

Large body size in the pygmy swordtail *Xiphophorus pygmaeus*

MOLLY R. MORRIS* AND MICHAEL J. RYAN

Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.

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Fishes in the genus *Xiphophorus* (swordtails and platyfishes) are well known for the influence of the pituitary (*P*) locus on variation of male size at maturity both within and among species. We report the discovery of large male size (>29 mm SL) in several populations of the swordtail *X. pygmaeus*, a species previously thought to consist of only small males (<29 mm SL). Large size is geographically restricted, and average male size varies significantly by site and year sampled in a pattern suggesting a recent origin and slow spreading of the large male phenotype. However, large male size is not strongly paternally inherited in this species, as it is in its two closest relatives, *X. nigrensis* and *X. multilineatus*, showing that large size does not result from the same genetic (*P* locus) mechanism. Large *X. pygmaeus* males do not court, can exhibit the gold morph, do not possess swords and have slender body shape. In these traits they resemble small conspecific males and small males of *X. nigrensis* and *X. multilineatus* rather than large males of these latter two species. This shows that correlations between morphological and behavioural traits that occur in *X. nigrensis* and *X. multilineatus* are absent in *X. pygmaeus*.

ADDITIONAL KEY WORDS:—alternative behaviour – biogeography – courtship – *P* alleles – Poeciliidae – sexual selection – *Xiphophorus nigrensis* – *Xiphophorus multilineatus*.

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INTRODUCTION

Poeciliids are small fish, most less than 5 cm in length, found in fresh to salt waters from tropical and subtropical latitudes of the New World. They

*Present address and correspondence to: Department of Natural Sciences, University of Maryland Eastern Shore Campus, Princess Anne, MD 21853-1299, U.S.A.

exhibit extensive variation in several life history traits (Reznick & Miles, 1989), including variation in adult male size and age at sexual maturity (*Xiphophorus spp.*, Kallman, 1983; Borowsky, 1987; *Poecilia latipinna*, Farr *et al.*, 1986; Travis & Trexler, 1987; *Brachyrhaphis episcopi*, Turner, 1938). Within the genus *Xiphophorus*, composed of swordtails and platyfish, variation in male size is strongly influenced by a Y-linked gene, the pituitary or *P* locus (Schreibman & Kallman, 1977; Kallman & Borkoski, 1978; Kallman, 1983). This locus is involved in activation of the hypothalamic-pituitary-gonadal axis in males. Upon activation of this axis, androgens are secreted, sexual maturation is initiated and growth ceases or drastically declines (Kallman, 1989). Social effects have also been shown to influence male size in some species (Borowsky, 1973; Campton, 1992), and at least in some cases, it has been suggested that *P* factors may control the size range within which social effects function (Sohn, 1977; Borowsky, 1987).

Xiphophorus pygmaeus is so named because when the species was described (Hubbs & Gordon, 1943), all known males were small as compared to the size of males in the closely related species of swordtails. Rauchenberger *et al.* (1990) proposed that *X. pygmaeus* is the sister species of *X. nigrensis* (Rosen, 1960) and *X. multilineatus*. Together these three species form a clade within the larger clade of northern swordtails. From north to south, within the Río Pánuco drainage in San Luis Potosí, Mexico, *X. nigrensis* is found in the Río Choy, *X. multilineatus* in the Río Coy, and *X. pygmaeus* is found in the Río Axtla system (Rauchenberger *et al.*, 1990).

X. nigrensis has three alleles at the Y-linked *P* locus: *s* males mature in a shorter time at a smaller body size, *I* males mature in an intermediate time at an intermediate size, and *L* males in a longer time and at the largest size (Morris & Ryan, 1990). The body sizes of sons and fathers are quite similar; narrow sense heritability was estimated from sire-son regressions as 0.92 (Kallman personal communication; Ryan & Wagner, 1987). *X. multilineatus* differs from *X. nigrensis* by having two *I* genotypes that give rise to intermediate-sized males (Zimmerer & Kallman, 1989, conducted prior to the assignment of specific status to *X. multilineatus*, Rauchenberger *et al.*, 1990). *X. pygmaeus* has two *P* alleles that produce two highly overlapping small size classes (Kallman, 1989). All males collected prior to this study had been less than 29 mm, and most were less than 24 mm (Rauchenberger *et al.*, 1990).

