male were averaged over the three tests before analysis.

Results

Behavior in the field.—The average number of large males observed on the 37 quadrats was 1.89 (SD = 1.11), whereas the average number of small males was 0.84 (SD = 0.75). The average number of females per quadrat was 7.24 (SD = 3.63). Both large and small males fed next to the females on the quadrat when not interacting with the females or other males. Female behavior was not quantified; however, females appeared to feed almost continuously.

The rate at which large males interacted with females was significantly correlated with the number of females on a quadrat, when number of large males and time of day were held constant (Table 1), suggesting that females per quadrat is a good indicator of opportunity to interact with females for large males. The number of females was also correlated to the number of large males on a quadrat, when rate of courtship and time of day were held constant (Table 1). The rate of sneak-chase was not correlated with the number of females, holding number of large males and time of day constant; however, the rate of sneak-chase behavior by small males increased as the number of large males on a quadrat increased, holding number of females per quadrat and time of day constant (Table 1).

Male-male competition in the field.—The number of females per male on field quadrats was significantly greater for large focal males ($\bar{x}$ = 3.45 females/male, n = 26, SD = 2.16) than small focal males ($\bar{x}$ = 2.06 females/male, n = 11, SD = 0.88; two-tailed Mann-Whitney U-test, Z = 2.18, P = 0.02). In addition, large males interacted more with females ($\bar{x}$ = 2.18 courtships/minute, n = 26, SD = 2.15) than did small males ($\bar{x}$ = 0.27 sneak-chases/minute, n = 12, SD = 0.46; two-tailed Mann-Whitney U-test, Z = 4.9, P = 0.001). We do not know whether similar

TABLE 1. PARTIAL CORRELATION COEFFICIENTS FOR VARIABLES INFLUENCING MALE BEHAVIOR AND DISTRIBUTION OF FEMALES.

Variables				
Tested	Held constant	Coefficients	df	*P*
Courtship	No. of lg. males			
No. of females	Time of day	0.551	23	<0.01
Sneak-chase	No. of lg. males			
No. of females	Time of day	0.235	8	n.s.
Sneak-chase	No. of females			
No. of lg. males	Time of day	0.666	8	<0.05
No. of females	Courtship			
No. of lg. males	Time of day	0.569	34	<0.01

rates of these two reproductive behaviors yield comparable probabilities of reproductive success. However, the duration of one courtship display approximates the duration of one sneak-chase, and therefore provides an index of time spent interacting with females. These field data suggest that large males have a greater opportunity to interact with females than do small males. This advantage could be due to male-male competition if large males are better at excluding other males, and/or female choice if females choose to spend more time around large males.

To determine whether male-male competition contributes to greater access to females by large males, we determined whether large males chased males away from females more than did small males. Twenty-two large focal males and nine small focal males were involved in male-male chases. Nineteen of the 22 large males always chased, whereas eight of the nine small males were chased exclusively (Table 2). This suggests that large males are more likely than small males to chase males away from females and that small males are more likely than large males to be chased.

The relative sizes of males were recorded in 71 out of 157 chases observed. The larger male always chased the smaller male. Large focal males chased other large or large intermediate males in 44 cases and chased small males in 12 cases. In the remainder of the 71 cases, the large focal males were chased by larger males (n = 14), and a small male once chased a smaller male. Because the relative sizes of the males involved in chases with focal males were not recorded in 54 cases, these results cannot be used to suggest that large males chased other large and intermediate males more than small males. They do demonstrate, however, that large males are chasing intermediate males and other large males in addition to small males in the field.

Male-male competition in the laboratory.—We found a significant positive correlation between male size and the average number of displays in the laboratory for the three 30-min trials ($r^2 = 0.32$, $P < 0.05$, n = 60) and a significant negative correlation between male size and the average number of sneak-chases per trial ($r^2 = 0.51$, $P < 0.01$, n = 60), as reported in previous studies demonstrating a link between behavior and size class (Ryan and Causey, 1989; Zimmerer and Kallman, 1989). The average rates of these behaviors in the laboratory experiment for large males ($\bar{x} = 0.62$ courtships/minute, SD = 0.5, n = 21) and small males ($\bar{x} = 0.27$ sneak-chases/minute, SD = 0.26, n = 19) were lower than the rates of these behaviors observed in the field. This difference is most likely due to the lower ratio of females to males used in the laboratory experiments (0.5 females/males) as compared to the average quadrat observed in the field (>2.0 females/males), as well as what appears to be an overall decline in behavior the longer males are kept in the laboratory.

