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A GENETIC POLYMORPHISM IN THE SWORDTAIL *XIPHOPHORUS NIGRENSIS*: TESTING THE PREDICTION OF EQUAL FITNESSES

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Abstract.—When a genetically determined polymorphism is selectively maintained in a population, the different morphs should have equal fitnesses at equilibrium. We empirically examined this prediction for the size polymorphism of the swordtail *Xiphophorus nigrensis*, in which a single locus on the Y chromosome controls male size. Small males mature earlier and chase females, whereas large males mature later and court females. We analyze our data with a model that uses the differential mating success and the ages at sexual maturity of the two morphs to calculate the per capita death rate necessary for them to have equal fitness. We demonstrate how female fecundity data can be used to determine whether the estimated death rate is biologically realistic. Our data support the hypothesis that morph fitnesses are equal, and the model is fairly robust to changes in population growth rate and differential death rates of morphs. However, the confidence intervals for our estimates are large, which suggests that the null hypothesis only be accepted with caution. We show that in many circumstances very large sample sizes will be needed to distinguish between alternative hypotheses concerning the relative fitnesses of the two morphs. We emphasize that despite the popularity of alternative mating behaviors, specifically, and mixed evolutionarily stable strategies, in general, there is almost no empirical evidence that alternative behavioral morphs have equal fitnesses. Also, the conclusion that morph fitnesses are equal does not address the hypothesis that frequency-dependent mating success is the mechanism maintaining the equilibrium of fitnesses. This requires additional evidence directly demonstrating the fitness effect of changes in morph frequency.

Alternative mating behaviors are common in many animals and can be maintained by several different mechanisms (Austad 1984; Dominey 1984; Gross, in press *a*). When a genetic polymorphism underlies the alternative mating behaviors, theory predicts that the various morphs should have equal fitnesses at equilibrium. This is thought to be accomplished by different morphs striking different balances between mating success and survival, two important components of fitness (Lewontin 1974; Maynard Smith 1989). The problem of maintaining a balance between mating success and survival is very general and is at the crux of arguments of life-history evolution (MacArthur and Wilson 1967; Pianka 1970), the evolution of sex (Gadgil 1972), and sexual selection (Darwin 1871; Fisher 1958). Although there has been considerable discussion as to how alternative mating behaviors *could* generate equal fitnesses—that is, that they are mixed evolutionarily stable strategies (Maynard Smith 1982; Alcock 1989; Gross, in press *a*)—there is very little empirical evidence to suggest that this is actually the case (Gross, in press *b*).

In this study, we test the hypothesis of equal fitnesses for a size polymorphism

in male swordtails, for which there is a simple Mendelian, Y-linked genetic basis. Males of one mating type are larger, mature later, and court females, whereas males of the other mating type are smaller, mature earlier, and chase females. We develop a model to analyze data bearing on the hypothesis that the opposing forces of sexual selection, due to greater mating success of larger males, and natural selection, due to higher survival to sexual maturity by smaller males, result in equal fitnesses of two mating types.

Studies of sunfish and salmon are relevant to results presented here. Gross (1985) estimated lifetime fitnesses of two sizes of morphs of coho salmon; his data supported the hypothesis that the fecundity advantage enjoyed by the hook-nose males, which mature at 3 yr, is balanced by the survival rate advantage enjoyed by jack males, which mature at 2 yr. Based on a more extensive analysis, Gross (in press *a*) now suggests that perhaps jacks have higher lifetime fitness. In bluegill sunfish there are alternative mating behaviors that are fixed within individuals, and it has been hypothesized these might have equal fitnesses maintained by negative frequency-dependent selection (Gross and Charnov 1980; Gross 1982). Recently, Gross (in press *b*) has demonstrated negative frequency-dependent selection in the sunfish; although he has not demonstrated equal fitnesses, this seems a likely possibility.