A suite of characters covary with male size in *X. nigrensis* and *X. multilineatus*, including mating behaviour. Small *X. nigrensis* males do not exhibit courtship, but instead chase females and attempt to force copulations (Ryan & Causey, 1989). Also, small males lack a well-developed sword or ventral extension of the caudal fin (Kallman, 1989), are more slender than larger males (Kallman, 1989), and exhibit a solid gold body colour, caused by a sex-linked gene (Zander, 1968; Kallman, 1989). Large males court females, possess swords, have greater body depth, and lack the gold morph; most of the intermediate males are similar to large males in these traits. The smallest of the intermediate males, however, chase females; it is possible either that these are males of the *s* genotype that have been misclassified, or that there are both mating strategies within the *I* genotype (Ryan & Causey, 1989). The relationships between male size, courtship, swordtails, body shape, and colour morphs are similar for *X. multilineatus* (Zimmerer & Kallman, 1989).

Ryan & Causey (1989) showed that in *X. pygmaeus* all males exhibited chasing

behaviour and lacked courtship, similar to the small males in *X. nigrensis* and *X. multilineatus*. *X. pygmaeus* males also lacked a well-developed sword and exhibited the gold morph, both traits that also typify small males in *X. nigrensis* and *X. multilineatus*. Courtship is exhibited by most of the species of swordtails (Heinrich & Schroder, 1986), although it is absent in many species of poeciliids (Farr, 1989). The lack of courtship in *X. pygmaeus* was surprising because non-courting behaviours are often thought to be exhibited by phenotypes that either are less competitive in male interactions or less attractive to females (Dominey, 1984). Furthermore, because Ryan & Wagner (1987) showed that female *X. pygmaeus* prefer larger courting *X. nigrensis* males to their own conspecifics, it appeared that sexual selection would favour large body size and courtship behaviour were it to arise.

Here we describe what appears to be the recent and geographically restricted appearance of large body size in *Xiphophorus pygmaeus*. We describe these large males and present data on the geographic distribution of large size among populations of *X. pygmaeus*. We also compare the relationships between morphology and behaviour of large size in *X. pygmaeus* to phenotypic correlations of large males in the closely related species *X. nigrensis* and *X. multilineatus*, and determine if the mechanism of inheritance of large body size in these related species produces the large males in *X. pygmaeus*.

MATERIAL AND METHODS

Size distributions

Distributions of male size were determined at ten sites: seven along the Río Huichihuayan, including the headwaters of a tributary located near the village of El Nacimiento and two sites above the town of Huichihuayan; two sites on the Río Tancuilín; and one site on the Río Axtla (Fig. 1). Between 1988 and 1993, standard length (snout to hypural plate) was measured in the field, and the males were either returned immediately, or taken back to the laboratory for further study. Fish had been collected from six of the ten sites prior to 1988. We determined size distribution for 10 museum collections made between 1939 and 1974, consisting of a total of 368 males. While some shrinkage occurs in preserved specimens (Lee, 1982), the percentage of shrinkage in standard length is assumed to be small. In those cases where we make comparisons across sites, we analysed measurements from live males only to eliminate any error that might arise in comparing measurements of live specimens to preserved specimens. To determine if male size differed among sites and/or was increasing over time, we examine the influence of site and year sampled on variation in male size with one-way and multiple ANOVAs. Not all sites were sampled on all visits. And so, to examine the influence of site and year separately, we also compared the variation in size at several sites all sampled during the same month and one site sampled over several years. Finally, the percentage of large males at El Nacimiento was compared to the percentage of large males at the two other main sites found downstream by year with a Kendall Rank Correlation Test. Only samples in which all three sites were collected during the same month were included in this final analysis.