TABLE 2. COMPARISON OF MALE-MALE CHASES FOR THE LARGE AND SMALL FOCAL MALES.

	Large males	Small males
Chasing*	19	1
Chased*	3	8

Pearson's χ^2 Test of Association = 15.74, $P = 0.001$.

* Large males classified as "Chasing" if they always did the chasing and were never chased. Small males classified as "Chased" if they were always chased and never did the chasing.

TABLE 3. COMPARISON OF THE AVERAGE NUMBER OF BLOCKS FOR LARGER AND SMALLER MALES IN EACH SIZE CLASS COMBINATION.

Size class combinations	(n)	Average size difference, mm (SD)	Average number of blocks (SD)	
			Larger male	Smaller male
L × L	6	0.98 (0.7)	20.5 (18.2)	2.5 (2.2)
L × I	5	5.48 (2.8)	14.2 (15.7)	2.5 (2.8)
L × s	4	11.30 (2.1)	5.8 (6.6)	1.3 (2.7)
I × I	5	1.96 (1.9)	13.2 (12.1)	5.0 (4.8)
I × s	5	6.10 (2.1)	10.0 (15.1)	1.0 (1.3)
s × s	5	0.72 (0.7)	4.3 (3.5)	0.9 (1.1)

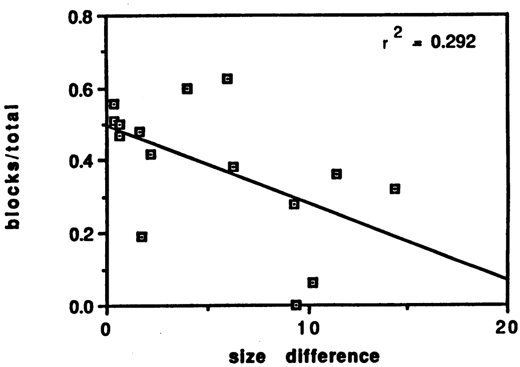

Fig. 1. Number of "blocks" by male from large size class compared to the difference in size between him and his competitor.

Males dominated access to females in the laboratory through "blocking" behavior. Although this behavior was not observed in the field, we considered it to be a competitive male behavior equivalent to male-male chases observed in the field because both behaviors prevent access to the female. The average number of blocks per trial was greater for the larger male of the pair ($\bar{x}$ = 11.74, SD = 13.38) than the smaller male ($\bar{x}$ = 2.23, SD = 2.88, Wilcoxon Test for Two Matched Samples, Z = 4.06, n = 30, $P < 0.0001$). Within each of the six size class combinations, the average number of blocks by the larger males was always greater than the average number of blocks by the smaller males (Sign test, n = 6, $P < 0.05$, Table 3). Therefore, irrespective of size class, the larger male of a pair dominated access to the female more often than did the smaller male.

To determine whether the intensity of competition for females depended on relative size of the opponent, we regressed the number of blocks used by the Y-*L* males against the size difference between the Y-*L* male and his opponent. We calculated the ratio of blocks to total behaviors to control for what appeared to be a decline in rates of behavior for fish that had been in the laboratory longer. Y-*L* males spent significantly more time blocking as the difference in size decreased ($r^2 = 0.29$, $P = 0.04$, Fig. 1). These results suggest that the intensity of male-male competition has the potential to be greater between larger males of similar size.

DISCUSSION

This study provides documentation that male size influences access to females in *X. nigrensis* in nature and that large males have increased access to females over small males due, in part, to male-male competition (i.e., large males actively chase smaller males away from females). Previous studies have shown that large males have greater mating success than do small males in nature and that females prefer large males in the laboratory (Ryan et al., 1990). Therefore, both female choice and male-male competition have the potential to contribute to a reproductive advantage for larger males in this species.

