



---

Patterns of Offspring Size at Birth in Clonal and Sexual Strains of *Poeciliopsis* (Poeciliidae)

Author(s): Stephen C. Weeks and Oscar E. Gaggiotti

Source: *Copeia*, Vol. 1993, No. 4 (Dec. 28, 1993), pp. 1003-1009

Published by: [American Society of Ichthyologists and Herpetologists](#)

Stable URL: <http://www.jstor.org/stable/1447077>

Accessed: 11/11/2010 16:12

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=asih>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



*American Society of Ichthyologists and Herpetologists* is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

<http://www.jstor.org>

## Patterns of Offspring Size at Birth in Clonal and Sexual Strains of *Poeciliopsis* (Poeciliidae)

STEPHEN C. WEEKS AND OSCAR E. GAGGIOTTI

**Females from two closely related reproductive complexes of *Poeciliopsis* reared under common conditions differed in weight of offspring at birth. The two fish strains from a more variable, upstream environment had significantly larger offspring than did three downstream fish strains. There was no consistent pattern of within-clutch variation for the two reproductive complexes. We interpret these data by examining the biotic and abiotic environmental factors in the natural habitats of these two reproductive complexes that may affect offspring size at birth and relate these observations to current adaptive explanations for differences in offspring size. Larger offspring were significantly less likely to be cannibalized by adult *Poeciliopsis*. Cannibalism, combined with the possibility of size-selective predation by insect predators in the upstream habitat, might lead to an advantage of producing larger offspring in these streams. No trends between these two reproductive complexes were found in within-clutch variation in offspring size consistent with predictions of “bet-hedging” life-history models.**

PATTERNS of energetic investment in offspring have figured predominantly in theoretical and empirical life-history studies (Smith and Fretwell, 1974; Stearns, 1976; Kaplan and Cooper, 1984). Investment in offspring, commonly measured in terms of size, can affect juvenile survival, growth rate, intraspecific competition, and resistance to stress (Bagenal, 1969; Brockelman, 1975; Kaplan, 1980). Life-history theory based on optimality models assumes that optimal parental investment maximizes offspring fitness per unit of energy invested (Smith and Fretwell, 1974). Thus, for any particular environment, there should be a single optimal investment per offspring, with “good” environments selecting for smaller offspring and “bad” environments selecting for larger offspring (McGinley et al., 1987). Any variation around this optimal investment can be considered “environmental noise” (McGinley et al., 1987).

A contrasting view is that there is no single optimal offspring size in any environment because of natural habitat heterogeneity (Capienera, 1979; Kaplan and Cooper, 1984). In these models, inter- or intraclutch variation in offspring size maximizes the likelihood of producing the appropriately sized offspring in spatially and temporally unpredictable environments. A correlated prediction is that organisms can also compensate for variable environments by increasing average offspring size (Schultz, 1991). In this model, intraclutch variation is only selected when environmental variability exceeds a threshold value.

Livebearing fishes in the family Poeciliidae

are useful for experimental assessment of offspring size variation (Thibault and Shultz, 1978; Reznick, 1982; Meffe, 1987) because of the wide range of reproductive mechanisms and environments in which poeciliid fish are found and their ease of rearing in the laboratory (Thibault and Schultz, 1978; Reznick and Miles, 1989). In the current study, we compared offspring size in five strains of *Poeciliopsis* reared in a common, controlled environment. These strains occur in two ecologically distinct reproductive complexes (Schultz, 1977; Vrijenhoek et al., 1978): the *monacha* complex, consisting of the sexual, *Poeciliopsis monacha*, and two associated triploid, gynogenetic clones (only one triploid clone was used in this study); and the *lucida* complex, consisting of the sexual, *Poeciliopsis lucida*, and two diploid, hybridogenetic clones [Schultz (1969, 1977) reviews gynogenetic and hybridogenetic reproduction]. The two complexes occur in contrasting portions of the Arroyo de Jaguari tributary of the Río Fuerte (Sonora, Mexico). The *monacha* complex dominates the upstream rocky arroyos (Platanos), whereas the *lucida* complex dominates the downstream sandy bottom portions of this stream (approximately at Agua Caliente, see Schenck and Vrijenhoek, 1986). The upstream habitat is more seasonally variable in water level, light intensity, and food resources than is the downstream habitat (Thibault, 1974a; Thibault and Schultz, 1978). Mature embryos of *P. monacha* weigh an average of 77% more than those of *P. lucida* in the field (Thibault and Schultz, 1978). These differences are qualitatively consistent with dif-