THE SYSTEM

In poeciliids, which include swordtails (*Xiphophorus*), males inseminate females with an intromittent organ, and fertilized eggs are retained in the ovarian follicles until the young are born. Breeding is continuous; all females collected at 8-wk intervals throughout the year had either eggs or embryos (Morris and Ryan, in press).

Xiphophorus nigrensis is found in the Rio Choy of the Rio Pánuco basin in the state of San Luis Potosí, Mexico. Males vary in size from 18 to 42 mm standard length (SL; tip of snout to hypural plate; hereafter all sizes are in SL). Much of the variation in size is due to a genetic polymorphism at the pituitary (*P*) locus (Kallman 1984, 1989). This locus determines onset of activation of the hypothalamic-pituitary-gonadal axis and thus the eventual secretion of androgens in males. As with other poeciliids, *X. nigrensis* males cease or drastically reduce growth at sexual maturity; hence, variation at the *P* locus underlies much of the variation in adult body size. Males have one of three alleles at the Y-linked *P* locus (*s*, *I*, and *L*), and *s* is fixed on the X chromosome. Males with the Y-*s* allele mature early at a body size less than 26 mm; males with the Y-*I* allele mature in an intermediate amount of time at an intermediate size, 26–32 mm; and males of the Y-*L* genotype take longer to mature and do so at a larger size, more than 31 mm. Narrow sense heritability for body size in males is 91% (Ryan and Wagner 1987; Kallman 1989).

Variation at the *P* locus affects traits in addition to age and size at sexual maturity. Ryan and Causey (1989) showed that small male *X. nigrensis* do not court but instead chase females and attempt to force copulation. Large males, on the other hand, court but rarely chase females. Males in the intermediate size

class usually court, but the smallest of the intermediate males chase and do not court. Thus, mating behavior (chase vs. court) is correlated with the Y-s and Y-L genotypes. Because there is some overlap in phenotypes between the Y-s and Y-I as well as between the Y-I and the Y-L genotypes, there is some ambiguity when inferring the genotype from the phenotype of certain individuals. It is not clear whether both mating behaviors exist in the Y-I genotype or whether the smallest males in the phenotypically determined intermediate size class were actually the Y-s genotype. Zimmerer and Kallman (1989) found similar results in *Xiphophorus multilineatus*, the sister species of *X. nigrensis* (formerly considered the same species; see Rauchenberger et al. 1990) from the nearby Rio Coy. These males can have one of four Y-linked P alleles: *s*, *I*, *II*, *L*. They found differences in mating behavior between males of the Y-s genotype (chase) versus those of the other three genotypes (court). In *X. multilineatus* the sizes of males of the Y-s and Y-I genotype also overlap; however, genotype can be distinguished by other phenotypic markers. Zimmerer and Kallman (1989) found that the dichotomy in mating behaviors remained even when Y-s males were larger than Y-I males. Thus, in *X. multilineatus* there is a strong genetic basis to polymorphism in mating behavior.

Ryan et al. (1990) showed that in *X. nigrensis* in the Rio Choy, sexual selection results in a decrease in the frequency of the Y-s allele after an episode of mating in nature, and Zimmerer and Kallman (1989) demonstrated the same result in aquarium experiments with *X. multilineatus*. Morris and Ryan (1990) calibrated otoliths in outdoor enclosures and showed that males do not add daily rings after growth ceases with the onset of sexual maturity; otolith number thus indicates age at sexual maturity. Using otoliths, they then determined the age of *X. nigrensis* males of each size class and showed, as expected, that small males mature at a younger age and larger males at an older age. In summary, small males of the genotype Y-s mature sooner, at a smaller body size, and chase females, and larger males of the Y-I and Y-L genotypes mature later, at a larger size, and court females.

The size polymorphism in *X. nigrensis* has been known since this species was discovered; collections from 1957 to 1987 contain males representing all three size classes (K. D. Kallman, personal communication). While this polymorphism appears to have existed for at least the last 3 decades, there are insufficient data to determine whether the morph frequencies have been stable over this time.