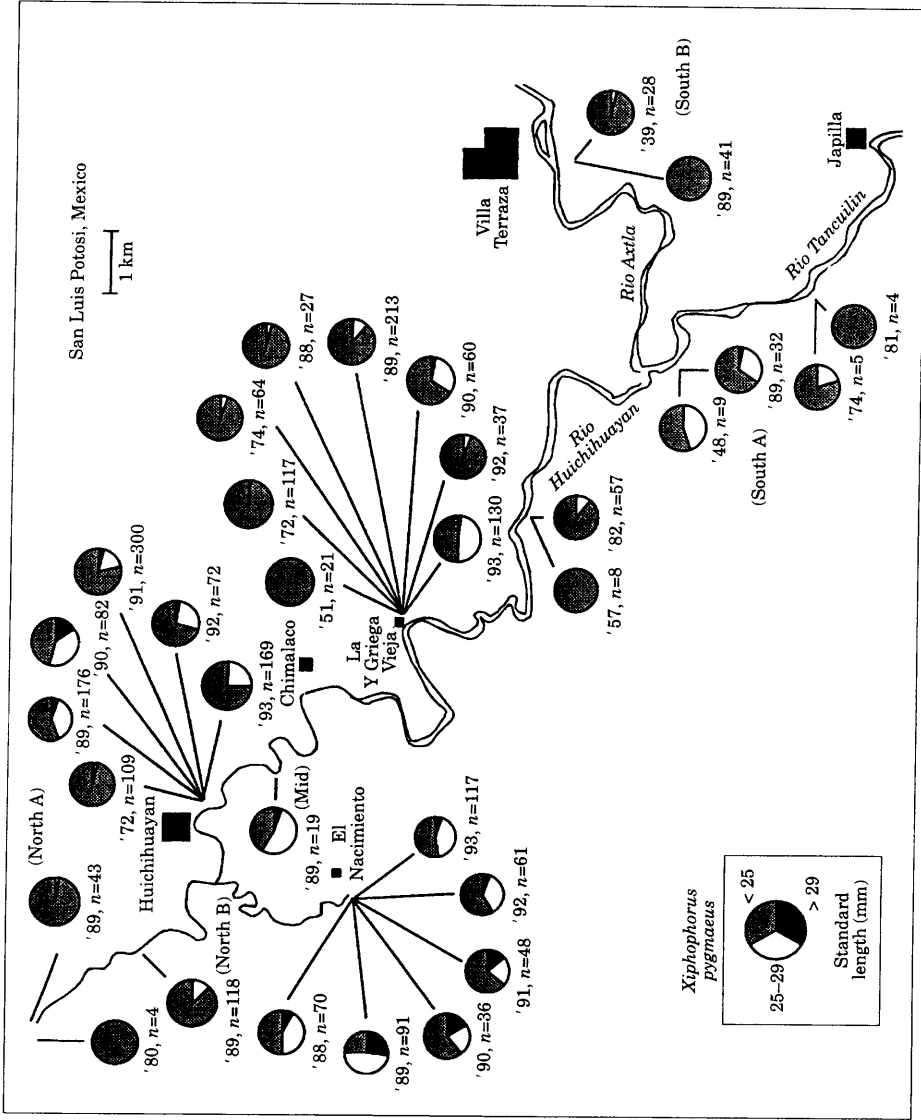


Figure 1. The distribution of *Xiphophorus pygmaeus* in the Rios Huichihuayan, Tancuilin, and Axtla as a function of body size. Dates of collection and sample sizes are shown.

Morphology

We compared the body shape of *X. nigrensis* and *X. pygmaeus* adult males. Specifically, we asked if the relatively deeper body size of larger males in *X. nigrensis* is also exhibited by larger males in *X. pygmaeus*. We measured standard length (SL) and depth (the shortest distance from the pelvic fin to the dorsal fin) in 29 male *X. nigrensis* and 31 male *X. pygmaeus*. Data were log transformed and we calculated the regression of log depth on log standard length. The slopes of the regression for each species were compared with analysis of covariance by examining the interaction term (species versus log standard length). Harvey & Pagel (1991) state that an analysis of covariance using least squares regression is more appropriate than reduced major axis or major axis regressions when one wishes to compare the size of characters after removing the variation due to differences in body size because the errors in the X and Y values are not correlated.

In addition, we noted the proportion of large male *X. pygmaeus* that possessed well-developed swords (>5 mm, measured from the distal edge of the caudal fin), and the proportion of gold morphs in both size classes in *X. pygmaeus*.

Courtship

We investigated the mating behaviour of large *X. pygmaeus* males following the methods of Ryan & Causey (1989). Ten large *X. pygmaeus* males from Nacimiento were placed separately in a 2.5 litre aquarium with a single female. Mating behaviour was video-recorded for 30 min and later reviewed for presence of courtship. Male size ranged from 29.1 to 35.5 mm.

Determinants of large size

We investigated the possibility that the large male phenotype in *X. pygmaeus* is inherited as in *X. nigrensis* and *X. multilineatus* by determining if there was a strong relationship between the size of wild-caught fathers and the size of their laboratory-bred sons at sexual maturity in *X. pygmaeus*. In the laboratory, *X. nigrensis* shows paternal inheritance of body size (Kallman, 1989), and large wild-caught fathers produce sons that reach sexual maturity at large body sizes in the laboratory (Morris and Ryan, unpublished data). We crossed ten wild caught large male *X. pygmaeus* each with a virgin female, and then compared the sizes of the sons at sexual maturity to the sizes of their fathers. Broods were fed brine shrimp twice a day and tetramin flakes daily. Upon reaching sexual maturity, which was determined by gonopodium differentiation (Rosen, 1960), males were removed from tanks and their SL was measured. A regression of the sizes of fathers and sons was not suitable for heritability estimations because the fathers were wild-caught and therefore the causes for variation in body size may be different for fathers and sons (Falconer, 1981).