ferences in both ova and offspring size from these strains reared in laboratory cultures (Schultz, 1969, 1982).

Our goal was to determine whether the reported differences in offspring size at birth between *P. monacha* and *P. lucida* could be replicated using individually reared females in a "common garden" experiment. We describe the differences in offspring size at birth for these two sexual and three associated clonal strains. We also present the results of a cannibalism study that show increased offspring size may reduce cannibalism.

#### MATERIALS AND METHODS

Two strains of the *monacha* complex (*P. monacha* and MML/I) and the three strains of the *lucida* complex (*P. lucida*, ML/VII, and ML/VIII) were used in this study. The *P. monacha* were third-generation females reared from outcrossed wild populations collected in the Platanos tributary of the Río Fuerte, Sonora, Mexico. The other four strains were maintained as laboratory stocks for 18–20 years before the present experiment. The *P. lucida* females were from an inbred strain originally collected from the Agua Caliente region of the Río Fuerte (Strain S68-4 PC; Angus and Schultz, 1983). This inbred strain shows no inbreeding depression in growth or fecundity over its many years in laboratory culture (Schultz, 1982). The three unisexual strains are divided into one gynogenetic form (*P. 2monacha-lucida*) and two hybridogenetic forms (*P. monacha-lucida*). The gynogenetic females (accession code: S68-4 MML/I) were artificially inseminated with sperm from a male of the *P. monacha* stock. Females of the two hybridogenetic stocks (accession codes: S68-4 ML/VII and T70-3 ML/VIII; Vrijenhoek et al., 1978) were artificially inseminated with sperm from a male of the *P. lucida* stock. Females of both sexual strains were naturally fertilized by males of their respective strains in large rearing tanks before initiation of the experiment.

Reproductively mature females were held for 2–3 months in individual 3.7-liter plastic containers in a 1500-liter, flow-through aquatic incubator. Temperature was 25 °C, and photoperiod was 12L:12D (Wetherington et al., 1989). All females were fed ad libitum twice daily with frozen brine shrimp adults.

Each plastic container was checked twice daily for newborn fish. Wet mass was determined for both offspring and parent. Fish were blotted dry on absorbent paper, transferred to a tared dish

containing a small quantity of water, and individually weighed to the nearest 0.1 mg. Offspring from the first and second clutch were used in another experiment (S. C. Weeks and R. C. Vrijenhoek, unpubl.) and, thus, were not included in the analyses. Only offspring of a single clutch were included for any one female.

Fifteen females of each of three strains (*P. monacha*, ML/VII, and ML/VIII) were grouped into 15 10-liter aquaria in monocultures of three for a total of five replicates per strain. All sides of aquaria were covered with opaque, white plastic to prevent visual disturbances. Females of similar sizes were used from all three strains (*P. monacha*:  $0.555 \pm 0.154$  g, ML/VII:  $0.549 \pm 0.178$  g, and ML/VIII:  $0.523 \pm 0.215$  g).

Juveniles of three size categories were introduced into each experimental aquarium, as follows: small ( $x < 0.0080$  g), medium ( $0.0094$  g  $< x < 0.0132$  g), and large ( $0.0152$  g  $< x < 0.0250$  g). Only juveniles from ML/VII were used so that differences in predation on the three size classes would not be confounded with genetic differences among juveniles. Four juveniles from each of the three size categories were simultaneously introduced into each aquarium for 10 min. Offspring were then removed, and the numbers of survivors were used to calculate the numbers eaten in each size group.

