Genetic Basis for Alternative Reproductive Tactics in the Pygmy Swordtail, Xiphophorus nigrensis

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GENETIC BASIS FOR ALTERNATIVE REPRODUCTIVE TACTICS IN THE PYGMY SWORDTAIL, *XIPHOPHORUS NIGRENSIS*

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Abstract.—Differences in adult male size and age at sexual maturity in the Río Coy (Mexico) population of *Xiphophorus nigrensis* (Pisces; Poeciliidae) are controlled by genetic variation at a Y-linked locus. Four genetic size-classes have been identified. The mating behavior of the males of the three largest size-classes consists exclusively of an elaborate courtship display, whereas that of the genetically small males ranges from display to a sneak-chase attempt at copulation. In the presence of large males, small males switch to the sneak-chase behavior. Females prefer the display of large males. In mating-competition experiments (two females with one large male and one small male), the large males are dominant and deny the small males access to females. From 20 such experiments, 601 large-male and 200 small-male progeny were obtained, indicating that the switch to sneak-chase behavior by small males is not particularly effective in overcoming the large-male advantage. By using the largest males of the genetically smallest size class and the smallest males of the genetically next-larger size-class, size was kept constant, whereas genotype was varied. When these males were tested in competition with genetically large males, only the males of the genetically smallest size class showed sneak-chase behavior. These observations suggest that the difference in mating behavior is not an indirect developmental effect of size but, rather, is under direct genetic control.

Size-dependent alternate mating strategies between males within a species have been observed in many animal groups, including mammals (Leboeuf, 1974; Hausfater, 1975), reptiles (Trivers, 1976), amphibians (Wells, 1977), fish (Barlow, 1967; Constantz, 1975; Gross, 1982, 1984, 1985; Warner et al., 1975), and insects (Alcock et al., 1977; Cade, 1979; Thornhill, 1979; Waage, 1973). Larger males are more likely to court females and defend both females and territories from other males. Because a male's success in defending a territory or courting a female is often related to his size, an alternate mating behavior may be the best strategy for a small male. Smaller males (which have been called subordinate or satellite males) often "sneak" copulation during the momentary absence of a larger male or, less frequently, spawn during the presence of the larger male. Small males may mimic females and submit to copulation with larger males to achieve successful copulation with females. The relative success of alternate mating strategies can best be judged by determining the paternity of offspring. Inferences on mating success based on who wins in male-male competitions or who spends the most time with females may be misleading and, in some cases, have been shown to be inaccurate (Duval et al., 1976). Most discussions of alternate mating tactics are weak, because paternity is difficult or impossible to determine.

The proposal (Maynard-Smith and Price, 1973; Maynard-Smith, 1976, 1981) that alternate mating tactics exist as an evolutionarily stable strategy (ESS) has gained much support (Brockmann et al., 1979; Hamilton, 1979; Rubenstein, 1980; Gross, 1982; Austad, 1984; Dominey, 1984). However, the assumption that behavioral polymorphisms are maintained (balanced) by natural selection is supported by little experimental evidence concerning the means of selection and the genetic basis on which this selection can work. Are the behavioral differences a direct effect of a specific gene for a given behavior, or are they caused indirectly by other genetic factors (e.g., those influencing size or

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TABLE 1. Average adult size, standard length of the four genotypes of male *Xiphophorus nigrensis* (Río Coy). Y-linked color patterns at the yellow (flavus) locus (nomenclature adapted from Zander [1968]) are as follows: con = flavus concolor (solid yellow); cm = flavus caudimarginatus (ventral and dorsal margins of caudal fin yellow); cp = flavus caudipinna (caudal fin yellow); + = absence of yellow (solid blue). Two lines each of II and L males were maintained with cp and cm patterns, respectively. In the experiments, all L males were cm, and all II males were cp.

Phenotypic size-class (line)	Genotype	Color pattern	N	Standard length (mm)	
				Mean ± SD	Range
Small (s)	X-*s*/Y-*s*	con, +	302	25.2 ± 1.20	22–28
Intermediate-1 (I)	X-*s*/Y-*I*	cm	135	27.4 ± 0.12	25–32
Intermediate-2 (II)	X-*s*/Y-*II*	cp	216	32.4 ± 2.06	29–38
Large (L)	X-*s*/Y-*L*	cm	154	37.5 ± 2.05	32–42

pigment patterns) or by environmental cues that act either during ontogeny or on adult social organization?