RESULTS

Size distributions

All fish collected between 1939 and 1974 were less than 29 mm SL (Fig. 1). All of these sites were resampled after 1988, and at four of the six sites

all males were less than 29 mm. In 1988 we discovered large males, between the sizes of 29.0 and 37.2 mm, at the headwaters of springs in El Nacimiento. This site had not been previously sampled. The large male phenotype has been found at this site in all of the last six years sampled (1988–1993, Fig. 1). On a yearly basis, the proportion of large males in the population fluctuated between 0.05 and 0.27 ($n = 6$ and 25 of 117 and 91, respectively); however, some smaller samples within each year failed to yield large males (Fig. 1).

In 1989 we also collected large males in the Río Huichihuayan in the town of Huichihuayan (Fig. 1). This site is downstream and south of the confluence of the springs originating at El Nacimiento and the Río Huichihuayan. Fish had been collected at this site in 1972, and no large males were found in a large sample ($n = 109$; Fig. 1). Also, K. Kallman and D. Morizot (personal communication) monitored this site during the early and mid-1980s and never found large males. Large males have been present at this site for the last five years sampled, 1989–1993. The proportion of large males at this site is lower than at El Nacimiento, and fluctuated between 0.006 and 0.16 ($n = 1$ and 13 of 169 and 82, respectively, Fig. 1).

We collected a total of eight large males at three other sites (Fig. 1): One large male at the site immediately downstream and south of Huichihuayan; six large males at La Y Griega Vieja, located immediately south of the town of Chimalaco; and one large male at site South A, located where the Río Tancuilín splits from the Río Axtla (Fig. 1).

There was a significant difference in male size between the three sites most extensively sampled (El Nacimiento, Huichihuayan, and La Y Griega Vieja, one-way ANOVA, $F = 110.2$, d.f. = 2, $P < 0.001$). If we limit the data analysed to those samples from 1988 and later (males measured live) the difference is still significant ($F = 59.7$, d.f. = 2, $P < 0.001$). Site also explains a significant amount of the variation in male size even when the large males (>29 mm) are eliminated from the analysis ($F = 29.40$, d.f. = 2, $P < 0.001$). Tukey's HSD posthoc comparisons of this final data set showed that there was no significant difference between Huichihuayan and La Y Griega Vieja ($F = 0.140$, $P = 0.709$), but these two sites differed significantly from El Nacimiento ($F = 58.56$, $P < 0.001$).

In a multiple analysis of variance of male size at the three main sites, there was a significant interaction between year and site sampled ($F = 18.29$, d.f. = 1,6, $P < 0.001$). Therefore, to examine variation in male size over time without the confounding influence of site, we examined the site that had been sampled over the longest period of time, La Y Griega Vieja. Average male size at La Y Griega Vieja increased over forty years of sampling by 3.5 mm (Kendall Rank Correlation Coefficient, $n = 8$, $\zeta = 2.47$, $P = 0.01$). Even if we exclude samples collected before 1988 as well as the large males (>29 mm) from the analysis, there was significant variation in male size due to year sampled at La Y Griega Vieja ($F = 21.8$, d.f. = 4, $P < 0.001$), and males from the 1990, 1992 and 1993 samples were significantly larger than males from the 1988 and 1989 samples (Tukey's HSD posthoc comparison, $F = 13.77$, $P < 0.001$).

Fish were collected from some sites more than once during a given year. To remove the confounding influence of changes in average male size due to month sampled, we determined how male size varied among sites by comparing the sizes of males from eight sites that were all collected in June 1989. There

TABLE 1. Comparison of the mean sizes of males sampled on June 1989 at eight sites (for locations see Fig. 1). Tukey's HSD posthoc tests from a one-way ANOVA of site on male size are given for comparisons between each site. *P* values corrected for multiple comparisons with Dunn-Sidak method