*Statistical analyses.*—A one-way ANOVA (females nested within strains) was used to determine the differences in mean offspring size. The nested factor "female" was considered random. Thus the strain mean square error was compared against the female mean square error for the F-ratio tests. Average female wet mass differed among strains for fish in the offspring mass study, with *P. monacha*, ML/VII, and ML/VIII females being larger, on average, than *P. lucida* and MML/I. Nevertheless, female mass was not found to be a significant covariate of offspring mass at birth nor intraclutch variation (see below) and, therefore, was not included in these analyses. Intraclutch size variation was measured by comparing the coefficient of variation for offspring mass per clutch among the five strains. A one-way ANOVA was used to compare strains.

Residuals for the ANOVA on the coefficient of variation data were normal, but the residuals of the offspring mass ANOVA were leptokurtic. Therefore, the probability values should be considered conservative for this test. Comparisons of means among strains were made using the Ryan-Einot-Gabriel-Welsch multiple range test [SAS (Statistical Analysis Systems) Institute,

TABLE 1. (A) ANOVA RESULTS FOR OFFSPRING MASS AT BIRTH FOR THE FIVE FISH STRAINS. (B) Pairwise comparisons of mean mass at birth. Strains are ranked from the largest to the smallest offspring size at birth. Underlined means are not significantly different at the  $P = 0.05$  level (Ryan-Einot-Gabriel-Welsch multiple range test).

(A)	Source	df	Sum of Squares	F ratio	P
	Strain	4	0.00060183	18.19	0.0001
	Female (Strain)	71	0.00058741	10.96	0.0001
	Error	484	0.00036551		
(B)	MML/I	<i>P. monacha</i>	ML/VII	ML/VIII	<i>P. lucida</i>
Mean	0.0096	0.0095	0.0077	0.0069	0.0067

Inc., 1985]. The numbers of juveniles consumed in the cannibalism study were compared using G-tests (Sokal and Rohlf, 1981).

### RESULTS

**Offspring Mass.**—Offspring mass at birth differed among strains (Table 1A). Mean offspring mass grouped according to the two reproductive complexes (Table 1B), with offspring from MML/I and *P. monacha* being 35% larger, on average, than those of the other three lines (Table 1B, Fig. 1). ML/VII was intermediate in size between the two sexual strains (31% of the difference between *P. monacha* and *P. lucida*) but grouped with *P. lucida* in the multiple range test (Table 1B). Neither MML/I nor ML/VIII were intermediate to their sexual relatives, both being closely matched with the sexual species with which they naturally coexist (Table 1B). Intracatch size variance differed among strains (Table 2A). There was no overall relationship

TABLE 2. (A) ANOVA RESULTS FOR COEFFICIENT OF VARIATION (CV) FOR OFFSPRING MASS AT BIRTH FOR THE FIVE FISH STRAINS. (B) Pairwise comparisons of CV for offspring mass at birth. Strains are ranked from the largest to the smallest CV. Underlined means are not significantly different at the  $P = 0.05$  level (Ryan-Einot-Gabriel-Welsch multiple range test).

(A)	Source	df	Sum of Squares	F ratio	P
	Strain	4	0.03910937	5.23	0.0010
	Error	68	0.12702733		
(B)	MML/I	<i>P. monacha</i>	ML/VII	ML/VIII	<i>P. lucida</i>
Mean	0.1334	0.1157	0.1115	0.1041	0.0710