Here, we use the pygmy swordtail, *Xiphophorus nigrensis*, to study alternate mating strategies. This species is found in two rivers, Río Coy and Río Choy (Río Panuco basin), in San Luis Potosí, Mexico. Males of this species differ in size by more than a factor of two and show size-related differences in mating behavior (Zimmerer, 1982). Size and age at maturation in this species and other *Xiphophorus* are determined by a sex-linked gene (P) (Kallman et al., 1973; Kallman and Borkoski, 1977; Kallman, 1983). As with males of most poeciliid fish, little growth occurs after maturation, resulting in genetically determined male size-classes.

In this paper we 1) describe mating behavior of males from the different size-classes, 2) present data showing relative mating success of genetically small and genetically large males, 3) document the behavioral shift in one of the genotypes (corresponding to the smallest mean size of males) and the inability for a similar shift in the genetically larger size classes, 4) give evidence for the association of some of these behaviors with specific P alleles, and 5) describe the role of female choice in these interactions.

MATERIALS AND METHODS

Male-competition experiments and single-male (control) matings were set up with newly matured, inexperienced males and virgin females. Behavior was not recorded for the first two weeks of each mating to allow the fish to adapt to new surroundings. Control matings each involved a single male

of one of four size classes (small, intermediate-1; intermediate-2, or large) and one female; male-male competition matings each involved two males of different size-classes (either small and large or intermediate-1 and large) with two females. Several male competition matings with large and small males were performed in 200–400-liter aquaria; all other matings were set up in 20-liter aquaria. All aquaria had gravel and aquatic plants to allow some cover; water temperature was maintained between 23° and 25°C. Fish were fed a diet of liver paste (Gordon, 1950), newly hatched brine shrimp, and daphnia (when available) 2–3 times daily. Thirty-minute observations were made twice monthly between 11:00 A.M. and 1:00 P.M. Behavior activities recorded included 1) time foraging for food, 2) time males spent with females, 3) number, duration, and types of male display to female(s), 4) male copulation attempts, 5) female response to male displays, and 6) number, duration, and types of male-male interactions.

Four size classes are known from the Río Coy, and these differ in their Y-linked P alleles (s, I, II, or L) and color genes (Table 1). All X chromosomes carry the s allele for small size and early maturation. Small males have two color phases, metallic blue and solid yellow, controlled by a Y-linked locus. Males of the other P genotypes are also metallic blue, but may have various yellow patterns in their caudal fins. The *X. nigrensis* stock used in this study was collected in the Río Coy in 1972, and has been maintained in lines corresponding to the male size-classes (s, I, II, and L) at the Genetics Laboratory of the New York Aquarium by breeding males of small and intermediate-1

TABLE 2. The mating behaviors of the four genotypes of male *Xiphophorus nigrensis* from the Río Coy. Table entries are mean numbers (±SD) per observation period.

Behavior	s	I	II	L
Frequency of frontal display	6.1 ± 4.5	13.1 ± 3.1	13.2 ± 4.2	12.1 ± 3.4
Duration of frontal display (sec)	1.6 ± 1.3	4.3 ± 1.2	—	5.5 ± 4.2
Frequency of sneak-chase	2.5 ± 3.0	0	0	0
Frequency of circle display	4.0 ± 3.8	0	0	0
Frequency of orientation	6.6 ± 6.0	0.08 ± 0.27	0	0

size-classes (lines s and I) to females from the L line and breeding males of intermediate-2 and large size-classes (lines II and L) to females from the s line (see Table 1).

To determine whether differences in behavior between small and intermediate-1 males (lines s and I) are under direct genetic control or are an indirect effect of size, only males of overlapping size phenotype were used (i.e., the largest s males and the smallest I males). Therefore, the s and I males used did not differ in size (mean ± SD = 25.6 ± 1.4 mm [$N = 20$] and 25.8 ± 0.72 mm [$N = 15$], respectively).

In order to determine whether s and L males sire equal numbers of offspring in the absence of competition, we recorded the number of progeny per brood for the first three broods (or for two broods if there was no third) of control matings sired by either blue s, yellow s, or L males. There were ten control matings with each of these three male phenotypes. A similar procedure was used to determine whether s and L males sire broods of equal size in competitive matings. The experimental matings were further subdivided into 1) those in which s males did not contribute to the progeny and 2) those in which both males contributed. Only those broods in which the male progeny was either all L or all s were counted.