	North A	North B	Nac.	Huich.	Mid.	La Y	South A	South B
NA	1.00							
NB	0.04	1.00						
Nac	0.02	0.02	1.00					
Hui	0.02	0.02	0.02	1.00				
Mid	0.02	NS	NS	NS	1.00			
La Y	0.02	NS	0.02	0.04	0.02	1.00		
SA	0.02	NS	0.02	NS	0.05	NS	1.00	
SB	NS	0.02	0.02	0.02	0.02	0.02	NS	1.00
\bar{X} (mm)	20.9	22.3	27.0	24.3	25.3	22.9	22.3	20.0
(SD)	1.9	1.82	3.39	2.92	2.24	1.81	1.14	1.59

was a significant effect of site on adult male size in this analysis, which explained a large proportion of the variance in male size ($r^2 = 0.421$, $F = 50.685$, d.f. = 7, $P < 0.001$). Tukey's HSD posthoc comparisons between the different sites sampled in June 1989 and the average male size for each site during this month are summarized in Table 1. Average male size appears to decrease the farther downstream the site is from the Nacimiento site (Table 1). Finally, there was a significant relationship between the proportion of large males at El Nacimiento and the proportion of large males at Huichihuayan and La Y Griega Vieja (Kendall Rank Correlation Coefficient, $n = 6$, $Z = 2.3$, $P = 0.02$).

In summary, large male *X. pygmaeus* now exist at several sites. They are most abundant at the headwaters of a spring in El Nacimiento. They are present downstream in Huichihuayan and La Y Griega Vieja in lower frequencies. One male was found at a site much farther downstream during the year the proportion of large males at El Nacimiento was greatest. Large males were not found farther south on the Río Axtla, nor were they found at any sites immediately to the north, upstream from Huichihuayan (Fig. 1). A significant proportion of the variation in male size can be explained by site and year sampled, with average male size increasing over our study period at La Y Griega Vieja. In general, males are largest at El Nacimiento, and yearly fluctuations in the proportion of large males at the sites downstream from El Nacimiento appear to coincide with the fluctuating proportion of large males at El Nacimiento.

Morphology

The body depth of *X. nigrensis* adult males is positively allometric, increasing at a greater than linear rate with standard length (slope = 1.27, SE = 0.05, $n = 22$; $P < 0.001$). Depth is also positively allometric in *X. pygmaeus* males (slope = 1.11, SE = 0.05, $n = 30$, $P < 0.001$), but significantly less strongly than in *X. nigrensis*, as is apparent from comparing the slopes of the two regressions ($F_{1,50} = 4.72$, $P = 0.035$). Thus larger *X. nigrensis* are significantly deeper than larger *X. pygmaeus* (Fig. 2).

Both small and large males exhibit the gold morph in *X. pygmaeus*. Thirty

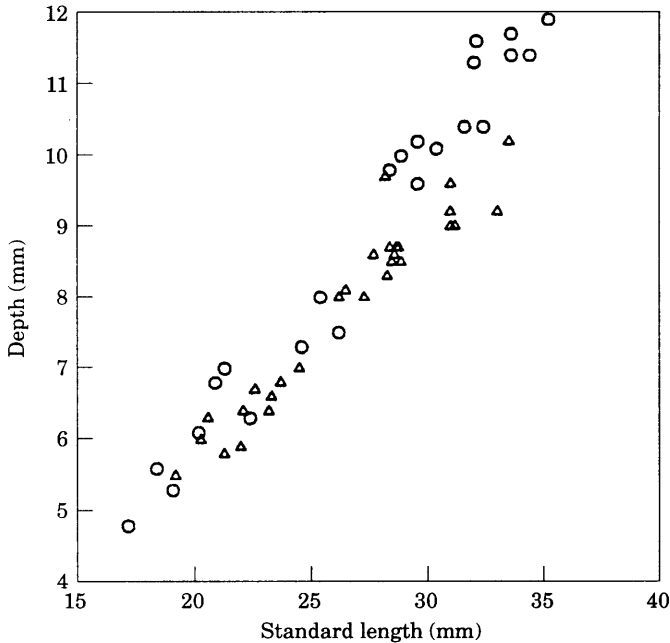


Figure 2. Body depth as a function of standard length in *X. pygmaeus* (△) and *X. nigrensis* (○).

two percent of the large males sampled at El Nacimiento and Huichihuayan (≥ 29 mm; $n = 46$) were gold rather than the typical 'wild type', which is a bluish tint that results from tyndall scattering. Gold males were slightly less common in the small *X. pygmaeus* males sampled (< 29 mm, 28.6%, $n = 192$) than the large *X. pygmaeus* males. We never observed any male *X. pygmaeus*, large or small, with a well-developed (< 5 mm) or pigmented sword.

