

BREEDING CYCLES IN NATURAL POPULATIONS OF *XIPHOPHORUS NIGRENSIS*, *X. MULTILINEATUS*, AND *X. PYGMAEUS*.—Poeciliid fishes are well studied in relation to demography and life-history evolution (Stearns, 1978; Constantz, 1979; Reznick and Miles, 1989); one of the critical variables in these studies is the breeding cycle. Therefore, it is surprising that, for most of the species in this family, breeding cycles in nature have not been documented. A series of studies on the alternative mating strategies in *Xiphophorus nigrensis* have shown that body size is correlated with mating strategy (Ryan and Causey, 1989), that variation in body size is due to a genetic polymorphism at the pituitary (P) locus (Kallman, 1984, 1989), and that the fitnesses of the two mating types are equal (Ryan et al., 1992). It was important to determine whether breeding was continuous or discrete in order to design an appropriate model to test the hypothesis of equal fitnesses of two mating strategies in this species. In the present study, we determine female breeding cycles in three species—*Xiphophorus nigrensis*, *X. multilineatus*, and *X. pygmaeus*—and discuss the relationships between brood size, female size, and time of year.

Materials and methods.—*Xiphophorus nigrensis* females were collected from the headwaters of the Rio Choy and *X. multilineatus* (formerly considered the same species, see Rauchenberger et al., 1990) from the Rio Coy, both in San Luis Potosi, Mexico. *Xiphophorus pygmaeus* females were collected from two sites on the Rio Huichihuayan, Mexico, the headwaters near Nacimiento (only sampled in Oct. and Jan.), and at Chimalaco. Water temperature ranged from 25.0–27.0 C at the headwaters of the Rio Choy, 24.0–27.0 C at the Rio Coy, 22.0–23.0 C at the Chimalaco site of the Rio Huichihuayan, and 20.5 to 23.0 at the Nacimiento of the Rio Huichihuayan. On one of the seven sample dates (Aug.), both the Rio Choy and Rio Coy were flooded, and therefore fish were collected only from the Rio Huichihuayan. Adult females, identified by a brood spot, were collected at random and preserved in Bouin solution. Sample sizes and dates are shown in Figure 1. We

recorded standard length (SL), the number of eggs, and the number of embryos for each female. Our egg classification included eggs that had clearly yolked (no longer small and opaque) and possibly had been fertilized (up to stage 4 as described by Tavolga, 1949). An embryo was recognized as such if it had reached stage 5 (0.9 day) as described by Tavolga (1949). Late embryos and yolked eggs were present together in 17% of the females examined. It is impossible to determine whether these eggs would have been reabsorbed or would have become part of the following brood. Therefore, to reduce the problem of overestimating brood size when late embryos and yolked eggs were present together, only the number of embryos was used in subsequent brood size analysis in these cases.

Results.—All sampled females from all four sites at all sample periods had either eggs or embryos and, therefore, were reproductively active. In addition, there were more females with eggs and embryos (fertilization had occurred) than females with only eggs (eggs may not have been fertilized) in every sample except for those collected in July in the Rios Coy and Huichihuayan (Fig. 1).

There was a significant correlation between female size and brood size for *X. nigrensis* ($r^2 = 0.34$, $df = 59$, $P = 0.00001$) and *X. multilineatus* ($r^2 = 0.13$, $df = 45$, $P = 0.02$) but not for either of the *X. pygmaeus* populations (Chimalaco, $r^2 = 0.0001$, $df = 48$, $P = 0.95$; Nacimiento, $r^2 = 0.08$, $df = 19$, $P = 0.21$). We determined whether brood size might also vary as a function of the time of year by using the residuals from the regression of female size on brood size in a one-way analysis of variance. Brood size varied significantly as a function of time of year for all three species (Table 1). Average female size and average brood size by site and time of year are shown in Table 2.

Discussion.—*Xiphophorus nigrensis*, *X. multilineatus*, and *X. pygmaeus* breed continuously. Reproductively active females were present throughout the year for all three species. Information on breeding cycles is important, because it can influence population size and because it can be used to choose between population models that assume continuous versus discrete breeding. It is common in many life-