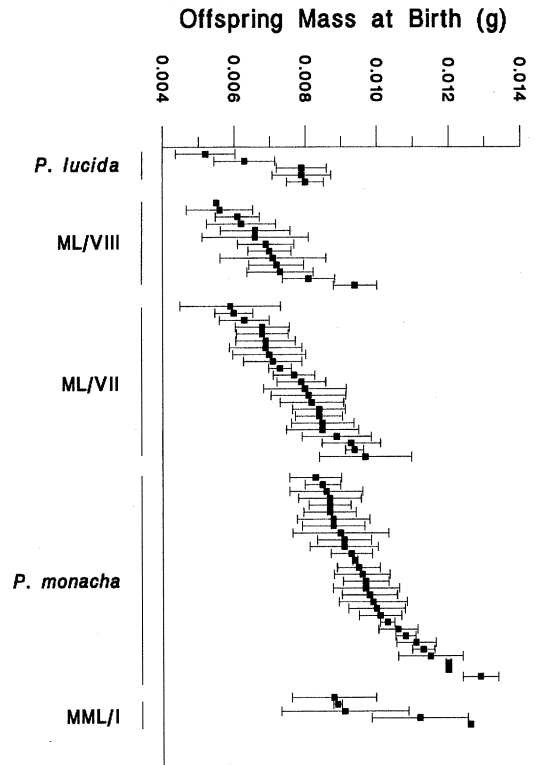


Fig. 1. Means  $\pm$  one standard deviation of offspring wet mass at birth within clutches for the five fish strains. Strains and clutches are ordered by increasing mean mass.

between reproductive complex and intracatch variation (Table 2B, Fig. 1). Like mean size, intracatch variation was not associated with dosage of sexual genotypes in the three clonal strains (Table 2B). Genetic variation in the outcrossed sexual strain (*P. monacha*) did not affect variation among the means or the standard deviation of offspring size when compared to either the inbred sexual strain (*P. lucida*) or the three clonal strains (Fig. 1).

**Cannibalism.**—Three to five times as many juveniles of the smallest size class were consumed relative to the other two size categories (Table 3;  $G = 19.95$ ,  $P < 0.001$ ). All three strains showed the same pattern of consuming the smallest size class (Table 3), which was verified by the independence of juvenile size and fish strain ( $G = 4.09$ , n.s.). *Poeciliopsis monacha* and ML/VII consumed a larger quantity of offspring than ML/VIII during the 10-min exposure period ( $G = 17.14$ ,  $P < 0.001$ ). Initial observations revealed that the consumption of different-sized offspring was due to the ability

TABLE 3. NUMBERS OF OFFSPRING CONSUMED IN EACH OF THREE SIZE CLASSES. Twenty offspring per size category were offered to 15 females per strain, for a total of 60 offspring per size category and 180 total offspring. All offspring were from the ML/VII strain.

Offspring size	Strain			Total
	ML/VII	ML/VIII	<i>P. monacha</i>	
Small	12	5	12	29
Medium	5	2	2	9
Large	2	0	4	6
Total consumed	19	7	18	44

of the juveniles from the larger size classes to avoid predation, rather than selective predation by the adults on the smaller fish.

#### DISCUSSION

We found a consistent pattern of offspring size at birth within two ecologically distinct reproductive complexes but a divergent pattern between complexes. The two strains of the *monacha* complex (*P. monacha* and MML/I) have larger offspring than the three strains of the *lucida* complex (*P. lucida*, ML/VII, and ML/VIII). Because the differences observed in the field (Thibault and Schultz, 1978) are qualitatively similar to our results under controlled, common garden conditions, differences in offspring size at birth appear genetically based. Unlike previous studies that showed ordering of ova sizes according to genomic dosage (Schultz, 1969), we found no consistent ranking of mean size or intraclutch variation in offspring size with genomic dosage in these five strains.

There are a number of possible "adaptive" and "nonadaptive" explanations for the observed differences in offspring size at birth. The nonadaptive explanations explain differences in offspring size as by-products of environmental effects or as "fixed" phylogenetic differences among lines. Two likely environmental factors that may affect offspring size in these two reproductive complexes are diet and temperature. However, previous studies with three of the five strains used in this experiment (*P. monacha*, ML/VII, and ML/VIII) show that diet and temperature do not alter the relative differences in ova size between these three strains (Weeks and Quattro, 1991; Weeks, 1993). Therefore, although the absolute sizes might differ in the natural environments, we expect that relative differences among the reproduc-

tive complexes will be similar to those reported here (i.e., there is no evidence for genotype-by-environment interactions for offspring size in these strains).

