Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*

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Summary. In a natural population, we document changes in the frequencies of alleles influencing body size and size-correlated alternative male reproductive tactics, and we examine the possible role of sexual selection in producing these changes. Male swordtails (*Xiphophorus nigrensis*, Rio Choy) exhibit three body size classes (small, intermediate, and large) that primarily derive from allelic variation (*s*, *I*, *L*) at the Y-linked pituitary (*P*) locus. Some XX individuals are male. They are small and can be fathered either by XX or XY males. We compared the frequencies of Y-linked *P* alleles across two generations in a natural population. There was a significant decrease in the Y-*s* genotype relative to Y-*I* and Y-*L* genotypes. Laboratory experiments suggest that the disadvantage of Y-*s* resulted, at least in part, from female preference for larger courting males relative to small chasing males. All larger courting males are of the Y-*I* or Y-*L* genotypes. Although the frequency of Y-linked *P* alleles changed across generations, there was no change in the distribution of male body size classes. The stability of the phenotypic distribution across generations, despite changes in *P* allele frequencies, was maintained by the production of small XX sons by Y-*I* and Y-*L* males.

Introduction

Males exhibit a variety of traits that reduce survivorship but are maintained by sexual selection (Darwin 1871; Fisher 1958; Kirkpatrick 1987). Sexual selection can be realized through competition within a sex (usually male-male competition) and choice between sexes (usually female mate choice). Although numerous studies now reveal that female choice can exert selection on male traits, direct evidence supporting the hypothesis that sexual selection has an evolutionary effect on these traits is less

common (Parker 1983; Boake 1986; but see Endler 1980).

Several approaches could provide arguments for such an effect. These include: (1) demonstration of a phylogenetic correlation between mating system and the degree of sexual dimorphism in a trait under sexual selection by female choice (e.g., Harvey et al. 1978; Harcourt et al. 1981; Carothers 1984; Ryan 1985), (2) demonstrated heritable variation for traits that directly influence female choice (e.g., Cade 1981; Butlin and Hewitt 1986; Majerus et al. 1986), and (3) documentation that the mean values of such traits change across generations, assuming directional selection (e.g., Endler 1980). Rarely is there an opportunity to measure changes across generations of phenotypes or genotypes that influence female choice in natural populations.

Studies on some poeciliid fish reveal that females exhibit mate choice, that female preferences can be based on heritable male traits, and that these preferences can have an evolutionary effect. Male Trinidad guppies (*Poecilia reticulata*) exhibit heritable color patterns (e.g., Haskins and Haskins 1951) that influence female mate choice (Kodric-Brown 1985; Breden and Stoner 1987; Houde 1987; Stoner and Breden 1988), just as heritable variation influences male courtship behavior (Farr 1977, 1980, 1983). And field, laboratory, and greenhouse experiments reveal that male color patterns in any particular gruppy population are the result of a balance between predation and sexual selection by female choice (Endler 1978, 1980, 1983). Thus the Trinidad guppy is one of the few species for which there is documentation of sexual selection by female choice and an evolutionary effect of this selection.

In many animals, male mating success correlates with body size (Thornhill and Alcock 1983; Clutton-Brock 1987). Because larger males often have superior competitive ability and/or greater ability to attract females, the evolution of alternative reproductive tactics in smaller males often is favored (Alcock 1979; Rubenstein 1980; Austad 1984; Dominey 1984; Gross 1984). There are

an increasing number of studies documenting alternative mating tactics in small males (e.g., Van Rhijn 1973; Kodric-Brown 1977, 1986; Thornhill 1979; Howard 1984; Arak 1988; Höglund and Lundberg 1989), especially fish (Dominey 1980; Gross 1982, 1985; Ryan and Causey 1989; Zimmerer and Kallman 1989; also see review in Gross 1984). Many size-correlated male alternatives may result simply from ontogenetic changes in behavior (Caro and Bateson 1986), but there are some documentations of genetically determined, size-correlated mating tactics (Gross 1985; Zimmerer and Kallman 1989). Furthermore, a growing number of field studies provide estimates of the relative reproductive success of alternative male tactics (e.g., Howard 1984; Gross 1985; Kodric-Brown 1977, 1986; Smith and Arcese 1989), but similar measures for known genetic alternatives are rare (Gross 1985).