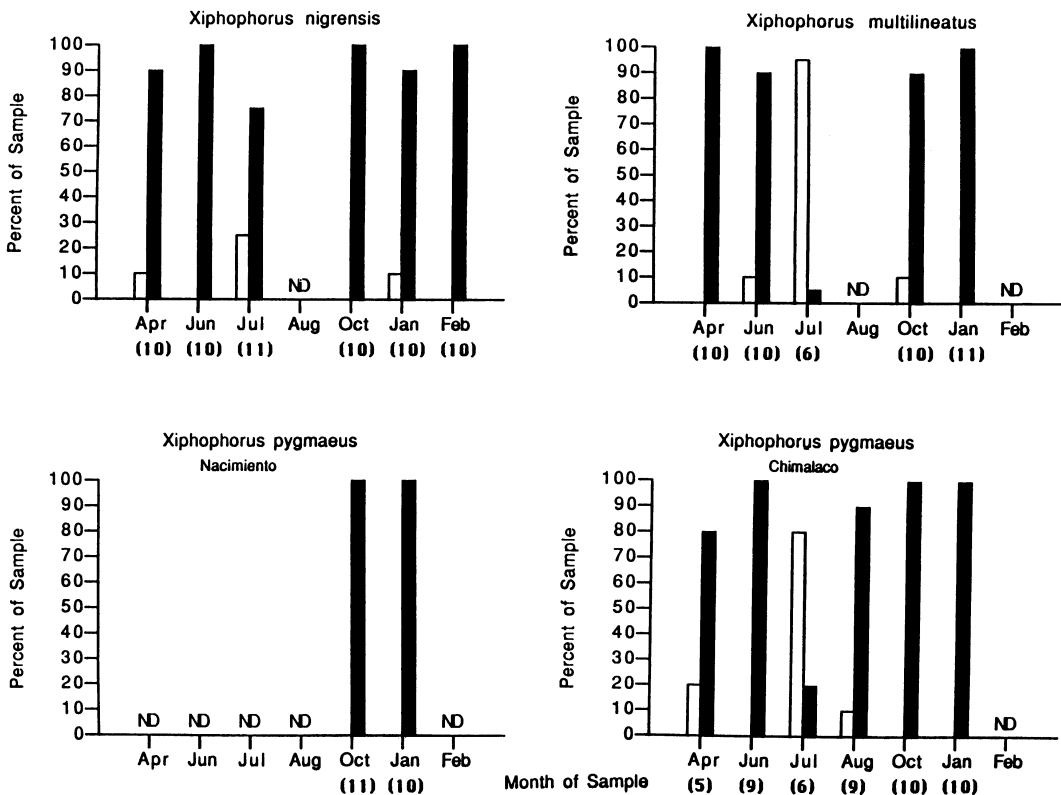


Fig. 1. Percent of females that were carrying only eggs (white bars) or were carrying eggs and embryos (black bars) for each sample period. ND = no data collected for that sample period. Sample sizes are given below each date.

history studies to assume that breeding is continuous, because this assumption allows for a more tractable model. Continuous breeding appears to be uncommon in most organisms but has been documented for another species of *Xiphophorus*, a population of *X. maculatus* that breeds in a constant temperature spring (Borowsky and Kallman, 1976).

Seasonal changes in brood size would also affect population growth rate and, thus, the degree to which an assumption of continuous breeding would be realistic. Brood size was influenced by the sample period in all three species. The influence of seasonal variation in brood size on population growth, however, would be smaller than the effects of a discontinuous breeding cycle.

Many variables are known to influence brood size in poeciliids (see Travis, 1989), including female size (approx. 50% of variance in brood size in ovoviviparous species; Reznick and Ender, 1982; Trexler, 1985; Reznick and Bryga,

1987), female nutritional condition (Wooten, 1979; Reznick, 1983), and time of year (Constantz, 1979). Although female size was correlated with brood size for *X. nigrensis* and *X. multilineatus* in this study, we did not find a statistical correlation between brood size and female size in *X. pygmaeus*. In addition, female size did not explain very much of the variation in brood size for *X. nigrensis* and *X. multilineatus*. The lack of

TABLE 1. ANALYSIS OF VARIANCE OF BROOD SIZE AS A FUNCTION OF TIME OF YEAR.

Species	df	F	P
<i>X. nigrensis</i>	5,55	3.8	0.005
<i>X. multilineatus</i>	4,41	4.09	0.01
<i>X. pygmaeus</i>			
Chimalaco	5,42	4.7	0.002
<i>X. pygmaeus</i>			
Nacimiento	1,19	6.52	0.02

TABLE 2. AVERAGE FEMALE SIZE AND BROOD SIZE FOR EACH SAMPLE PERIOD.

	April	June	July	Aug.	Oct.	Jan.	Feb.
<i>H. nigrensis</i>							
Female (mm)	27.7	29.1	29.2		29.4	25.9	26.7
SD	(3.15)	(2.46)	(3.15)		(2.27)	(1.91)	(2.23)
Brood size	6.0	6.2	4.8		4.0	3.6	5.1
SD	(4.03)	(1.55)	(2.40)		(0.94)	(1.35)	(2.33)
<i>H. multilineatus</i>							
Female (mm)	29.3	31.6	28.4		31.0	29.0	
SD	(3.05)	(2.83)	(2.81)		(3.41)	(2.50)	
Brood size	10.1	9.12	4.3		6.4	5.6	
SD	(4.50)	(4.90)	(1.50)		(2.59)	(1.69)	
<i>H. pygmaeus</i>							
Female (mm)	23.8	25.2	27.0	27.5	26.4	22.0	
SD	(1.53)	(1.28)	(1.04)	(0.87)	(2.37)	(1.62)	
Brood size	4.0	2.9	1.4	4.7	4.1	5.2	
SD	(2.28)	(0.74)	(1.74)	(1.33)	(1.37)	(1.83)	

correlation in *X. pygmaeus* could be due to either the smaller range of female body sizes in the Chimalaco sample or the small sample sizes. However, the overall low correlation with female body size in these species could also be due to the confounding effect of time of year on brood size.