The goal of this study was to determine whether the different-sized morphs have equal fitnesses. To do this, we analyzed data on *X. nigrensis* using a model that takes into account the differential effects of sexual selection together with the different ages to sexual maturity and, consequently, the different probabilities of reaching sexual maturity. Because the males of the Y-I and Y-L genotypes tend to exhibit the same mating behaviors, we followed Ryan et al. (1990) and combined these two genotypes for analysis.

Using data on age at first reproduction and the relative fecundities of the two morphs, we used the model to predict the daily mortality rate necessary to balance the fitness of the two mating types. We then investigated whether our mortality estimate was consistent with known demographic patterns. To demonstrate

how the model could be expanded to account for a growing population or different rates of postmaturation mortality on the two morphs, we examined how our prediction would change under these two additional assumptions. Finally, we used a bootstrap to determine the accuracy of the fit between the data and the predictions.

THE MODEL

We modeled the males of each size morph as clonally reproducing populations, since the various morphs breed true. Assume that individuals of morph i are subject to a constant per capita death rate of δ_i , first reproduce at age f_i , and have per capita fecundity of m_i per unit time thereafter. Under these assumptions and the additional assumption that generations overlap, the asymptotic growth rate of morph i , r_i , is the largest root of the Euler equation,

$$1 = m_i \int_{f_i}^{\infty} e^{-\delta_i x} e^{-r_i x} dx. \quad (1)$$

As is well-known, the population will be at a stable age distribution when it is growing at the asymptotic growth rate.

We knew the ages at first reproduction (f_1 and f_2) for males of each size class. Morris and Ryan (1990) determined that the small males first reproduce at 78 d ($N = 15$), whereas the intermediate and large males first reproduce on average at 107 d ($N = 27$).

We also had data that could be used to compute the relative reproductive success of the two morph classes, that is, m_1/m_2 . Ryan et al. (1990) compared the frequencies of small and intermediate plus large males in the adult population (π_1^A and π_2^A , below) to the frequencies of small and intermediate plus large male offspring that were obtained from a random sample of gravid females (π_1^O and π_2^O , below). The 197 offspring (98 males and 99 females) of a sample of 27 gravid females were found to be 11% of the small morph class and 89% of the intermediate and large morph classes; among a sample of 249 adult males taken from the same population at the same time, 22% were of the small morph class, and 78% were of the intermediate and large morph classes. Since $m_1/m_2 = \pi_1^O \pi_2^A / \pi_1^A \pi_2^O$, then, $m_1/m_2 \approx 0.44$.

To predict the per capita death rate making the fitnesses of the two morphs equal, assume that both morphs are subject to the same per capita death rate, that is, $\delta_1 = \delta_2 = \delta$, and that the per capita growth rate of both populations is zero, $r_1 = r_2 = 0$. (Note that in order for the fitnesses of the two morphs to be equal, it is only necessary that $r_1 = r_2$, not that $r = 0$; the consequences of relaxing the additional assumption that the per capita growth rates are zero will be developed later.) These two assumptions together with equation (1) demonstrate that

$$\delta = \frac{\ln(m_2/m_1)}{f_2 - f_1}. \quad (2)$$

By substituting the above estimates into equation (2), we attained the prediction $\delta \approx 0.028 \text{ d}^{-1}$. We had no direct empirical estimates of the per capita death rate against which to test this prediction. However, we were able to determine whether the death rate that we predicted would be needed to maintain the two morphs in genetic equilibrium was biologically realistic. It would not be realistic if it resulted in a population that rapidly reached extinction or grew at an exceedingly fast rate. Specifically, we predicted that when the death rate is combined with independent estimates of the birth rate, they should result in a stable population size; that is, r should be approximately zero. It is critical to point out that the predicted death rate was being tested with data on female rather than male fecundity and that these data were not used to calculate the predicted death rate. Additionally, to predict the death rate we used the relative reproductive success of the morphs (the ratio m_1/m_2) and not their absolute reproductive success (m_1 and m_2 separately). This calculation would be nontrivial even if we used male fecundity data and even if there were not an extra degree of freedom, because, if any assumption we made in estimating the per capita death rate were empirically incorrect, it could cause the estimate of δ to be incorrect.