RESULTS

Mating Behavior of I, II, and L Males.— Males of these three genotypes begin their mating displays by approaching females with their dorsal and caudal fins rigidly expanded. This initial approach is followed by a series of slow, rigid glides either in front or somewhat to the sides of the females. The distance between male and female is seldom more than 3 cm or less than 0.5 cm, except when followed by a copulation attempt. Duration of this behavior, which we call "frontal display," varied between 1 and 36 seconds. Occasionally, the males momentarily swam backwards toward the females, but in none of these instances did the male's sword ever come into contact with the female. The displays of L, II, and I males were essentially identical (Table 2), with the exception of a shorter mean display duration for I males relative to L males (ANOVA, $F_{[1, 15]} = 6.23$, $P < 0.05$). Copulation attempts were rare, occurring at a frequency of less than 0.25 per observation period and having a mean duration of less than one second. Of all mating displays described for *Xiphophorus* species (Franck, 1964, 1968), the display of *X. nigrensis* most closely resembles that of *X. cortezi*.

Mating behavior of s Males. —The s males have a much broader repertoire of mating behavior than larger males. Three types of behavior were observed in s males which could represent points along a behavioral continuum. At one extreme, the frontal display is virtually identical to that in L, II, and I males; it differs only in its shorter mean duration (Table 2). As with the males of the other genotypes, copulation attempts after the frontal display were rarely observed. The opposite end of the behavioral continuum is characterized by a sneak attempt at copulation which we call "sneak-chase." The male darts in toward the female and often follows this by gonopodial thrusts and attempts at copulation. The approach by the male can be from any direction but usually is from behind the female. Because of the speed and short duration of this behavior, it was not possible to quantify precisely the gonopodial thrusts or to judge their effectiveness. The female's usual response to this behavior is flight; the male often follows with a series of darting motions. The third display, called the "circle display," appears to represent a midpoint between the sneak-chase and frontal displays. The male

darts in toward the female, but instead of attempting a copulation and chase, the male makes a series of fast, abrupt passes or circles around the female. If the female responds by flight, the male may give chase and repeat the circle display or revert to sneak-chase behavior; but if the female remains passive, the circle display may (rarely) be followed by an attempted copulation. The frequencies of the frontal-display behavior in L and s males differ significantly (Student's $t = 4.16$, $d.f. = 92$, $P < 0.001$; Table 2). The combined mean frequency ($\pm$SD) of the three behaviors (frontal display, circle, sneak-chase) for s males is 13.2 $\pm$ 6.1, which does not differ significantly from the frequency of frontal display exhibited by males of the other three genotypes.

A fourth behavior associated mostly with s males involves a male positioning his body in a plane such that he points directly toward the female. This "orientation" behavior often results in the male assuming an attitude that differs from the normal horizontal posture when he is a distance of 10–20 cm from the female. This behavior may be identical to "anschleichen" (creeping up) described by Franck (1964, 1968) for X. helleri, X. pygmaeus, and X. cortezi. Orientation behavior usually precedes an approach to the female, but the method of approach is highly variable. The male may either dart toward the female swiftly and abruptly or approach her in a series of small slow swimming episodes. The approach can be discontinued at any time. The incidence of orientation behavior was highly variable among s males; it occurred at a frequency ($\pm$SD) of 6.6 $\pm$ 6.0 per observation period and preceded a mating display 43% of the time. Orientation positioning was never performed by L or II males and was performed infrequently by I males (observed four times out of nine matings during a total of 50 observation periods).

Competition Between s and L Males. — High frequencies of male-male as well as male-female interactions were observed in mating competitions between s and L males (14 matings in 75 observation periods). The predominant interaction involved chase of the s male by the L male. The chase rarely lasted more than two seconds and usually ended with the s male hiding in the aquatic vegetation. In 1% of all male-male interactions the s male did not flee but instead responded with a counterdisplay. These displays involved the two males swimming parallel to one another, 1–2 cm apart, with their dorsal and caudal fins extended; occasionally one nipped or slapped his tail at the other fish. Similar agonistic behavior also occurs in X. pygmaeus, X. helleri, and X. maculatus (Clark et al., 1954; Franck, 1964). Chase behavior by the L male was usually elicited by the emergence of the s male from hiding or its approach to the female. The persistent aggression of L males toward s males resulted in L males spending a greater amount of time with the females than did s males (81.7% vs. 14.0% of observation periods; $t = 2.51$, $d.f. = 90$, $P = 0.01$).

In mating competitions with L males, behavior of the s males did not differ qualitatively from behavior in the control matings; however, overall s-male mating activity decreased. Not all behaviors were affected in the same manner: the frequencies of frontal display and circle display decreased (two-level nested ANOVA [Sokal and Rohlf, 1981 p. 293], $F_{[1, 17]} = 10.28$, $P < 0.005$), but the frequency of sneak-chase behavior increased significantly ($F_{1, 17]} = 8.26$, $P < 0.005$). The frequency of orientation behavior of s males also increased in the competition matings (9.7 $\pm$ 7.0 [SD] vs. 6.6 + 5.6, Student's $t = 2.25$, $d.f. = 90$, $P < 0.01$) and preceded a mating display at a higher frequency (83% vs. 43%). Orientation behavior was equally likely to precede any of the three mating behaviors.