In this study we investigate size-correlated male alternatives in the swordtail *Xiphophorus nigrensis* (Poeciliidae), a species in which the genetic basis of alternative mating behavior patterns is known. We explore how the frequencies of these specific alleles change across two generations, and address the general question of how sexual selection by female choice may contribute to these changes. In this species, simple, Mendelian, sex-linked inheritance results in three body size classes, and heritability for body size variation is high. Genetic variation is restricted to one locus on the Y chromosome, resulting in a strong father-son correlation in body size (Kallman 1984); consequently, paternity can be determined by progeny analysis. This allows differential reproductive success in nature to be measured directly, rather than being estimated by other factors such as rate of courtship behavior or number of copulations. Furthermore, smaller *X. nigrensis* males exhibit alternative mating behaviors (Ryan and Causey 1989; Zimmerer and Kallmann 1989). Thus progeny analysis provides information on the relative reproductive success of the size-correlated alternative male reproductive tactics in a natural population.

We address three questions. Is there a change in the distribution of alleles that determine body size across generations? Does this change in allelic frequencies result, in part, from female preference for larger males? What is the phenotypic effect of sexual selection?

The species

The genus *Xiphophorus* is distributed throughout much of eastern Middle America (Rosen and Bailey 1963; Kallman 1975; Rosen 1979). *X. nigrensis* is restricted to the Rio Panuco Basin, in eastern Mexico. We studied a population at the headwaters of the Rio Choy near Cuidad Valles, San Luis Potosi.

Kallman (1984, 1989) showed that *X. nigrensis* from the Rio Choy exhibits three alternative alleles at the *P* locus on the Y chromosome. These alleles result in three body size classes due to variation in time to maturity, the time at which male growth dramatically decreases

Table 1. Genotypes of *Xiphophorus nigrensis* (Rio Choy) that influence sex and adult size (Kallman 1984, 1989), and the behavior patterns correlated with these phenotypes (Ryan and Causey 1989). "–" indicates that the allele has no effect on sex and size

Genotype	Sex	Size phenotype (mm)	Behavior
X-*s* X-*s* A-	female	indeterminate growth	
X-*s* X-*s* aa	male	small (<25 mm)	chase
X-*s* Y-*s* –	male	small (<25 mm)	chase
X-*s* Y-*I* –	male	intermediate (26–31 mm)	chase, court
X-*s* Y-*L* –	male	large (>31 mm)	court

(Table 1). XY individuals are males and can be one of three body size classes. Some XX individuals, however, may also be males, since an autosomal gene with two alleles, (*A*, *a*), produces males when present in the homozygous recessive state (Kallman 1984). XX males are small because the *s* allele is fixed on the X chromosome, and these small males can result from matings between heterozygous (*Aa*) females and either XY (*Aa* or *aa*) or XX males.

In *X. nigrensis* the size of the father is a good predictor of the size of his sons; heritability for body size is 91% (Kallman 1984; Ryan and Wagner 1987). Kallman (personal communication) has raised offspring under different feeding regimes, and results suggest that within a genotype, the time to sexual maturation may vary but the size at maturation does not. This is further supported by data showing that among random samples of males raised either in the laboratory, in large outdoor pools, or in nature, there are drastic differences in the age at sexual maturity but not in adult size (Morris and Ryan 1990). Also, Borowsky (1987) showed that in male *X. variatus*, social conditions have only a minor effect on adult size relative to the effect of the *P* allele, and that changes in environmental conditions that affected growth rate influenced the time to maturity but not size at maturity.

