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Life History of *Brachyrhaphis rhabdophora* (Pisces: Poeciliidae)

DAVID REZNICK, AXEL MEYER, AND DAVID FREAR

We describe the life-history pattern of *Brachyrhaphis rhabdophora* from several Costa Rican locations. This species is nonsuperfetating, meaning that it carries only one brood of developing young at a time. They are also lecithotrophic (ovoviviparous), meaning that there is no evidence of maternal provisioning of the young after the eggs have been fertilized. These female life-history traits are typical of other species in the tribe Gambusiini, as illustrated with a multivariate analysis. We also found considerable variation among populations for offspring size, fecundity, reproductive allocation, and fat content of the females. The size distribution of mature males was bimodal in two of four samples, significantly skewed in a third, and normal in a fourth. Because there is believed to be little growth after maturity, bimodality suggests genetic polymorphism for age and size at maturation, as described for other species of Poeciliidae.

A virtue of comparative studies is that they allow one to perceive patterns that are not attainable in any other fashion. This is true because compiling data from a large number of species reveals a range of variation not found within any one species. It is then possible to generate testable hypotheses for the evolution of these patterns and develop the appropriate experiments or observations to test them.

The comparative study of the family Poeciliidae is a good example of this process. Reznick and Miles (1989) summarized the diversity in life-history patterns present within this family and demonstrated strong associations among the different components of the life history. They also established trends in the distribution of different life histories. For example, there is an association between the mode of reproduction

(superfetation vs nonsuperfetation) and reproductive allotment, litter size, and interbrood interval.

Such relationships can be used to evaluate the costs and benefits associated with evolving a given form of reproduction, such as the derivation of superfetation (the ability to carry two or more developing broods simultaneously) from non-superfetation. Reznick and Miles also found that both modes of reproduction may be found in at least four tribes, suggesting that this change in reproduction has evolved on multiple occasions. If this proves to be true, one could then make paired comparisons among the most closely related species with contrasting modes of reproduction and deduce the possible causes of the evolution of these modes (following Felsenstein, 1985).

In both applications, it is necessary to have a large group of related species for which the same suite of variables has been estimated. One important realization of this recent review is that, in spite of the presence of interesting patterns within this family, and in spite of the degree to which this family has been studied, there is actually very little information available on the life histories of these fish. For example, Reznick and Miles were only able to find estimates for interbrood interval, offspring size, brood size, and reproductive allotment for eight of the estimated 180 species in this family. All of the above patterns are, therefore, based on a very sparse data set. Our goal is, thus, to characterize the life history of additional species of Poeciliids. To do so efficiently, we will concentrate on species in tribes or genera for which there is currently little or no data.

We describe here the life-history pattern of *Brachyrhaphis rhabdophora*. This genus is in the tribe Gambusiini, which also contains *Gambusia* and *Belonesox*. High quality information is available on some species of *Gambusia*, especially *G. affinis* (e.g., Milton and Arthington, 1983; Reznick, 1981; and Stearns, 1983), and on the one species of *Belonesox* (Turner and Snelson, 1984), but there is as yet very little known about any species of *Brachyrhaphis*.

The only available information from this genus is on *Brachyrhaphis episcopi* from Panama (Turner, 1938). Turner studied the seasonal cycle of reproduction and found that the minimum size of reproducing females was 25 mm, the mean size was 33.4 mm, and the mean number of young per brood was 7.4 (estimated from his Table III). He also reported that the species developed only one brood at a time (i.e., was nonsuperfetating) and was lecithotrophic, meaning that there was no evidence of a transfer of nutrients from the mother to the young after fertilization. He found an unusually large range of sizes for mature males, with length ranging from 15–36 mm. In most regards, reproduction in this species is similar to the other members of the tribe Gambusiini.

MATERIALS AND METHODS

Collections.—A sample of females was collected by AM from the Palo Verde National Park, Guanacaste Province, on 22 July 1985. Two small collections of females were made by DR from the Guacimal River, Puntarenas Province, in the vicinity of the Presa Main Dam on 23 July 1987. One collection was made from the river itself (Guacimal B), whereas the other was made from an irrigation ditch alongside the riv-

er (Guacimal A). Two collections of males and females were made by DR in two small tributaries to the Rio Piedras, Guanacaste Province, on 31 Aug. 1989. The remaining data on males were based on collections made by AM, from the Corcovado National Park on 15 Aug. 1984, and a second from the Rio Quebrada Hondo, in the vicinity of Colon, San Jose Province, on 20 July 1985. The fourth collection of males was made by W. Bussing from Quebrada 36, Puntarenas, Puntarenas Province on 1 May 1967 (UCR collection #111–3). The only available measurements of immature males were for the samples from Rio Piedras. The laboratory stocks used to estimate interbrood interval were descended from fish collected from the vicinity of the city of Colon, San Jose Province.