The rainy season in the central part of Mexico is from mid-April through Dec., and it is during this time that the rivers often flood. When rivers are turbulent and murky, mating may become more difficult. There is some indication from our data that females of the same size may have smaller broods during the rainy season. Even though poeciliid fishes are capable of storing sperm (Van Oordt, 1928), there is evidence that brood size may decrease with decreased mating (Travis, 1989). In addition, the samples in which there were more females without embryos than females with eggs and embryos were all in July, which is the middle of the rainy season. Borowsky and Diffley (1981) found that *X. variatus* females suspended reproduction during traumatic conditions, such as warm stagnant water. More work is needed to determine how seasonal factors, such as flooding, might influence breeding in these species.

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LITERATURE CITED

- BOROWSKY, R. L., AND J. DIFFLEY. 1981. Synchronized maturation and breeding in natural populations of *Xiphophorus variatus* (Poeciliidae). *Env. Biol. Fish.* 6:49–58.
- , AND K. D. KALLMAN. 1976. Patterns of mating in natural populations of *Xiphophorus* (Pisces: Poeciliidae). *Copeia* 1976:792–796.
- CONSTANTZ, G. D. 1979. Life history patterns of a livebearing fish in contrasting environments. *Oecologia* 40:189–201.
- KALLMAN, K. D. 1984. A new look at sex determination in poeciliid fishes, p. 95–171. *In: Evolutionary genetics of fishes*. B. J. Turner (ed.). Plenum Publishing Company, New York, New York.
- . 1989. Genetic control of size at maturity in *Xiphophorus*, p. 163–184. *In: Ecology and evolution of livebearing fishes (Poeciliidae)*. G. K. Meffe and F. F. Snelson (eds.). Prentice-Hall, New York, New York.
- RAUCHENBERGER, M., K. D. KALLMAN, AND D. C. MORIZOT. 1990. Monophyly and geography of the

- Rio Panuco Basin swordtails (*Xiphophorus*) with descriptions of four new species. *Amer. Mus. Nov.* No. 2975.
- REZNICK, D. N. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. *Ecology* 64:862–873.
- , AND H. BRYGA. 1987. Life-history evolution in guppies (*Poecilia reticulata*): I. Phenotypic and genetic changes in an introduction experiment. *Evolution* 41:1370–1385.
- , AND J. A. ENDLER. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Ibid.* 36:160–177.
- , AND D. B. MILES. 1989. A review of life history patterns in poeciliid fishes, p. 125–148. *In: Ecology and evolution of livebearing fishes (Poeciliidae)*. G. K. Meffe and F. F. Snelson (eds.). Prentice-Hall, New York, New York.
- RYAN, M. J., AND B. CAUSEY. 1989. "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *X. pygmaeus* (Pisces: Poeciliidae). *Behav. Ecol. Sociobiol.* 24:241–248.
- , C. PEASE, AND M. R. MORRIS. 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. *Am. Nat.* 139:21–31.
- STEARNS, S. C. 1978. Interpopulational differences in reproductive traits of *Neoheterandria tridentiger* (Pisces: Poeciliidae) in Panama. *Copeia* 1978:88–91.
- TAVOLGA, W. N. 1949. Embryonic development of the platyfish (*Platypoecilus*), the swordtail (*Xiphophorus*), and their hybrids. *Bull. Amer. Mus. Nat. Hist.* 94:161–229.
- TRAVIS, J. 1989. Ecological genetics of life history traits in poeciliid fishes, p 185–200. *In: Ecology and evolution of livebearing fishes (Poeciliidae)*. G. K. Meffe and F. F. Snelson (eds.). Prentice-Hall, New York, New York.
- TREXLER, J. C. 1985. Variation in the degree of viviparity in the sailfin molly, *Poecilia latipinna*. *Copeia* 1985:999–1004.
- VAN OORDT, G. J. 1928. The duration of life of the spermatozoa in the fertilized female of *Xiphophorus helleri* Regan. *Tijdschrift der Nederlandsche Dierkundige Vereeniging.* 1:77–80.
- WOOTEN, R. J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. London* 44:133–159.
- MOLLY R. MORRIS AND MICHAEL J. RYAN, *Department of Zoology, University of Texas, Austin, Texas 78712*. Accepted 15 Oct. 1991.