I Males in Competition With L Males. — The pattern of male-male interactions in competition mating involving I and L males is similar to that observed in interactions involving s and L males. A high frequency of chase by the L male (15.6 $\pm$ 6.0, 8 matings, 45 observations) and flight by the I male was observed. In 0.8% of the male encounters, the I male responded with a counterdisplay. This momentary challenge was always short-lived and was followed by a hasty retreat. The percentages of the observation periods spent with or near females were also similar to those observed for male competition matings with s and L males (L males: 81.7%; I males: 11.7%).

Mating behavior of I males in the pres-

TABLE 3. A comparison of the mean frequencies (±SD) per observation of the mating behaviors of s and I males in competition with L males.

	Behavior			
Male	Frontal display	Sneak-chase	Circle	Orientation
s	1.3 ± 2.0*	4.2 ± 3.5**	0.96 ± 0.8**	9.4 ± 8.3**
I	2.9 ± 6.8	0	0.04 ± 0.2	1.3 ± 3.1

* $P < 0.05$; ** $P < 0.01$.

ence of L males differs greatly from that observed in similar competition matings involving s males (Table 3). In eight matings and in 45 observation periods, no sneak-chase and only two questionable circle displays were observed. Orientation behavior by I males occurred at a frequency of 1.34 ± 3.1 and frontal display at a frequency of 2.9 ± 6.8. The frequency of frontal display by L males in the absence of competition (mean = 12.1, SD = 3.4) did not differ significantly from that in mating competition with s males (mean = 10.42, SD = 5.0) or with I males (mean = 10.5, SD = 5.8) (two-level nested ANOVA, $F_{[2, 24]}$ = 3.3, $P >$ 0.05).

Female Response. —Female pygmy swordtails exhibited few recognizable courtship behaviors or responses. Females responded to male courtship negatively by flight. Female behaviors indicating a negative response toward male courtship, such as nipping, tail slapping, s-curving, or backing behavior, have been described in the platyfish, *X. maculatus* (Clark et al., 1954), but were either not observed or rare (two instances of nipping) in our study. A positive response to male courtship was difficult to determine. If a female did not evade a courting male, she either continued foraging for food or remained motionless. Flight was scored as a negative response to male behaviors and all other female responses were scored as positive responses. In competition matings involving s and L males, females swam away from only 2.7% of L-male displays but swam away from s males after 13.2% of the frontal displays, 42.1% of the circle displays, and 96.1% of the sneak-chase encounters. Female response in I-male control matings was similar to that observed for L-male displays (flight in 4.1% of the encounters). The difference between female response to frontal display of L and I males on the one hand and that of s males on the

other is significant (t = 4.6, *d.f.* = 120, $P <$ 0.001), and we tentatively attributed this to female preference for a longer display (Table 2), rather than for large male size. The females showed no recognizable reaction to orientation behavior.

Mating Success. —L males had greater reproductive success than did s males in the competitive matings: L males made up 75% of the male progeny (601 L, 200 s ♂♂). Five matings produced only L males, and 12 matings produced L and s progeny in various proportions; no matings resulted exclusively in s-male progeny. Data from three matings are not included here, because of the death of one male before the first brood was produced. Mating success of blue s males was the same as that of yellow s males. The sex ratio of the progeny of the 17 competitive matings did not deviate significantly from unity (793 ♀♀, 801 ♂♂).

The mating success of L males was slightly greater in the 200–400 liter aquaria (seven aquaria; 312 L vs. 47 s male offspring, 51 broods) than in the 20-liter ones (ten aquaria; 289 L vs. 153 s male offspring, 103 broods). Mating success of s males was slightly higher in later broods of the same mating. This is possibly a result of male-male habituation with time, because some of these matings lasted more than one year. This did not appreciably affect the results, other than adding a slight bias toward s-male mating success.

In control matings, L males sired a larger number of offspring per brood than did s males (ANOVA, $F_{[1, 83]}$ = 8.42, $P < 0.01$; Table 4). The length of time from the date the mating was initiated to the birth of the first brood did not differ significantly between L and s control matings (Table 4). Thus, the greater reproductive success of the L males in the experimental crosses must be attributed to a combination of their greater competitive ability, their ability to

TABLE 4. Number of broods, number of fry per brood ($\bar{x} \pm$ SD), and length of mating time prior to birth of the first brood ($\bar{x} \pm$ SD) in *Xiphophorus nigrensis* lines descended from fish collected in the Río Coy.