Not only does a male's phenotype indicate its genotype, but it also indicates both the father's phenotype and genotype since variation is Y-linked. Because small males can be XX individuals, however, fathered by phenotypically larger males (Y-*I* or Y-*L* males), the number of small male progeny is a maximum estimate of the reproductive success of males of the Y-*s* genotype, while the number of sons of intermediate and large body size are minimum estimates of the reproductive success of males of the Y-*I* and Y-*L* genotypes. However, the proportions of small males of the XY-*s* and XX *aa* genotypes can be estimated by the frequency of males with yellow caudal fins, because the gene for yellow caudal is Y-linked, and analysis by Kallman (1984) suggests that this allele is fixed on the X chromosome. Thus small males with yellow caudal must be XY, and males without yellow caudal are XX.

Stereotyped courtship behavior of many *Xiphophorus* species has been well described (Franck 1964, 1968; Heinrich and Schroder 1986). *X. nigrensis* males exhibit one of two stereotyped forms of mating behavior (Ta-

ble 1). There is a strong correlation between mating be-
havior and body size, and between mating behavior and
genotype (Ryan and Causey 1989; Zimmerer and Kall-
man 1989). In a laboratory study of males from the
Rio Choy (Ryan and Causey 1989), males in the large
size class attempted to gain access to females through
courtship behavior, whereas males in the small size class
quickly chased females, attempting to force copulation.
As a phenotypic class, intermediate males exhibited both
behaviors. Most of these males courted, but the smallest
males in this size class chased. Relative to genotype,
Y-s and Y-L males almost exclusively chased or courted,
respectively. The mating behavior of Y-I males is less
clear. If the smallest males in this size class were actually
of the Y-s genotype, then all Y-s chased. If they truly
were Y-I males, then this genotype exhibited both forms
of mating behavior. Zimmerer and Kallman (1989) show
that in Rio Coy X. nigrensis males, behavior is correlated
with genotype and not simply with body size.

Methods

Allelic and phenotypic frequencies in the parental population. On
2 days in March 1987, male *X. nigrensis* in the Rio Choy were
captured. Each sexually mature male (indicated by presence of
gonopodium) was measured (standard length, i.e., snout to hypural
plate), temporarily marked with a small caudal fin-clip (fin-clips
eventually regenerate), and then released. The fin-clip allowed iden-
tification of males captured for the first time versus males that
were recaptured. On the third day the population was sampled
without replacement (all fish were returned at the end of this day),
and the percent of recaptured males in each size class was noted.
These data were used to test the null hypothesis that there was
no significant difference in recapture rate among size classes.

   Small males were inspected for presence of yellow caudal, indi-
cating they were Y-s. Small males without a yellow caudal were
classified as XX. The body sizes of XY males were used to estimate
the frequencies of Y-linked *P* alleles (as in Table 1). The body
sizes of all males, XY and XX, were used to determine the frequen-
cies of each size class.

Allelic and phenotypic frequencies in the progeny. Females were col-
lected from the Rio Choy the same days we estimated male geno-
typic and phenotypic frequencies, and were transported back to
our laboratory in Austin, Texas. Gravid females were individually
placed in a 20-l aquarium, and females were removed immediately
after dropping broods. Three times per day broods were fed a
diet of live brine shrimp, liver paste, and Tetra-min fish flakes.
Upon reaching sexual maturity, which was judged by the complete
differentiation of the gonopodium, a male was removed from the
brood tank, temporarily immobilized by MS 222, and standard
length was measured to the nearest 0.1 mm with dial calipers. All
measures were rounded to the nearest mm for analysis. The allelic
and phenotypic frequencies were estimated from body sizes as in
the parental population.

Female choice tests Female preference among alternative males of
different body size was examined in a choice paradigm conducted
in an aquarium 45 × 90 × 41 cm (width, length, and height, respec-
tively) as in Ryan and Wagner (1987). The tank was divided into
five equal sections. The sections at each end were separated from
the three central sections by plexiglass. A male was placed in each
of the end sections 10 min prior to testing. The plexiglass partition

insured that females were exposed only to visual cues. An opaque
cylinder, 11 cm in diameter and higher than the water column,
was placed in the middle section. A female was placed in the cylin-
der and allowed to acclimate for 10 min. Field collected males
and females were kept in a large communal tank and isolated
at least 4 days prior to experiments. In this species, female prefer-
ence for males is not influenced by female reproductive condition
(dropped brood 24 h before testing versus dropped brood 7 days
before testing; Ryan and Wagner, unpublished data).