The birth rate estimated from female demographic information exactly balances the death rate. Females produce an average of 15 individuals and thus 7.5 females per brood. The mean time between broods is 30 d, so the fecundity is $7.5/30 \approx 0.25 \text{ d}^{-1}$ (Kallman 1989). The age at sexual maturity in female *Xiphophorus nigrensis* has not been directly determined, but Kallman (1984) indicated that in this *P* locus system, females mature early as do small males since the *P* genotype is the same (*X-s X-s* vs. *X-s Y-s*). Thus we assume that females reach maturity at 78 d. By substituting our female demographic data together with the predicted death rate into equation (1), we found a resulting r of 0.00. This calculation shows that the death rate that would result in equality of fitnesses of the two morphs is consistent with our general expectation of a stable population size.

It is of interest to investigate the robustness of our predicted per capita death rate to assumptions of the underlying model. In particular, when the population size is not constant (r does not equal zero), one can show that the predicted δ is

$$\delta = -r + \frac{\ln(m_2/m_1)}{f_2 - f_1}. \quad (3)$$

In a growing as compared to a stationary population, a relatively smaller per capita death rate is required to balance the fecundity advantage enjoyed by a morph with a delayed age of sexual maturity. Figure 1 shows the per capita death rates predicted from the *X. nigrensis* data assuming the per capita growth rate is in the range -0.01 to 0.01 . The extreme growth rates of this range correspond to the population decreasing by half or increasing by twofold in 70 d. Even within this range of r , δ is between 0.018 and 0.038.

Large and small morphs might have different per capita death rates, and the per capita death rates of the sexually immature individuals may differ from those of the sexually mature individuals. We have no a priori basis to predict even the magnitude of differences in postmaturation mortality in the *X. nigrensis* system.

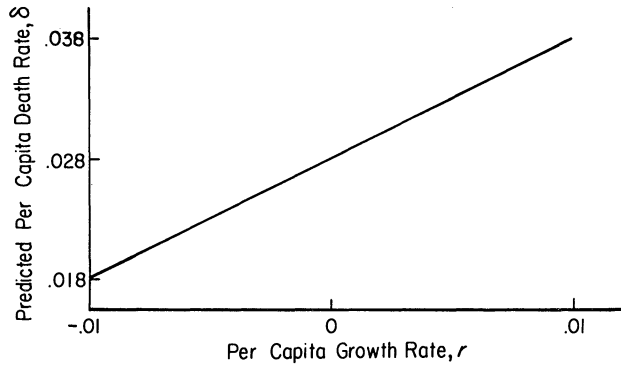


FIG. 1.—Predicted per capita death rates assuming different per capita growth rates

In many animals, males that display conspicuously are more susceptible to predation (Cade 1975; Tuttle and Ryan 1981), which may suggest that the larger, courting males should have higher postmaturation mortality. However, the smaller males are probably more susceptible to a wider range of predators, especially the abundant, smaller cichlids and *Astyanax* that inhabit these waters (M. J. Ryan and M. R. Morris, personal observations). To evaluate how these considerations would change our prediction, assume that both morphs have the same per capita death rate before reaching sexual maturity, δ^J , and that the per capita death rate of morph i after sexual maturity is δ_i^A . In this case, a generalization of the above model shows that

$$\delta^J = -r + \frac{1}{f_2 - f_1} \ln \frac{m_2(r + \delta_1^A)}{m_1(r + \delta_2^A)}. \quad (4)$$

If we arbitrarily take $\delta_1^A/\delta_2^A = 1.2$ and $r = 0$ and use the values of m_1/m_2 , f_1 , and f_2 estimated above, we would predict that $\delta^J \approx 0.034$. Conversely, if $\delta_1^A/\delta_2^A = 0.8$, then $\delta \approx 0.021$.