Phylogenetic constraints may also explain the observed differences in offspring size. Average offspring mass can vary fivefold within the genus *Poeciliopsis* (Reznick and Miles, 1989). Yet, several experiments on poeciliids have shown offspring size to be responsive to local biotic and abiotic conditions. Population differences in offspring size have been documented in *Poecilia reticulata* (Reznick and Endler, 1982), *Gambusia affinis* (Stearns, 1983), *G. holbrooki* (G. K. Meffe, 1990, unpubl.), and *Poeciliopsis occidentalis* (Constantz, 1979). These intraspecific differences can be threefold (see Reznick and Miles, 1989). Because offspring size seems readily modifiable, the argument that the observed differences among the strains used in this study are due to fixed differences among species is less tenable. Also, the three clonal strains used in this study grouped according to habitat rather than to genomic dosage, which further indicates that the differences in offspring size may be adaptations to local conditions rather than be indicative of fixed phylogenetic differences.

For the above reasons, we feel that the observed differences in offspring size may be better explained by adaptive scenarios rather than these nonadaptive ones. We, thus, discuss the fit of the observed patterns of offspring size and intraclutch variation to those predicted by several life-history models.

*Differences in mean offspring size.*—Allocation of energy per offspring should be sensitive to the increase in offspring survival per unit of increased energy invested (Smith and Fretwell, 1974; Morris, 1987; Winkler and Wallin, 1987). Increased offspring size can positively affect a number of life-history traits, including (a) increased interference and exploitative competitive ability (Brockelman, 1975; Constantz, 1979; Morris, 1987), (b) increased ability to withstand environmental stresses (e.g., starvation stress; Calow and Woollhead, 1977; Schultz, 1991), or (c) decreased likelihood of size-selective predation (Reznick, 1981; Reznick, and Endler, 1982).

Differences in offspring size at birth in *P. occidentalis* have been interpreted as an adaptation to local competitive regimes in Arizona streams (Constantz, 1979). Constantz (1979) suggested that larger offspring are better competitors for the limited resources in the food-limited population (Monkey Spring), but detailed analyses to verify this assertion were not conducted. In

the current case, the downstream habitats of the Arroyo de Jaguari are more productive than upstream (Thibault and Schultz, 1978), but no data exist for a comparison of the relative densities of fish in these two habitats. Therefore, we are unable to determine the importance of (a) in the explanation of the differences in mean offspring size between these two reproductive complexes until detailed field studies have been conducted.

Unfortunately, long-term measures of biotic and abiotic sources of stress in these habitats are lacking. Nevertheless, numerous collections in these two habitats suggest that the upstream environment is more seasonally variable in water levels, light intensity, and food resources than is the downstream environment (Thibault, 1974a; Thibault and Schultz, 1978; R. C. Vrijenhoek, pers. comm.). In fact, Thibault and Schultz (1978) attribute the differences in offspring developmental patterns between *P. monacha* and *P. lucida* to an adaptation of *P. monacha* to a more unreliable food supply in the upstream habitats. Therefore, it is possible that the increased mean offspring size in the upstream habitat is caused, in part, by a response to increased environmental stress (McGinley et al., 1987; Schultz, 1991).