Mating	Male	Number of broods	Number of fry per brood	Range	Weeks to first brood
Control	s (yellow)	28	8.6 ± 0.7	3–18	7.4 ± 1.88
	s (blue)	29	9.1 ± 1.1	2–22	6.6 ± 0.63
	L	28	10.6 ± 1.6	2–28	6.8 ± 0.56
Experimental					
Both males sired progeny	s	28	9.0 ± 0.9	2–24	7.2 ± 0.55
	L	31	9.1 ± 1.2	2–26	
Only L males sired progeny	L	28	11.4 ± 1.3	1–26	5.6 ± 0.84

sire a greater number of young per brood, and female preference for their longer display.

In four competitive matings, the s males sired an appreciable number of offspring. Over periods of many months, the L and s males of these four crosses had consistently different mating success with the two females of each pair (Table 5), which suggests that individual females may vary in their choice of males.

DISCUSSION

Males of the pygmy swordtail, *X. nigrensis,* exhibit size-related differences in courtship behavior. The three largest size-classes (I, II, and L) engage exclusively in frontal display, primarily in front of the female, while s males use a variety of behavioral approaches, from frontal display to sneak-chase attempts at copulation. The s males shift their behavior in response to the presence of large (L) males: they perform predominantly frontal displays in the absence of L males but switch to sneak-chase attempts when in competition with L males. A similar phenomenon has been documented in the Gila topminnow, *Poeciliopsis*

TABLE 5. Reproductive success of L and s males with different females in four separate competitive matings.

		Number of male progeny sired		Number of broods
Mating	Female	L male	s male	
1	1	38	1	7
	2	0	20	5
2	1	26	2	5
	2	0	25	6
3	1	13	3	4
	2	0	35	4
4	1	10	11	5
	2	6	26	5

occidentalis: large dominant males maintain territories and court females, and smaller subordinate males show "sneak" attempts at copulation in the presence of a dominant male but become aggressive and territorial when the dominant male is removed (Constantz, 1975). Constantz (1975) postulated an "ontogenetic switch mechanism" contingent upon body size at maturity but did not elaborate further on its physiological basis.

In fish, the most common phenotypic correlate to small size is some kind of sneak behavior. Such size differences and associated behaviors may be environmentally induced. For example, size within *P. occidentalis* populations is essentially normally distributed; discrete genotypes for small size have not been identified. Thus, the possibility remains that small males may have the same genotype as large males. The alternate behaviors associated with small size may therefore be "phenotypic" (Austad, 1984). Male size and courtship behavior may also be environmentally induced in the pupfish, *Cyprinodon* sp. (Kodric-Brown, 1977). However, the size distribution of mature pupfish males in breeding condition is discontinuous, with distinct large and small size classes, and the situation is further complicated by the presence of many males in nonbreeding condition. In sunfishes (*Lepomis*), satellite males and female mimics grow at the same rate as nesting males until the age of two years. Then, the former become mature (a process accompanied by a strongly reduced growth rate that is perhaps an indirect effect of gonad maturation), but the latter remain immature for several more years (Dominey, 1980; Gross, 1982). Satellite males and female mimics are always smaller than nesting males, and the former

do not eventually develop into nesting males (Gross, 1982). (Nothing is known concerning the cue that controls the switch at two years of age. Dominey (1980) postulated that a genetic polymorphism was involved but later abandoned this view on the basis of some preliminary evidence to the contrary [Dominey, 1984].) The males of *Lepomis* thus become locked into their size categories and reproductive tactics. A similar situation occurs in several species of salmon (Gross, 1984).

There are few examples of alternate behavior patterns with a known Mendelian basis. Alternate plumage colorations in the ruff, *Philomachus pugnax,* are most likely genetically controlled and are closely correlated with certain behavior patterns (van Rhijn, 1973). Whether the effects on plumages and behaviors are pleiotropically mediated by a single locus or controlled by two closely linked loci is not known. The differences in behavior could be under indirect genetic control and result from the interaction between birds of different plumages.