   After acclimation, the cylinder was removed and the amount
of time the female spent in each section, either the center section
or in one of the sections adjacent to a male, was recorded for
10 min. After the first trial the female was returned to the cylinder,
the two males were exchanged between the end sections of the
tank, a 10 min acclimation period was allowed, and the trial was
repeated. This procedure controlled for potential side-biases. In
all trials the females and males vigorously interacted with one an-
other, attempting to reach one another through the plexiglass parti-
tion. If either of the males failed to move toward the female and
attempt to interact with her during the experiment, the experiment
was terminated. Likewise, if the female failed to interact with either
male during the experiment, the trial was terminated. Thus the
bioassay was not merely association, but behavioral interaction.
In guppies (*Poecilia reticulata*), female interactive behavior strongly
correlates with female "willingness" to actually copulate (Houde
1987). Since females could be interacting with either male, or when
located in the middle third of the tank interacting with neither
male, our criteria for preference was that females spent on average
significantly more time interacting with one of the two males. The
null hypothesis of no difference in time spent interacting with each
male was tested with a two-tailed paired *t* test.

Results

*Changes in the distribution of Y-linked P alleles across
generations*

In this analysis, and in the phenotype analysis that fol-
lows, we concentrate on differences between the fre-
quency of Y-s alleles relative to Y-I plus Y-L alleles,
and the small phenotype versus the intermediate plus
large phenotype. Thus we refer to these two phenotypic
groups as *small* and *larger* males. We do so for several
reasons. First, in the body size distribution of XY males
in both the adult and progeny populations (Fig. 1A),
and in the analogous distributions of the XX plus XY
males (Fig. 1B), there is an obvious discontinuity be-
tween the small male size class and the intermediate size
class, but a less obvious one between the intermediate
and large size classes. Although there are three Y-linked
P alleles, our data reveal only two clearly defined pheno-
types. Thus we are more confident in assigning genotype
to Y-s versus Y-I plus Y-L. Second, in all of the four
distributions (Fig. 1) there is no significant difference
between the number of Y-I and Y-L genotypes or be-
tween the intermediate and large phenotypes; all conclu-
sions we reach would be identical if we treated the Y-I
and Y-L genotypes and the intermediate and large phe-
notypes separately. Third, Ryan and Causey (1989) iden-
tified two mating phenotypes (chasing and courting) of
this population that coincide fairly well (within 1 mm)
with the two well defined size classes apparent in nature
(Fig. 1).
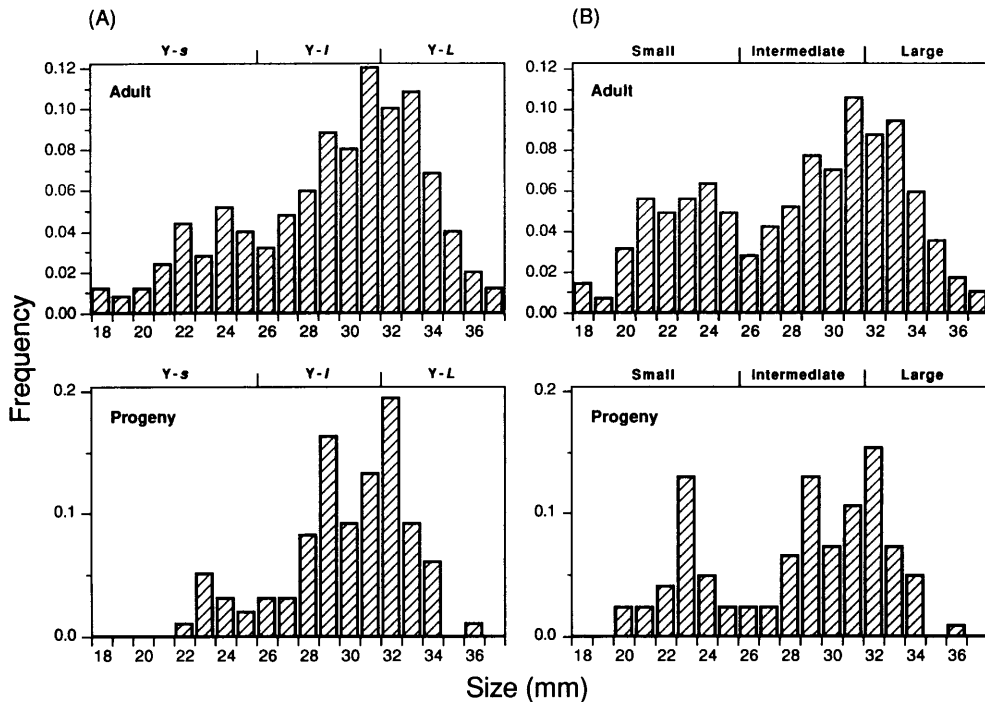
Fig. 1. (A) The frequency distributions of body sizes of XY males of *X. nigrensis* in nature (adult) and of the body sizes of their sons at sexual maturity (progeny). These data were used to estimate the frequency of Y-linked *P* alleles in each generation. (B) The frequency distributions of body sizes of all (i.e., XY and XX) males of *X. nigrensis* in nature (adult) and of the body sizes of their sons at sexual maturity (progeny). These data were used to determine the frequency distribution of body size classes in each generation