Courtship

None of the ten large *X. pygmaeus* males tested showed a courtship display. All of the males, however, exhibited the fast chase. Therefore, although some populations of *X. pygmaeus* have males of the same size as large male *X. nigrensis*, the mating behaviour is not courtship as it is in the large heterospecifics, but is chasing, as it is in their small conspecifics and small heterospecifics.

Determinants of large size

Twenty one sons were obtained from 10 crosses of virgin females and large El Nacimiento males (1–4 sons/father). Fathers ranged in size from 31.6–35.7 mm, while sons ranged in size from 23.0–24.2 mm at sexual maturity. The sizes of the large fathers and their sons did not overlap in *X. pygmaeus* as they do in all three size classes of *X. nigrensis* (Fig. 3). These data suggest that large size is not determined in the same manner in *X. pygmaeus* as it is in *X. nigrensis* and *X. multilineatus*. It is not clear from these crosses if there is any heritable genetic basis to large size in *X. pygmaeus*.

DISCUSSION

We report the discovery of large males (>29 mm) in several populations of the swordtail *X. pygmaeus*, a species previously thought to consist of only small males. Rauchenberger *et al.* (1990) reported that most males of *X. pygmaeus* are less than 24 mm. Their comment that sometimes males reach 38 mm was based upon our data on large males that we report here. These large *X. pygmaeus* males do not appear to be produced by the same *P* allele system as the large males in *X. nigrensis* and *X. multilineatus*. The genetic basis underlying the expression of large male size in *X. nigrensis* and *X. multilineatus*, which results in a strong relationship between the body sizes of fathers and sons, is not present in *X. pygmaeus*.

Kallman's (1989) successful introgression of the *L* allele from *X. nigrensis* into *X. pygmaeus* demonstrated that large size would appear in *X. pygmaeus* if this allele were to occur. Kallman crossed a large *X. nigrensis* male with a female *X. pygmaeus* and then back-crossed large males of the F¹ and several subsequent generations to female *X. pygmaeus*. This resulted in males that had most of the *X. pygmaeus* genome, but were large because they possessed the *L* allele at the *P* locus from *X. nigrensis*. The introgressed large males produced sons that matured at a large size, typical of *P* locus systems, while in our crosses the large *X. pygmaeus* males that occur in nature did not. This suggests that there are no constraints, e.g. maternal effects or paternal genetic backgrounds in *X. pygmaeus* that would prohibit the expression of large size via the same *P* locus system found in other closely related species.

At this point, we have no evidence to indicate if large size in *X. pygmaeus* is a genetic or a totally environmentally-induced phenotype. The effects of social and environmental factors on growth and maturation in poeciliids are reviewed by Snelson (1989). He suggests that the interactions between all of these factors are complex and vary from case to case. So, for example, interactions between genetic and social control of sexual maturation have been shown for both *X. variatus* and *X. maculatus* (Sohn, 1977; Borowsky, 1987), but social interactions do not appear to influence size or age at maturity in *P. latipinna* (Farr & Travis, 1989) or *G. heterochir* (Yan, 1987). The social environments were very similar between this study and the *X. nigrensis* study we used for comparison of the correlations between paternal size and size of sons at maturity. While we have shown that a *P*-allele similar to that which produces large males in *X. nigrensis* is not functioning to produce the large males in *X. pygmaeus*, we have not demonstrated the factors that produce large males in this species.

Several of the characters that are specific to the small size classes in *X. nigrensis* and *X. multilineatus* are found in the large males in *X. pygmaeus*. Mating behaviour of males has been shown to be correlated with genotype in *X. nigrensis* and *X. multilineatus*. Large *X. pygmaeus* males, however, do not court but use instead sneak-chase behaviour like the small males in *X. nigrensis* and *X. multilineatus*. In *X. multilineatus* and *X. nigrensis* the gold phenotype is exhibited by only the small males (Rauchenberger *et al.*, 1990; personal observation). Rauchenberger *et al.* (1990) do not report small gold males in *X. nigrensis*; however, we have occasionally found small gold males in this species as well. Both small and large males exhibit the gold morph in *X. pygmaeus*. Large *X. pygmaeus* males lack well-developed swords even though large males in the other