The range of mating behaviors in *X. nigrensis* is not purely "phenotypic," because size is controlled by alternate alleles at a Y-linked locus. Fish with the *s* allele at this locus can switch between frontal display and sneak-chase behaviors, whereas those with the *I, II,* and *L* alleles are locked into the frontal-display tactic: with two possible exceptions, none of the L ($N = 26$), II ($N = 3$), or I ($N = 15$) males exhibited sneak-chase or circle displays. The difference in behavior among males with different P genotypes does not appear to be a simple function of size but, rather, is due to an indirect effect of the P locus. In the competition experiments (s vs. L males and I vs. L males), the sizes of the s and I males were standardized by choosing fish from the area of size overlap (the largest s males and the smallest I males); yet none of the I males showed sneak-chase behavior. This raises the question of whether the alleles at the P locus themselves are directly responsible for the behavioral differences or whether a second, closely linked locus with two or more alleles controls alternate behaviors. A Y-linked factor that influences size at sexual maturity and shows no crossing-over (Kallman, unpubl.) would permit the evolution

and further linkage of traits adaptive for a specific size. This occurs in *X. nigrensis* of the Río Coy, where the allele for solid-yellow body coloration and the suppressor of vertical barring are always linked to *s* on the Y chromosome but are never associated with any other P allele on the X or Y (Zimmerer and Kallman, 1988). We cannot assign a function to the trait yellow body coloration, but the vertical-bar pattern is a signal for aggression and dominance. Its suppression could be advantageous to small males which rarely, if ever, win in encounters with L males. During aggressive interactions between males of the three larger size classes, the vertical-bar pattern disappears in subordinates. A third trait, male growth rate, is always associated with certain P factors. The s males grow at the slowest rate, and I, II, and L males grow increasingly faster, in that order. The same relationship exists in the *X. nigrensis* population inhabiting the Río Choy. There is no compelling reason to assume that the differences in growth rate, which become apparent within a few days after birth, are a direct effect of the P factors that stipulate size at maturity. We note that males of the different P genotypes of *X. maculatus* and *X. montezumae* grow at the same rate (Kallman, 1983).

Sneak-chase behavior has also been reported for *X. helleri, X. cortezi,* and *X. pygmaeus* (Franck, 1964). Adult males of *X. pygmaeus,* the sister species of *X. nigrensis,* are of relatively uniform small size, yet they exhibit only sneak-chase behavior. Frontal display, the various components of which are species-specific, is therefore present in all but one of the 17 described species of *Xiphophorus* (Franck, 1964, 1968, 1970) including *X. milleri,* in which most males are as small and uniform as those of *X. pygmaeus.* It is not clear whether the two behaviors evolved or are maintained as a response to a wide spectrum of adult male size, be it environmentally or genetically induced.

The developmental pathways that lead from a specific genetic condition to a particular behavior pattern are poorly known. Most behaviors are polygenically inherited (Franck, 1974; Noakes, 1986), and it is unlikely that a single gene controls sneak-chase behavior in *X. nigrensis.* The expression of

sneak-chase, orientation, and circle behaviors is facultative in smaller males and increases significantly in frequency in response to the presence of larger males. In control matings of I males, orientation behavior is rare, and sneak-chase and circle behaviors are unknown; however, in competition matings with L males, the incidence of orientation behavior by I males increases significantly. Therefore, the manifestation of these behavior patterns may represent a threshold phenomenon which could be controlled by allelic variation at a locus linked to the *P* locus. Such control of alternate behavior does not involve the evolution of new polygenic patterns but merely modifies what is already present. This view implies that most *Xiphophorus* possess the genetic basis for these types of behavior but that the expression and frequency of a particular behavior depends upon which particular allele is present at the postulated locus that governs the threshold. The frequency of the various components of the male courtship behavior of *Poecilia reticulata* is also inherited as a Y-linked trait (Farr, 1983). Manning (1967) has argued that mutations (i.e., allelic variation) primarily affect the threshold and frequency of a given behavior and not the nature of the pattern itself. Such mutant alleles could have electrophysiological effects that alter membrane excitability (see Ganetzky and Wu, 1986).

The greater reproductive success of L males in the competition experiments must be attributed to the selective advantage gained by their use of the frontal display, their dominance and their inherent ability to sire more fry per brood. The females' responses to the different behaviors of s males show that they prefer males that engage in frontal display. Females of *X. pygmaeus* prefer heterospecific males of *X. nigrensis* that display over conspecifics that do not (Ryan and Wagner, 1987). However, preference for L males may vary among individual females (Table 5) such that some s males sire an appreciable number of offspring even in the presence of L males.

