

PHENOTYPE, GENOTYPE, SWIMMING ENDURANCE AND SEXUAL SELECTION IN A SWORDTAIL (*XIPHOPHORUS NIGRENSIS*).—Many swordtails and platyfish (*Xiphophorus*, Poeciliidae) are characterized by a discrete polymorphism in body size. This polymorphism derives from allelic variation at the pituitary (P) locus on the Y chromosome. Males of *Xiphophorus nigrensis* possess one of three alleles, S (small), I (intermediate), or L (large) (Kallman, 1984). These alleles determine the onset of activation of the pituitary-gonadal axis, which then results in the secretion of androgens in males. Upon reaching sexual maturity, growth in males ceases or is reduced drastically (Kallman et al., 1973; Schreibman and Kallman, 1977). Males possessing the S allele mature early and are small (<25 mm), I males mature at an intermediate time and are of intermediate size (25–32 mm), and L males mature later and are large (>32 mm). The S allele is fixed on the X chromosome. Thus females mature early, but size is indeterminant because sexual maturity does not result in the cessation of growth. Laboratory analysis of progeny from fathers of

known genotypes shows a narrow sense heritability for body size of 0.91 (analysis of data provided by Kallman, pers. comm.). This strong father-son correlation is maintained under a variety of feeding regimes; variation in the amount of food influences the time to but not the size at sexual maturity (Kallman, pers. comm.).

All three size morphs exist in nature, even though progeny analysis reveals that larger males have a much greater absolute and relative reproductive success (Ryan et al., unpubl.). This bias in reproductive success can derive from several sources. Sexual selection theory indicates the importance of both female choice and male competition in effecting biases in reproductive success. In *X. nigrensis*, some of the observed variance in male mating success is due to female preference for larger males (Ryan and Wagner, 1987). Another potential factor, which has received somewhat less attention, is the differential ability of males to be present at the arena where sexual selection takes place (e.g., Koenig and Albano, 1986). For example, studies of butterflies (Watt et al., 1986), birds (Gibson and Bradbury, 1985), and frogs (Ryan, 1983, 1985) have shown that male mating success is positively correlated with male presence at the mating arena.

In nature, male *X. nigrensis* often court females that are feeding on algal-covered rocks in strong current. Males often appear to have difficulty in maintaining their location in space while courting females and patrolling the areas in which females occur. The purpose of this study is to ascertain the ability of males of different genotypes and phenotypes to maintain their location in space in a constant current. Specifically, I tested the null hypothesis that there was no difference in the amount of time that males of different genotypes and phenotypes could continuously swim in a constant current; that is, there were no differences in swimming endurance. If the null hypothesis were rejected, I then asked if endurances differed such that these differences might contribute to differential reproductive success among size morphs.

Methods and materials.—Male *X. nigrensis* used in these experiments were either collected in the field, at the headwaters of the Rio Choy, near Ciudad Valles, Mexico, or were first generation progeny of these fish. Males were isolated from one another in still water for several days prior to testing to reduce variation in mo-

tivation due to social factors. The size of fish was measured as SL (the tip of the snout to the hypural plate) to the nearest 0.1 mm using dial calipers. The length of the ventral portion of the caudal fin (tL, the distance from the caudal peduncle to the posterior end of the tail), which is differentiated to form a sword-like appendage in swordtails, was similarly measured.

The flow chamber was 1.62 m long and 70 mm internal diameter. Water was pumped into the chamber through a single inflow valve of 8 mm internal diameter with a 0.17 horse power submersible utility pump at an average rate of 3.92 cm/sec. This is within range of the flow rates I measured at the Rio Choy in Feb. 1987: ca 0–4 m/sec. Flow rate was varied by a gauge between the pump and the inflow valve. The chamber consisted of two sections, the first section was 1.27 m long. This section was not accessible to the fish and served to enhance laminar flow and reduce turbulence before reaching the fish. The two sections were partitioned by three diffusion grids placed 3.5 mm apart with a mesh of 0.5 mm. The diffusion grids served to further reduce turbulence and laminar flow. The second section contained the fish and was 0.35 m long. The outflow end of this chamber had a large-mesh metal grid 1 cm from the outflow valves. Water exited by way of two outflow valves of 8 mm internal diameter. For these dimensions and flow rate the Reynolds number is ca 2700. Given the Reynolds number, the distance from the fish to the inflow, the presence of the diffusion grid, and the fact that fish tended to swim in the center of the tube, it can be assumed that the fish experienced primarily laminar flow (Schlichting, 1955).