The third hypothesis has some empirical support in other poeciliids. Reznick (1982), Reznick and Endler (1982), and Reznick et al. (1990) showed that guppies (*Poecilia reticulata*) coexisting in streams with a fish predator (*Rivulus hartii*) that preys primarily on smaller individuals produce larger offspring than in streams without this size-selective predation pressure. Larger offspring are thought to be at a selective advantage in these streams because they can more rapidly outgrow their chief predator (Reznick, 1982). In the Platanos, fish of the *monacha* complex coexist with larger numbers of predaceous notonectids (esp., *Buenoa arizonis*), which are over 40 times as abundant in the upstream as in the downstream portions of this river (Thibault, 1974a). Notonectids prey primarily on other insects but occasionally consume small fish (Borror and DeLong, 1954; Thibault, 1974a; S. C. Weeks, pers. obs.). The only other potential predator of young at these two localities is *Cichlasoma beani* which is in low abundance at Agua Caliente (Thibault, 1974a). Although *C. beani* consume *Poeciliopsis* juveniles in the lab, none were found in gut analyses of over 30 *C. beani* from the field (Thibault, 1974a). Thibault suggested that "the preferred deep pool habitat of cichlids combined with preferences of young *Poeciliopsis* for shallow water may effectively reduce predator-prey interactions" at Agua Cal-

iente (Thibault, 1974a). Thus, the likelihood of predation on smaller size classes of *Poeciliopsis* appears to be much higher in the *monacha* complex habitats, which may result in selection for larger offspring and possibly increased growth rates in these upstream pools.

A corollary of this size-selective predation hypothesis is that increased size may reduce the likelihood of cannibalism. Thibault (1974b) showed a significant difference in cannibalism between *P. monacha* and *P. lucida*, with the former exhibiting cannibalism in over 95% of the cases studied, whereas the latter showed no indication of cannibalistic behavior. In the present study, one clone (ML/VII) had a cannibalism rate as high as *P. monacha*, in contrast to intermediate levels of cannibalism reported by Thibault (1974b). However, Thibault's data are difficult to interpret because at the time it was not recognized that the "clonal" forms used in his study were actually an assemblage of ecologically and behaviorally distinct clones (Schenck and Vrijenhoek, 1986, 1989; Weeks et al., 1992). Also, because the current experiment was specifically designed to measure differences in size-specific predation and not overall predation rates among these three lines, it is premature to assume that these data correctly reflect overall cannibalistic tendencies. Nevertheless, because *P. monacha* is the numerically dominant strain in the upstream complex, and the low-cannibalism strains are numerically dominant in the downstream complex (Schenck and Vrijenhoek, 1986; S. C. Weeks, unpubl.), it is likely that the reported differences in rates of cannibalism between these two reproductive complexes (Thibault, 1974b) accurately reflect the differences in selective pressure on offspring size in these habitats. Thus, increased cannibalism on the smaller size classes of offspring in the Platanos might be an additional (if not primary) selective factor causing the observed differences in offspring size at birth between the upstream and downstream portions of the Arroyo de Jaguari.

*Differences in intraclutch variation.*—Offspring sizes vary within and between clutches, and this variation may be adaptive in variable environments (Capinera, 1979; Kaplan and Cooper, 1984; Schultz, 1991). However, offspring size may vary for a number of nonadaptive reasons. The ability of an organism to precisely control offspring size may be constrained by genetic factors such as pleiotropy or environmental effects during offspring development (McGinley et al., 1987). Unless observed offspring variation can be correlated clearly with the predic-

tions of the above models, the null hypothesis of nonadaptive variation in offspring size should be accepted (McGinley et al., 1987; Schultz, 1991).

A few studies have specifically tested the possibility of an adaptive benefit to offspring variation. Crump (1981) found no difference in CV for egg size in tropical tree frogs (*Hyla*) from permanent and temporary ponds but did find egg sizes were platykurtic in temporary and leptokurtic in permanent ponds. Crump suggested these differences in egg distributions were indicative of "bet hedging" strategies in the temporary ponds. Meffe (1990) measured offspring size variation of mosquitofish (*Gambusia*) in thermally ambient and thermally fluctuating ponds. The fish in these contrasting environments showed no consistent trend of increased offspring variability in the thermally variable environment, and Meffe reasoned that this variability was more likely a reflection of environmental factors than a genetic response to a variable environment.