Bussing (1988) suggested that fish currently described as *B. rhabdophora* may actually represent two species. The northern populations, represented here by samples from Palo Verde, the Guacimal River, and Rio Piedras, may be renamed as *B. ololina*. The southern populations, represented here by samples from Corcovado, Colon, and Quebrada 36, would remain as *B. rhabdophora*.

Characterization of the life history.—The size distribution of reproducing females, fecundity, offspring size, and reproductive allotment were estimated from wild-caught, formalin-preserved females following the methods of Reznick and Endler (1982). Interbrood interval was estimated from the birth records of seven females then on 31 of their offspring. Each female was kept isolated in 38-liter aquaria fitted with a permeable partition which allowed the young to swim through but retained the female.

The pattern of maternal provisioning to developing young was characterized by regressing mean dry weight of developing embryos on the stage of development, following the methods of Reznick (1981). The absence of maternal provisioning after fertilization (lecithotrophy) is expected to be correlated with an approximately 35% loss in dry weight during development. The presence of some maternal provisioning after fertilization (matrotrophy) is expected to be correlated with less weight loss or even an increase in dry weight during development (Turner, 1937).

Males were characterized by the size distribution of mature and immature individuals. Males were scored as mature, based on the complete development of the terminal structures of the gonopodium, or metamorphosed anal fin, following methods similar to those described by Turner (1941) for *Gambusia affinis*.

TABLE 1. DESCRIPTIVE STATISTICS FOR FEMALE LIFE-HISTORY TRAITS FROM FIVE LOCALITIES. Numbers in parentheses equal one standard error.

	n ^a	Min. size of gravid female (mm)	Reproductive ^c allotment (%)	Mean embryo ^d dry weight (mg)	Slope of female weight-litter size, regression	Intercept
1. Palo Verde	9/18	— ^b	13.1 (1.0) ²	1.55 (0.12) ¹	0.143 (0.017)**	-6.14 (3.45)
2. Guacimal A	5/6	— ^b	14.2 (1.4) ²	2.87 (0.16) ³	0.076 (0.46) ns	-8.96 (32.47)
3. Guacimal B	4/13	— ^b	6.7 (1.6) ¹	3.92 (0.18) ⁴	0.014 (0.012) ns	1.70 (5.62)
4. Rio Piedras A	19/39	22	11.1 (0.7) ^{1,2}	2.07 (0.08) ^{2,3}	0.035 (0.007)**	1.98 (0.72)
5. Rio Piedras B	8/20	24	8.1 (1.1) ¹	2.45 (0.13) ²	0.053 (0.009)**	-2.07 (1.24)

	Litter size for a 215 mg female	Slope of stage of development—mean embryo weight regression	Intercept	Percent ^d fat females	Percent ^d fat offspring
	24.6	-0.017 (0.006)*	2.06 (0.21)	5.6 (0.9) ¹	15.0 (1.1) ¹
	7.4	-0.051 (0.014)*	4.39 (0.46)	16.6 (2.9) ³	17.1 (3.1) ¹
	4.7	-0.012 (0.026) ns	4.29 (0.68)	11.4 (0.8) ²	15.6 (2.1) ¹
	9.6	-0.012 (0.006)†	2.43 (0.19)	6.2 (0.4) ¹	17.8 (1.2) ¹
	9.3	+0.010 (0.014) ns	2.12 (0.42)	6.2 (0.7) ¹	14.1 (0.8) ¹

^a Numerator equals the number of females with developing embryos. Denominator equals the total number dissected. The numerator represents the sample size for all analyses.

^b Insufficient sample to estimate this variable.

^c Proportion of total dry weight which consists of developing embryos.

^d Numbers group together means that do not differ significantly from one another in the analyses summarized in Table 2. Means were compared with Scheffé's test (a posteriori) and a 0.05 criteria for significance.

* $P < 0.05$.