Table 2. The proportion (absolute number) of genotypes of adult XY male *X. nigrensis* at the Rio Choy and their XY sons, and the proportion (absolute number) of phenotypes of all (XY and XX) adult males and their sons (XY and XX). Combining days 1 and 2, 287 males were captured. On day 3, 126 males were captured of which 27% were recaptures. Twenty-seven of the 30 gravid females, simultaneously collected, produced a total of 197 offspring: 74 female and 123 male. Results of tests of independence comparing the phenotype and genotype frequencies of adult and progeny males are given

	Genotype		Phenotype	
	Y-*s*	Y-*I*+Y-*L*	small	intermediate + large
Adult	0.32 (93)	0.68 (194)	0.22 (55)	0.78 (194)
Progeny	0.11 (11)	0.89 (87)	0.29 (36)	0.71 (87)
	$G = 5.85$		$G = 0.40$	
	$df = 1$		$df = 1$	
	$P = 0.016$		$P = 0.53$	

The proportion (and number) of males of each genotype (excluding small XX males) is reported in Table 2, and the body sizes of XY males are shown in Fig. 1A. Recapture rates did not differ significantly among size classes ($G = 2.42$, $df = 2$, $P = 0.30$), suggesting that recapture probability was not biased by body size. We assume it was also not biased by genotype as there are no obvious behavioral or ecological differences among XX and XY small males to cause such a bias.

The gravid females produced offspring at a sex ratio (number of males/total number of offspring) of 0.62 (Table 2). There were 25 XX *aa* small males, based on the absence of yellow caudal criterion, and thus the ratio

of XY to XX individuals was 0.50. Kallman (1984) determined the frequency of *a* as 0.26, as estimated by the frequency of XX *aa* males. Using this same procedure to estimate the frequency of *a* in our progeny sample, 25 of the 99 XX individuals were males and thus the frequency of *a* was 0.50.

There was a significant change in the distribution of genotypes of XY males across generations (Table 2; Fig. 1A). The proportion of the Y-s genotype decreased while that of the Y-*I* plus Y-*L* genotype increased. If a body size of 24 mm or 26 mm, rather than 25 mm, was used to discriminate the Y-s males from the Y-*I* plus Y-*L* males, the conclusions are the same. Also, the conclusions are robust to an approximately 18% underestimation of the Y-s genotype among males in the small size class.

Female preference for male size

Laboratory experiments were used to determine if changes in allelic frequencies were influenced by female preference for larger males. Females exhibited a strong tendency to spend more time interacting with the larger of two males when given a choice between a pair of males that were small versus large, small versus intermediate, and intermediate versus large (Fig. 2A–C). Females also preferred the larger of two males within the intermediate class, even when the size difference was only 3 mm (Fig. 2D). Females usually lacked a preference involving a 3 mm size difference between classes (Fig. 2E–I).