The most straightforward measure of the relevance of these models to the current data is to compare the relative environmental variability of the upstream and downstream habitats. As indicated above, the upstream environment is thought to be more variable than is the downstream environment (Thibault, 1974a; Thibault and Schultz, 1978). Therefore, for the observed offspring variation to be adaptive, we would expect fish of the *monacha* complex to show either an increase in offspring variation (Capinera, 1979; Kapland and Cooper, 1984) or both an increase in average size and in intraclutch variation (Schultz, 1991) compared to fish of the *lucida* complex. These expectations were not met. Offspring of the *monacha* complex were larger than offspring from the *lucida* complex, perhaps partially a result of increased environmental variability (see above), but there was no consistent increase in coefficients of variation for offspring size in the upstream reproductive complex. Thus, we accept the null hypothesis of no adaptive benefit of the observed intraclutch variation in these five strains. In that multiple clutches were not measured per female, offspring size variation among successive clutches may be important in these fish (Kaplan and Cooper, 1984), but this possibility remains to be tested.

In summary, we confirmed a genetic basis of offspring size differences between two related reproductive complexes in Mexico. The consistent pattern of these differences under a number of laboratory-rearing conditions and in the field (Thibault and Schultz, 1978; Weeks and

Quattro, 1991; Weeks, 1993) and the observations of locally adapted populations of other poeciliids (Reznick and Endler, 1982; Stearns, 1983; Meffe, 1990) suggests an adaptive explanation. These preliminary results indicate that larger offspring size at birth might prove adaptive in habitats subject to higher environmental stress, size-selective predation, or cannibalism. The current data, though, show no adaptive benefit to patterns of intraclutch size variation. Further experimental work should concentrate on possible adaptive benefits of larger size in these habitats—other than reduced cannibalism—to estimate the contributions of these factors to the evolution of offspring size in these *Poeciliopsis* populations.

#### ACKNOWLEDGMENTS

We thank E. Fielding, D. Fletcher, G. K. Meffe, and D. L. Schultz for critically reviewing the manuscript and R. J. Schultz and R. C. Vrijenhoek for supplying the fish strains and for use of lab space. This study was funded in part by a National Science Foundation doctoral dissertation support grant (BSR-8815423) and by contract DE-AC0976SROO-819 between the United States Department of Energy and the University of Georgia to SCW and a Fulbright fellowship to OEG.

#### LITERATURE CITED

- ANGUS, R. A., AND R. J. SCHULTZ. 1983. Meristic variation in homozygous and heterozygous fish. *Copeia* 1983:287-299.
- BAGENAL, T. B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish Biol.* 1:167-182.
- BORROR, D. J., AND D. M. DELONG. 1954. An introduction to the study of insects. Holt, Rinehart, and Winston, New York, New York.
- BROCKELMAN, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* 109: 677-699.
- CALOW, P., AND A. S. WOOLLHEAD. 1977. The relationship between ration, reproductive effort and age-specific mortality in the evolution of life-history strategies; some observations on freshwater triclads. *J. Anim. Ecol.* 46:765-781.
- CAPINERA, J. L. 1979. Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* 114:350-361.
- CONSTANTZ, G. D. 1979. Life history patterns of a livebearing fish in contrasting environments. *Oecologia* 40:189-201.
- CRUMP, M. L. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. *Am. Nat.* 117:724-737.
- KAPLAN, R. H. 1980. The implications of ovum size variability for offspring fitness and clutch size with-