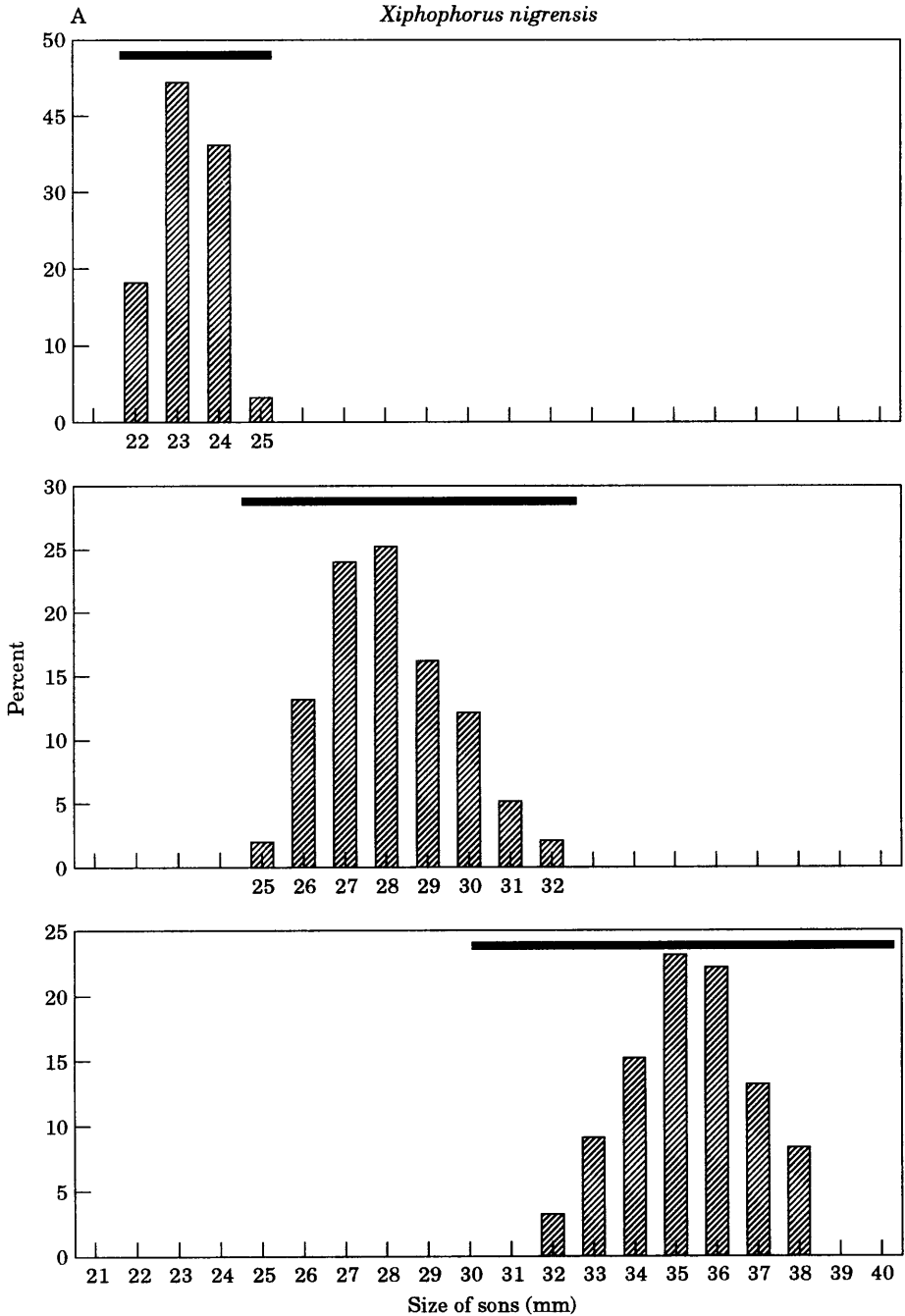


Figure 3. (A) Size distribution of fathers and sons for all three size classes of *X. nigrensis* males (Kallman, personal communication) and (B) the size distribution of large wild-caught *X. pygmaeus* males and their sons. The black bar indicates the size range of fathers.

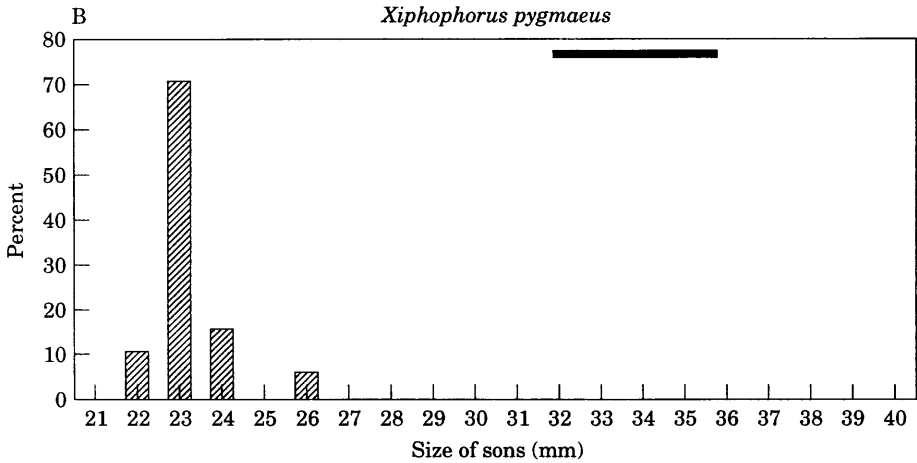


Fig. 3 (continued)