These results show that in some comparisons females preferred larger males. In most cases in which females
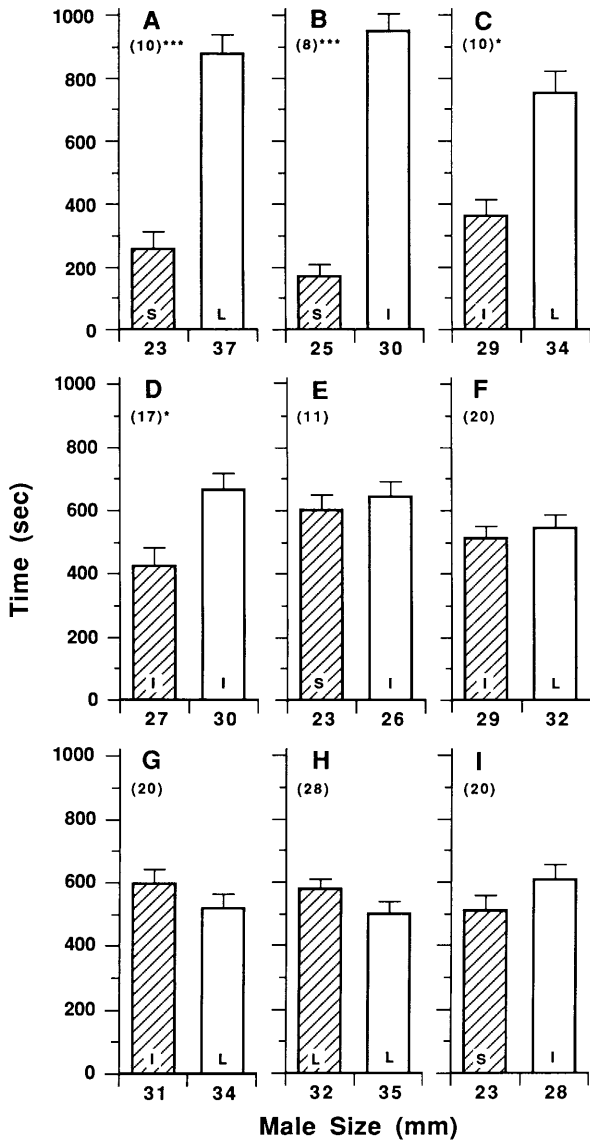
Fig. 2. The average amount of time (plus one standard error) spent by female *X. nigrensis* with each conspecific male in a paired choice test. Sample sizes are in parentheses and size classes in each histogram bar (S = small, I = intermediate, L = large). ** *P* < 0.001, by a paired t test

were given a choice between a male of the Y-*s* genotype and a male of either the Y-*I* or Y-*L* genotype, the female preferred the latter. When interpreted along with other ethological data (Ryan and Causey 1989), these results indicate that female preferences were based on the form of mating behavior. Females discriminated between small males that chased and larger males that courted, but did not discriminate among two smaller males that chased (Fig. 2E, I), or among two larger males that courted (Fig. 2F, G, H), regardless of the size differences. As in the study by Ryan and Causey (1989), these results suggest that females treat the smaller males of the intermediate size class similar to males of the small size class. These results also suggest that female choice for larger courting males contributes to the mating disadvantage of Y-*s* males observed in nature.

Across-generation changes in the distribution of body size classes

Finally, we determined the phenotypic effect of selection on Y-linked *P* alleles. As small males can be XX, there is not necessarily a correspondence between genotypic and phenotypic frequencies. The analysis of phenotypes includes XY and XX males and shows that there is no significant change in the proportion of phenotypes across generations (Table 2; Fig. 1B). When a body size of 24 mm or 26 mm, rather than 25 mm, was used to discriminate the small size class from the intermediate plus large size class, the conclusions were the same.