It has often been assumed that intersexual and intrasexual selection act in concert. We could not separate the effects of female choice and male-male competition in the field. However, our laboratory experiments suggested that these two mechanisms selected for different characters and may ultimately produce different patterns of mating success in this population. Female-choice experiments demonstrated a difference in the time females spent with large courting males over small noncourting males and large courting males over intermediate noncourting males, but no difference was detected between the time spent with large courting and intermediate courting males (Ryan et al., 1990). Our study has shown, however, that male-male competition should select for larger size within and among all three size classes. In other words, female choice appeared to be selecting for courtship, which is correlated with male size, whereas male-male competition would select more directly for male size.

The predicted patterns of mating success due to the different mechanisms of sexual selection in *X. nigrensis* can be compared to a field measure of relative reproductive success for this same population. Males from the large size class have a significantly greater reproductive success than do males from the small size class but not significantly greater than intermediate males (Ryan et al., 1990). Results from the present study predict that selection on male size due to male-male competition should produce a difference in male reproductive success between the large and intermediate size classes. Although theoretically the mating patterns predicted by female choice and male-male competition are different, it may be difficult to resolve these differences from the kind of data collected (i.e., one data point per size class). In addition, it is possible that male-male competition does not affect reproductive success at a constant rate throughout the breeding season. The reproductive success data of Ryan et al. (1990) only represented a single sample of the entire breeding season, and therefore a difference in mating success between large and intermediate males due to male-male competition might exist at a different time of year. Variation in factors such as population density (Farr, 1989) and operational sex ratio could influence the effect male-male competition has on reproductive success.

The rate of courtship increased with the number of females on a large male's quadrat, but we did not find a significant correlation between the number of females on a small male's quadrat and the rate of his interactions with females. Instead, small males showed a greater rate of sneak-chase on quadrats with more large males, irrespective of the number of females on a quadrat. Our laboratory results suggest that large males are blocking other large males more than small males. This is consistent with the hypothesis that small males may have more opportunities to sneak-chase females when there are more large males present, because the large males distract each other. If increased sneak-chase behavior resulted in increased mating success, then the mating success of small males could possibly be dependent on the density of large males.

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Literature Cited

Arnold, S. J. 1983. Sexual selection: the interface of theory and empiricism, p. 67–107. *In:* Mate choice. P. Bateson (ed.). Cambridge Univ. Press, Cambridge, England.

Bradbury, J. W., and M. B. Andersson (eds.). 1987. Sexual selection: testing the alternatives. John Wiley and Sons, Chichester, England.

Darwin, C. 1871. The descent of man, and selection in relation to sex. John Murray, London, England.

Farr, J. A. 1989. Sexual selection and secondary sexual differentiation in Poeciliids: determination of male mating success and the evolution of female choice, p. 91–123. *In:* Ecology and evolution of livebearing fishes (Poeciliidae). G. K. Meffe and F. F. S. Snelson (eds.). Prentice Hall, Edgewood Cliffs, New Jersey.

Gwynne, D. T. 1984. Sexual selection and sexual differences in mormon crickets (Orthoptera: Tettigoniidae, *Anabrus simplex*). Evolution 38:1011–1022.

Kallman, K. D. 1984. A new look at sex determination in poeciliid fishes, p. 95–171. *In:* Evolutionary genetics of fishes. B. J. Turner (ed.). Plenum Publ. Co., New York, New York.

———. 1989. Genetic control of size at maturity in *Xiphophorus*, p. 163–184. *In:* Ecology and evolution of livebearing fishes (Poeciliidae). G. K. Meffe and F. F. S. Snelson (eds.). Prentice Hall, New Jersey.

Kodric-Brown, A. 1988. Effects of sex-ratio manipulation on territoriality and spawning success of male pupfish, *Cyprinodon pecosensis.* Anim. Behav. 36:1136–1144.

Krupa, J. J. 1989. Alternative mating tactics in the Great Plains toad. *Ibid.* 37:1035–1043.

Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. Evolution 44:315–331.

Morris, M. R., and M. J. Ryan. 1990. Age at sexual maturity of *Xiphophorus nigrensis* in nature. Copeia 1990:747–751.

Ryan, M. J., and B. J. Causey. 1989. "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus.* Behav. Ecol. Sociobiol. 24:341–348.

———, D. K. Hews, and W. E. Wagner, Jr. 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis. Ibid.* 26:231–237.

———, and W. E. Wagner, Jr. 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. Science 236: 595–597.

ZIMMERER, E. J., AND K. D. KALLMAN. 1989. Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis.* Evolution 43: 1298–1307.

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