two closely related species have swords. And finally, the body shape of large *X. pygmaeus* males is more slender than the large males in *X. nigrensis*, and more similar to the small males in *X. nigrensis*.

The introgressed large males from Kallman's study (1989) developed neither swords nor the greater body depth typical of larger *X. nigrensis* males. In these traits, the introgressed large *X. pygmaeus* males were more similar to the newly discovered *X. pygmaeus* males in nature. It appears that the presence of the *L* allele is not sufficient to cause development of the sword or greater body depth. Therefore, phenotypic differences among the small and larger males of *X. nigrensis* and *X. multilineatus* are not due to differences at the *P* locus per se, but might derive from epistatic interactions with other loci to yield genetically correlated traits (Kallman, 1989). For example, gold body colour is determined by the sex-linked *con* locus (Kallman, 1989; also see Zander, 1968). In *X. nigrensis* and *X. multilineatus* the alleles at this locus are in linkage disequilibrium with alleles at the *P* locus: only *s* males have the alleles for gold body colour.

Because non-courting behaviours are expected to be exhibited by males that are less competitive or less attractive to females, it was perplexing when Ryan & Causey (1989) showed that courtship was lacking in *X. pygmaeus*. These males, all of which were thought to be small, exhibited an 'alternative' mating behaviour despite the lack of larger, courting males in this species. The lack of courtship in the newly found large *X. pygmaeus* males might make matters more confusing, but we suggest that it can be understood if the occurrence of large size in *X. pygmaeus* is independent of large size in the other pygmy swordtails. In *X. nigrensis* and *X. multilineatus* there is a correlation between *P* alleles and mating behaviour: *s* males chase while most *I* and *L* males court and do not chase (Ryan & Causey, 1989; Zimmerer & Kallman, 1989). Kallman (1989) concludes that expression of mating behaviour is under direct genetic control that is Y-linked. Farr (1983) has also shown that variation in courtship components in *Poecilia reticulata* is paternally inherited. Large size was lost either in the species *X. pygmaeus* or in the ancestor to the pygmy swordtail clade. Along with the alleles for large size, it appears that other correlates of large size, such as courtship, deeper bodies, and well-developed swords were also

lost. Thus when large size reoccurred in *X. pygmaeus*, whether its reoccurrence derives from genetic mechanisms other than *P* alleles, is due to purely environmental effects, or some gene \times environment interaction, it did so against a background lacking genetic variation for these correlated traits. We suggest that if large size in *X. pygmaeus* is an evolved trait rather than due to purely environmental effects, it is not a synapomorphy of large size in *X. nigrensis* and *X. nigrensis*.

The absence of large size and courtship in *X. pygmaeus* could have been due to the loss of large males and correlated variation for courtship or, alternatively, absence of large males could be the ancestral condition. Kallman (1989) suggested that the *P* alleles for large size in *X. nigrensis* and *X. multilineatus* are different from the *P* alleles for large size in other *Xiphophorus* species, and that the small males habitus in those species and in *X. pygmaeus* was the ancestral condition. Alternatively, the alleles for large size in *X. nigrensis* and *X. multilineatus* could be derived from the alleles for large size found in species outside of this clade. Parsimony optimization of large size (MacClade package: Maddison & Maddison, 1992) using the phylogenetic hypothesis of northern swordtails proposed by Rauchenberger *et al.* (1990) supports this second interpretation, and suggests that large size was lost in *X. pygmaeus*.

This study suggests a recent origin of large size in *X. pygmaeus*, and clearly documents a recent spread of this phenotype to sites where it did not previously occur. This phenomenon presents an unusual opportunity to document the historical spread of a new phenotype, and to monitor phenotypic correlations with large size that might evolve, specifically those phenotypes that are correlated with large male size in closely related species. It also presents an opportunity to ascertain the influence of this new phenotype on patterns of sexual selection with special reference to Ryan & Wagner's (1987) demonstration of a female preference for large size in populations lacking large size.

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