All tests were conducted between 0800–1800 h. Water temperature averaged 22 C. Fish were placed in the chamber and allowed 30 min to acclimate. In all tests the pump was started and flow rate was increased at a fairly constant rate over a 40 sec period until the desired velocity was reached. Endurance was measured as the amount of time from when the pump was turned on until the animal lost its righting ability. Loss of righting ability was determined as when the fish was forced against the back metal grid for more than 5 sec. Flow rate was determined after each test. These techniques are standard for measures of swimming endurance (reviewed in Beamish 1978).

Five fish in each of the three size classes were tested three times each. Fish were never tested more than once every 2 d. There was no evi-

dence of a training effect or decreased performance among tests.

Data were analyzed by genotype and phenotype. Genotype is a categorical variable, thus differences in endurance among genotypes (size classes) were analyzed by a nested analysis of variance, with trials nested within individuals and individuals nested within genotypes. Genotype was inferred from male size (Kallman, 1984).

Phenotype is a continuous variable, thus regression analysis was used to determine the relationship between size (SL) and endurance. There were small differences among tests in flow rate, and males also differed in tL as well as in SL. Thus a stepwise multiple regression was used to determine that portion of the variance in the independent variable, endurance, explained by the three dependent variables: SL, tL, and flow rate. Individual means were used in the analysis. For all analyses size was rounded to the nearest mm.

Results.—Mean endurance was greater among larger males, decreasing with size class: L males (\bar{x} = 1435 sec, SE = 151); I males (\bar{x} = 1053 sec, SE = 83); S males (\bar{x} = 658, SE = 86). The nested analysis of variance showed that differences among size classes were statistically significant (Table 1). There also were significant differences among individuals within size classes. Thirty-seven percent of the total variance was partitioned among size classes and 32% of the total variance was partitioned among individuals within size classes.

Consistent with the above results, SL, regardless of size class, was a good predictor of endurance ($F = 18.3$, $df = 1, 13$, $P < 0.005$). SL explained more of the variance in the regression analysis ($r^2 = 58.4\%$) than did size class in the nested analysis of variance. tL and flow rate did not explain a significant portion of the variance in endurance and thus their effect was not computed in the stepwise multiple regression analysis. Therefore, although flow rate varied slightly among tests, this variation did not result in an experimental artifact.

Discussion.—This study shows that under the experimental conditions to which males of *X. nigrensis* were subjected, larger males exhibit greater endurance in a constant rate of current flow. Furthermore, more of the variance in endurance is explained in the regression analysis, in which the independent variable, SL is con-

TABLE 1. NESTED ANALYSIS OF VARIANCE PARTITIONING VARIANCE IN ENDURANCE AMONG AND WITHIN SIZE CLASS.

Source of variation	Mean square	Degrees of freedom	F statistic	Probability
Among size classes	2.26	2	6.88	<0.005
Among individuals	0.33	12	3.29	<0.01
Error	0.13	30		

tinuous, than in the nested analysis of variance, in which the dependent variable, size class, is discreet. This suggests that the differences in endurance among size classes are due to differences in body size, attributed mainly to allelic variation at the P locus, and not to other factors correlated with P alleles. Variation among individuals within groups might also derive from differences in SL. Sample sizes are not sufficient to test this hypothesis. These results are consistent with other studies that reveal a positive relationship between size and swimming endurance (Boyar, 1961; Beamish, 1974; Webb and Corolla, 1981).

tL did not explain a significant portion of the variation in endurance. This suggests that the sword-like appendage of the caudal fin does not create significant hydrodynamic drag, or if so, the drag is of such small magnitude that it could not be revealed in this experimental design.

Field observations have shown that males court females and patrol areas frequented by females in areas of high current flow, and that some males have difficulty in maintaining their location in space in these currents. Regardless of a male's attractiveness to females or his ability to compete with other males, a male will have reduced reproductive success if he is limited in the time he can be attendant where mating occurs. This study suggests that in areas of high currents larger males might have an advantage due to their greater swimming endurance. These results are consistent with, although do not document the causation of, the greater mating success of larger males (Ryan et al., unpubl.). I suggest that in this species the correlation of large body size with greater reproductive success is derived, in part, from both female choice (Ryan and Wagner, 1987) and greater swimming endurance.

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