In summary, our simplest model shows equality of fitnesses between the two mating types, even though it does not incorporate nonzero population growth rates and differences in postmaturation mortality. Furthermore, inclusion of these variables does not substantially alter our prediction. Although our nonstatistical analysis supports the hypothesis of equal fitnesses, we wanted to determine the accuracy of the fit statistically.

We constructed a bootstrap statistic and used it to quantify the uncertainty in the estimate of δ from 1,000 randomized versions of the data used to compute f_1 , f_2 , and m_1/m_2 . To compute a single one of these 1,000 values of δ , we drew with replacement from the raw data used to compute the mean age of first reproduction of small females a sample of the same size ($N = 15$) as the original data set. A random sample was also drawn with replacement from the data set that gave large and intermediate male age at first reproduction ($N = 27$). The empirical estimates of the relative frequencies of small juvenile and adult males in the population were based on sample sizes of 98 and 249 and were estimated to be 0.11 and 0.22, respectively. In each iteration we drew a number from these two

binomial distributions, and from this we computed values of m_1/m_2 . The estimates of f_1 , f_2 , and m_1/m_2 obtained from these randomized data sets were then used to estimate δ . The 95% confidence interval was derived from the 1,000 estimates of δ .

The 95% confidence interval for δ that we determined by using the bootstrap described above is 0.006–0.066 d^{-1} . This confidence interval is conservative because it assumes that the offspring used to estimate the relative fecundities were statistically independent of each other, an assumption that effectively inflates the true sample size and that does not hold because some of these progeny had the same male parent. This large confidence interval for δ suggests that we only accept the null hypothesis of equal morph fitnesses with caution. We also offer a caveat regarding the match of the predicted death rate with the female fecundity data. We assume that males and females have the same death rate. This is likely to be true for juveniles but less likely to be true for mature adults. However, in the absence of any information on even the direction of potential differences in mortality between the sexes, equal mortality is a logical assumption.

DISCUSSION

Behavioral polymorphisms are ubiquitous and are especially common in the form of alternative mating behaviors (West-Eberhard 1986). In most alternative mating behaviors, the behavior expressed is conditional because it is dependent on factors such as the individual's age, size, and nutritional condition, or population variables such as density and sex ratio (e.g., in gerrids [Rubenstein 1984; Hayashi 1985], scorpion flies [Thornhill 1981], pupfish [Kodric-Brown 1986], sail-fin mollies [Farr et al. 1986], toads [Arak 1988; Høglund and Robertson 1988], bullfrogs [Howard 1984], and red deer [Clutton-Brock et al. 1979]). When alternatives are conditional, it is not expected that their fitnesses are equal (Dominey 1984; Gross, in press *a*).

By contrast, there are other systems in which the alternative mating behaviors are fixed throughout an individual's life and are thought to represent genetic polymorphisms in which the alternative genotypes have equal fitnesses. For example, there are winged and unwinged forms of male fig wasps. The unwinged males fight over emerging females, whereas the winged males search for figs with emerging females and without unwinged males (Hamilton 1979). In crickets there are calling males and noncalling males. Calling males are more likely to attract females but suffer higher rates of parasitism, and there is a heritable genetic component to the amount of calling by males (Cade 1975, 1981). In several species of fish there are age-independent differences in male size; some (usually larger) males court females, whereas other (usually smaller) males sneak matings (e.g., wrasses [Warner et al. 1975], sunfish [Dominey 1980; Gross and Charnov 1980], and salmon [Gross 1985]). And in the European ruff, a color polymorphism is associated with the type of mating behavior exhibited in the lek (van Rhijn 1973). In the above examples, a genetic basis to the polymorphism in mating behavior has only been conclusively demonstrated for crickets (Cade 1981), but it has been suggested for sunfish (Gross, in press *a*) and seems possible for the other systems.