- in several populations of salamanders (*Ambystoma*). *Evolution* 34:51–64.
- , AND W. S. COOPER. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the “adaptive coin-flipping” principle. *Am. Nat.* 123:393–410.
- MCGINLEY, M. A., D. H. TEMME, AND M. A. GEBER. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Ibid.* 130:370–398.
- MEFFE, G. K. 1987. Embryo size variation in mosquitofish: optimality vs. plasticity in propagule size. *Copeia* 1987:762–768.
- . 1990. Offspring size variation in Eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae) from contrasting thermal environments. *Copeia* 1990: 10–18.
- MORRIS, D. W. 1987. Optimal allocation of parental investment. *Oikos* 49:332–339.
- REZNICK, D. 1981. “Grandfather effects”: the genetics of interpopulation differences in offspring size in the mosquito fish. *Evolution* 35:941–953.
- . 1982. Genetic determination of offspring size in the guppy (*Poecilia reticulata*). *Am. Nat.* 120:181–188.
- , AND J. ENDLER. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 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, Englewood Cliffs, New Jersey.
- , H. BRYGA, AND J. A. ENDLER. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- SAS INSTITUTE, INC. 1985. SAS user's guide: statistics, version 5 edition. Cary, North Carolina.
- SCHENCK, R. A., AND R. C. VRIJENHOEK. 1986. Spatial and temporal factors affecting coexistence among sexual and clonal forms of *Poeciliopsis*. *Evolution* 40: 1060–1070.
- , AND ———. 1989. Coexistence among sexual and asexual *Poeciliopsis*: Foraging behavior and microhabitats, p. 39–48. *In*: Evolution and ecology of unisexual vertebrates. R. M. Dawley and J. P. Bogart (eds.). Bulletin 466, New York State Museum, New York.
- SCHULTZ, D. L. 1991. Parental investment in temporally varying environments. *Evol. Ecol.* 5:415–427.
- SCHULTZ, R. J. 1969. Hybridization, unisexuality, and polyploidy in the teleost *Poeciliopsis* (Poeciliidae) and other vertebrates. *Am. Nat.* 103:605–619.
- . 1977. Evolution and ecology of unisexual fishes. *Evol. Biol.* 10:277–331.
- . 1982. Competition and adaptation among diploid and polyploid clones of unisexual fishes, p. 103–119. *In*: Evolution and genetics of life histories. H. Dingle and J. P. Hegmann (eds.). Springer-Verlag, New York, New York.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108:499–506.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman, San Francisco, California.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* 51:3–47.
- . 1983. The genetic basis of differences in life-history traits among six populations of mosquitofish (*Gambusia affinis*) that shared ancestors in 1905. *Evolution* 37:618–627.
- THIBAUT, R. E. 1974a. The ecology of unisexual and bisexual fishes of the genus *Poeciliopsis*: a study in niche relationships. Unpubl. Ph.D. diss., Univ. of Connecticut, Storrs.
- . 1974b. Genetics of cannibalism in a viviparous fish and its relationship to population density. *Nature* 251:138–140.
- , AND R. J. SCHULTZ. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution* 32:320–333.
- VRIJENHOEK, R. C., R. A. ANGUS, AND R. J. SCHULTZ. 1978. Variation and clonal structure in a unisexual fish. *Am. Nat.* 112:41–55.
- WEEKS, S. C. 1993. Phenotypic plasticity of life-history traits in clonal and sexual fish (*Poeciliopsis*) at high and low densities. *Oecologia* 93:307–314.
- , AND J. M. QUATTRO. 1991. Life-history plasticity under resource stress in a clonal fish (Poeciliidae: *Poeciliopsis*). *J. Fish Biol.* 39:485–494.
- , O. E. GAGGIOTTI, R. A. SCHENCK, K. P. SPINDLER, AND R. C. VRIJENHOEK. 1992. Feeding behavior in sexual and clonal strains of *Poeciliopsis*. *Behav. Ecol. Sociobiol.* 30:1–6.
- WETHERINGTON, J. D., S. C. WEEKS, K. E. KOTORA, AND R. C. VRIJENHOEK. 1989. Genotypic and environmental components of variation in growth and reproduction of fish hemiclones (*Poeciliopsis*: Poeciliidae). *Evolution* 43:635–645.
- WINKLER, D. W., AND K. WALLIN. 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* 129:708–720.

(SCW) UNIVERSITY OF GEORGIA, SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29802; AND (OEG) CENTER FOR THEORETICAL AND APPLIED GENETICS, P.O. BOX 231, COOK COLLEGE, RUTGERS UNIVERSITY, NEW BRUNSWICK, NEW JERSEY 08903. Submitted 6 April 1992. Accepted 8 Dec. 1992. Section editor: W. J. Matthews.