Discussion

Our study shows that there was a significant change in the frequencies of Y-linked *P*-alleles across the generations sampled, and that this change may have resulted, in part, from female preference for larger, courting males, all of whom were of the Y-*I* or Y-*L* genotype. Phenotypic frequencies, however, did not change across generations because the small male size class was maintained by the contribution of small XX *aa* males fathered by larger males. This sample represents only one measure of selection over a narrow time frame, and more such samples and accompanying progeny analyses are needed to assess the generality of this phenomenon.

Kallman (1984) proposed that the high frequency of *a* suggests that it might be maintained by natural selection. Our estimate of the frequency of *a* was similarly high. It is the high frequency of this allele that appears responsible for the lack of phenotypic change across the generations we sampled, despite a significant decrease in the Y-*s* genotype.

The female choice tests suggest that the relative reproductive disadvantage of Y-*s* males reflected in our samples, at least in part, might result from female preference for males that courted – all of these males are thought to be of the Y-*I* or Y-*L* genotype (Ryan and Causey 1989). Females never showed a statistically significant preference for the smaller of the two males. Lack of discrimination by females among males in Fig. 2E–I may be due to small differences in courtship display rates, as the tendancy to perform a display and display rates are both correlated with body size (Ryan and Causey 1989). These results are consistent with the study of Ryan and Wagner (1987) showing that the heterospecific preference of *X. pygmaeus* females for *X. nigrensis* males that were of a similar body size also appears to be based on courtship. Finally, although selection against small males should be incurred by all males of the small phenotype, both XX *aa* and Y-*s* (since their mating behavior is similar; Ryan and Causey 1989), only the latter is relevant in assessing the effect of sexual selection on Y-linked *P* alleles.

Our results are similar to those reported by Zimmerer and Kallman (1989) for another population of *X. nigrensis* in the nearby Rio Coy. Their laboratory experiments

also revealed that Y-*s* males were at a reproductive disadvantage due to female preference for larger males that court.

Female preferences are unlikely to explain all of the variance in male reproductive success. Male-male interactions might also contribute to size-biased reproductive success. For example, males can have difficulty maintaining their location in space during male-male and male-female interactions in fast currents, and Ryan (1988) has shown that swimming endurance increases as a function of body size. Field and laboratory studies show that larger *X. nigrensis* males do have greater access to females through male competition (Morris et al. 1989). Sperm competition could also bias reproductive success. The progeny analysis suggests that single broods can contain offspring from more than one father, and the female reproductive tract of poeciliids appears to offer a sufficient arena for sperm competition, although there are no data available to suggest a body size advantage would be reflected in sperm competition (Borowsky and Kallman 1976; Constanz 1984; Yan 1986).

Factors favoring larger males, including female choice, might be circumvented to some extent by small chasing males. Our results show that the alternative mating strategy of chasing, which is exhibited by all Y-*s* males, is at a disadvantage relative to courtship behavior, which is exhibited by most Y-*I* males and all Y-*L* males, although the alternative mating behavior can result in fertilization.

Some studies have demonstrated that female preference based on male traits can account for variance in male mating success in nature (reviews in Searcy and Andersson 1986; Kirkpatrick 1987). This field study adds to the small but growing list of studies providing evidence suggesting that sexual selection by female choice has a direct genetic effect on alleles determining the expression of male traits. Additionally, since the males of the Y-*s* genotype rely primarily on chasing behavior to gain access to females, this is among the few studies to document the relative reproductive success of males of a genetically-correlated alternative mating behavior (field: Gross 1985; lab: Zimmerer and Kallman 1989).

This study does not address the maintenance of the genetic polymorphism for body size in the face of sexual selection by female choice against the Y-*s* genotype. There are several non-exclusive hypotheses: (1) natural selection favors small males because their shorter generation time results in a greater intrinsic rate of increase and probability of reaching sexual maturity; (2) natural selection favors small males because they experience lower mortality; and (3) the success of small males depends on their relative frequency in the population. Also, the relatively high frequency of *a* demands attention. These issues currently are under investigation.

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