If a polymorphism has a genetic basis, theory predicts that at equilibrium the fitnesses of the alternative genotypes will be equal. This is a well-known concept that has generated considerable discussion in behavioral and evolutionary genetics under the rubric of mixed evolutionarily stable strategies (see, e.g., Maynard Smith 1982; Alcock 1989). Our study shows how difficult it might be to demonstrate equal fitnesses conclusively. In most systems, direct measures or estimates of reproductive success and survival rate are likely to include substantial sampling error, and the large sample sizes thus required for robust conclusions are usually difficult to obtain. Furthermore, a clear genetic polymorphism responsible for alternative mating behaviors might be rare (Gross, in press *a*).

In *Xiphophorus nigrensis* there is a genetic basis to the polymorphism, and we present data bearing on the hypothesis that the fitnesses of the morphs are equal. The genetically determined polymorphism in mating behavior in *X. nigrensis* is unusual in that it derives from a single-locus, haploid (Y-linked) mechanism. Thus, the inheritance of the *P* locus actually meets the assumptions of the many haploid, asexual models investigating the maintenance of polymorphisms (Maynard Smith 1982). Although most fully explored in the swordtails and platys (genus *Xiphophorus*; Kallman 1984, 1989), the Y-linked *P* locus may be more widespread in the diverse family of poeciliid fishes (see, e.g., Travis 1989). However, we believe this simple system can serve as an exemplar for more complicated systems, just as in many theoretical treatments in which the conclusions of single-locus, asexual, haploid populations are extended to diploid, polygenic, sexual populations (see, e.g., Maynard Smith 1982).

Although Gross (1985) was able to measure directly the survival rate differences between the two morphs of salmon, it is difficult to obtain accurate empirical estimates of survival for most species; this is especially true for many poeciliid fishes (Snelson and Meffe 1989). Although the ideal means to test the validity of the predicted death rate is to measure it directly, the death rate has population effects that can be quantified if birth rate is known. In most systems, there is the general expectation that population growth is stable when averaged over ecologically long periods of time. In many systems it is possible to estimate lifetime female fecundity and to combine this estimate with the predicted death rate to determine *r*. There are clear outcomes that would cause the rejection of the calculated death rate and thus reject the validity of the model's prediction (i.e., unrealistic population decline or growth).

Even when the data necessary to compare lifetime fitnesses can be collected, there is still the problem of statistically testing the hypothesis of equal fitnesses (Austad 1984). The confidence limits we calculated for the death rate in this study demonstrate how easy it would be to conclude that a data set fits the prediction of equal fitnesses when, statistically, it would be difficult to reject alternative hypotheses. This problem plagues many studies. For example, Austad (1984) demonstrated with the data on relative mating success of the callers and the satellites in the green tree frog *Hyla cinerea* (Perrill et al. 1978) how confidence limits can be used to determine the accuracy with which the data fit the hypothesis of equal fitnesses. In that study, callers mated in 17 cases and satellites in 13, which is consistent with the hypothesis that they have equal mating success, as

well as the hypotheses that callers mate 2.5 times as often or that callers mate 0.6 times as often as the satellites (Austad 1984). We argue along with Austad that the calculation of confidence limits is an important consideration for studies of this kind.

Our analysis asked whether the different-sized morphs of male swordtails have equal fitnesses. Once equal fitnesses have been demonstrated, an additional question is how the morphs are maintained in the population. In theoretical terms, this is the difference between showing that an equilibrium exists and showing that it exists and is stable. The data we currently have for swordtails are consistent with the prediction that the various morphs have equal fitnesses, but we have not asked how these morphs are maintained in the population.

It is likely that negative frequency dependence maintains the equilibrium in morph frequency (Maynard Smith 1982). However, negative frequency-dependent selection is demonstrated by showing that the reproductive success of each morph is dependent on morph frequencies. Showing that the fitnesses of the morphs are equal does not demonstrate frequency-dependent selection. To our knowledge, this has only been directly demonstrated by Gross's (in press *b*) study of sunfish; although equal fitness of morphs exhibiting alternative mating behaviors seems likely in these fish, it still has yet to be demonstrated.

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