Fish density may also have an effect on the relative reproductive success of L and s males. Under high density or in restricted space, it may be easier for L males to monopolize females. Conversely, under low density, an s male would be less likely to come in contact with L males and should have greater reproductive success. The results from the 200-liter aquaria matings show that, if anything, the opposite is true. Under laboratory and field conditions, the fish form loose aggregates and do not disperse randomly. This allows L males to monopolize females, even under conditions of low fish density. It also allows us, with some confidence, to apply our laboratory observations to what happens in the field.

Do s males shift mating behavior to maximize mating potential? In the presence of L males, it appears to be uneconomical for s males to display; the alternative is a sneak-chase attempt at copulation. Whether this tactic is more economical is debatable: in spite of the marked shift of s males from display to sneak-chase behavior under competitive conditions, s males sired only one-third as many progeny as L males (200 vs. 601). Thus, under experimental conditions, the shift to sneak-chase could not overcome the effects of L-male dominance and display behavior. Our observations do not let us assess the effectiveness of sneak-chase attempts. Most of the attempts may be merely "thrusting," which in *X. maculatus* and *X. helleri* does not lead to insemination (Clark et al., 1954). It is also not known what proportion of the s progeny can be attributed to sperm transfer after sneak-chase episodes or to the much rarer copulations after frontal display.

The adaptive significance of mating variation among *P* genotypes must be considered in a larger context. In spite of the shift in behavior of s males under competitive conditions, their reproductive success was still well below that of L males. Other factors must play a role in order to compensate for the inferior ability of s males in competition with larger males. Although immature L males possess a higher growth rate than immature s males, it takes the former almost twice as long to mature (26.6 weeks, range = 20–34) than s males (14.4 weeks, range = 12–17). Although L males sire larger broods, the intrinsic rate of natural increase (Cole, 1954) of s males is still more than twice that of L males. Moreover, the frequency of the smaller morphs in the Río Coy is much higher than that of the larger

ones (Kallman, unpubl.). Therefore, a majority of the male-female and male-male interactions will involve only s males. This is a situation quite different from that for sunfish and salmon, in which the precocious, small males exhibiting sneak behavior do not gain access to females or eggs unless a large late-maturing male is present (Gross, 1984). The genetically controlled size polymorphism of *X. nigrensis* from the Río Coy is undoubtedly maintained by the interaction of many variables, including growth rate, size and age at maturity, pigment patterns, behaviors, and perhaps habitat preference. Differences in some of these traits are direct or indirect effects of the *P* factors, while the differences in others are probably due to allelic variation at hitchhiking genes.

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LITERATURE CITED

ALCOCK, J., C. E. JONES, AND S. L. BUCHMANN. 1977. Male mating strategies in the bee *Centrus pallida* Fox (Anthophoridae: Hymenoptera). Amer. Natur. 111:145–155.

AUSTAD, S. N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. Amer. Zool. 24:309–319.

BARLOW, G. W. 1967. Social behavior of a South American leaf fish *Polycentrus schomburgkii*, with an account of recurring pseudofemale behavior. Amer. Midl. Natur. 78:215–234.

BROCKMANN, H. J., A. GRAFEN, AND R. DAWKINS. 1979. Evolutionarily stable nesting strategy in a digger wasp. J. Theoret. Biol. 77:473–496.

CADE, W. 1979. The evolution of alternative male reproductive strategies in field crickets, pp. 343–380. *In* M. S. Blum and N. A. Blum (eds.), Sexual Selection and Reproductive Competition in Insects. Academic Press, N.Y.

CLARK, E., L. R. ARONSON, AND M. GORDON. 1954. Mating behavior patterns in two sympatric species of xiphophorin fishes: Their inheritance and significance in sexual isolation. Bull. Amer. Mus. Nat. Hist. 103:135–226.

COLE, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 20:103–137.

CONSTANTZ, G. D. 1975. Behavioral ecology of mating in the male gila topminnow, *Poeciliopsis occi-*

dentalis (Cyprinodontiformes: Poeciliidae). Ecology 56:966–973.

DOMINEY, W. J. 1980. Female mimicry in male bluegill sunfish—A genetic polymorphism? Nature 284:546–548.

———. 1984. Alternative mating tactics and evolutionarily stable strategies. Amer. Zool. 24:385–396.

DUVAL, S. W., I. S. BERNSTEIN, AND T. P. GORDON. 1976. Paternity and status in a rhesus monkey group. J. Reprod. Fert. 47:25–31.

FARR, J. A. 1983. The inheritance of quantitative fitness traits in guppies. Evolution 37:1193–1209.

FRANCK, D. 1964. Vergleichende Verhaltensstudien an lebendgebärenden Zahnkarpfen der Gattung *Xiphophorus*. Zool. Jahrb. Physiol. 71:117–170.

———. 1968. Weitere Untersuchungen zur vergleichenden Ethologie der Gattung *Xiphophorus* (Pisces). Behaviour 30:76–95.

———. 1970. Verhaltensgenetische Untersuchungen an Artbastarden der Gattung *Xiphophorus* (Pisces). Z. Tierpsychol. 27:1–34.

———. 1974. The genetic basis of evolutionary changes in behaviour patterns, pp. 119–140. *In* J. H. F. van Abeelen (ed.), The Genetics of Behaviour. Elsevier, N.Y.

GANETZKY, B., AND C. F. WU. 1986. Neurogenetics of membrane excitability in *Drosophila*. Ann. Rev. Genet. 20:13–44.

GORDON, M. 1950. Fishes as laboratory animals, pp. 345–449. *In* E. J. Farris (ed.), The Care and Breeding of Laboratory Animals. Wiley, N.Y.

GROSS, N. R. 1982. Sneakers, satellites, and parentals. Polymorphic mating strategies in North American sunfishes. Z. Tierpsychol. 60:1–26.

———. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes, pp. 55–75. *In* G. W. Potts and R. J. Wootton (eds.), Fish Reproduction, Strategies and Tactics. Academic Press, N.Y.

———. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47–48.

HAMILTON, W. D. 1979. Wingless and fighting males in fig wasps and other insects, pp. 167–220. *In* M. S. Blum and N. A. Blum (eds.), Sexual Selection and Reproductive Competition in Insects. Academic Press, N.Y.

HAUSFATER, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*): A quantitative analysis. Contrib. Primatol. 7:1–150.

KALLMAN, K. D. 1983. The sex determining mechanism of the poeciliid fish, *Xiphophorus montezumae*, and the genetic control of the sexual maturation process and adult size. Copeia 1983:733–769.

KALLMAN, K. D., AND V. BORKOSKI. 1977. A sexlinked gene controlling the onset of sexual maturity in female and male platyfish (*Xiphophorus maculatus*), fecundity in females and adult size in males. Genetics 898:79–119.

KALLMAN, K. D., M. P. SCHREIBMAN, AND V. BORKOSKI. 1973. Genetic control of gonadotroph differentiation in the platyfish, *Xiphophorus maculatus* (Poeciliidae). Science 181:678–680.

KODRIC-BROWN, A. 1977. Reproductive success and the evolution of breeding territories in pupfish (*Cyprinodon*). Evolution 31:756–766.

LeBoeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14:163–176.

Manning, A. 1967. Genes and the evolution of insect behavior, pp. 44–60. *In* J. Hirsch (ed.), Behaviour-Genetics Analysis. McGraw-Hill, N.Y.

Maynard Smith, J. 1976. Evolution and the theory of games. Amer. Sci. 64:41–45.

———. 1981. Will a sexual population evolve to an ESS? Amer. Natur. 117:1015–1018.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature 246:15–18.

Noakes, D. L. G. 1986. Genetic basis of fish behaviour, pp. 3–22. *In* T. J. Pitcher (ed.), The Behavior of Teleost Fishes. Johns Hopkins Univ. Press, Baltimore, MD.

Rubenstein, D. I. 1980. On the evolution of alternative mating strategies, pp. 65–100. *In* J. E. R. Staddon (ed.), Limits to Action: The Allocation of Individual Behavior. Academic Press, N.Y.

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

Sokal, R. R., and F. A. Rohlf. 1981. Biometry, 2nd Ed. Freeman, San Francisco, CA.

Thornhill, R. 1979. Adaptive female-mimicking behavior in a scorpionfly. Science 205:412–414.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–269.

van Rhijn, T. J. 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax* (L.). Behaviour 47:153–229.

Waage, K. 1973. Reproductive behavior and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). Behaviour 47:240–256.

Warner, R. R., D. R. Robertson, and E. G. Leigh, Jr. 1975. Sex change and sexual selection. Science 190:633–638.

Wells, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58:750–762.

Zander, C. D. 1968. Uber die Vererbung von Y-gebundenen Farbgenen des *Xiphophorus pygmaeus nigrensis* Rosen (Pisces). Molec. Gen. Genet. 101:29–42.

Zimmerer, E. J. 1982. Size related courtship strategies in the pygmy swordtail, *Xiphophorus nigrensis*. Amer. Zool. 22:910.

Zimmerer, E. J., and K. D. Kallman. 1988. The inheritance of vertical barring (aggression and appeasement signals) in the pygmy swordtails (*Xiphophorus*, Poeciliidae, Teleostei). Copeia 1988:299–307.

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