† $0.05 < P < 0.10$.

ns = not significant.

Statistical analysis.—The relationship between brood size and female size, or mean embryo dry weight and stage of development was characterized with bivariate regressions, using the Statistical Analysis System Regression Procedure (SAS Institute, 1985). Variations in reproductive characteristics among localities were evaluated with one-way analyses of variance or covariance, treating localities as fixed effects, following methods similar to Reznick and Endler (1982) (GLM Procedure; SAS Institute, 1985). The size distribution of mature males was characterized with the normal probability distribution statistics available through the Normal Procedure (SAS Institute, 1985). If the sample size was less than 51, then the comparison was made with the Shapiro-Wilk W statistic. For larger samples, the comparison was made with the Kolmogorov D statistic. We also report the skewness and kurtosis of the size distribution, based also on the Univariate Procedure. We only report on results for samples with more than 20 mature males. These include one of our Rio Piedras tributaries, then our Colon, Corcovado, and Puntarenas samples. The female life-history pattern was compared to the life histories of other members of the family Poeciliidae with a discriminant function analysis (as in Reznick and Miles, 1989). The class variable was the mode of reproduction, i.e., whether the species was superfetating or nonsuper-

fetating. The dependent variables were the mean female size, the predicted litter size for the average length female, mean offspring size, and interbrood interval.

RESULTS

Female life history.—Females appear to attain maturity and begin to develop yolking ova at 22–24 mm standard length in the two Rio Piedras collections (Table 1). All females below these sizes only contained oocytes, whereas most larger females contained either yolking ova or developing embryos. Sample sizes were not sufficient in our remaining collections to allow us to estimate this minimum size class.

Fecundity was strongly correlated with female dry weight (Fig. 1), with somatic dry weight accounting for from 60–91% of the variation in brood size in the three larger collections (Table 1). The average size female weighed 215 mg, was 32.4 mm long (standard length) and produced 12.6 offspring. Reproductive allotment averaged 10.9% (range 6.7–14.2% for locality means; Table 1) and was not correlated with either female size or the stage of development of the embryos. Offspring size averaged 2.29 mg dry weight and was not correlated with female size but tended to be negatively correlated with the stage of development (Table 1, see below). The fat content of the females av-

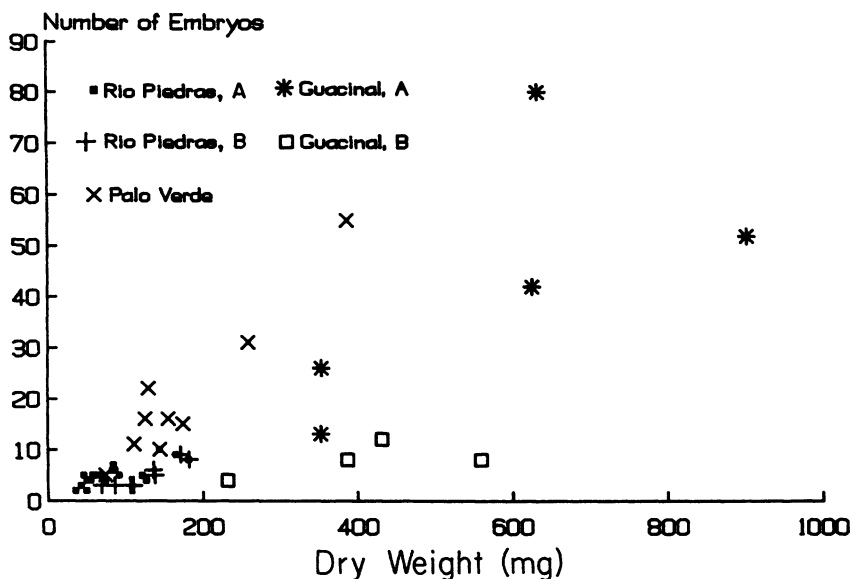


Fig. 1. Dry weight-fecundity distributions for all five collections of females. "Dry weight" equals the somatic dry weight of the female, or the weight after the reproductive tissues are removed.

eraged 7.7% (range 5.6–16.6% for locality means), whereas the fat content of offspring averaged 16.3% (range 14.1–17.8%; Table 1).

The slope of the regressions of embryo weight on the stage of development of the embryos was negative in four of the five collections and significantly negative in two of the four. A third population with a negative slope had a probability of 0.0515 that the slope was different from zero (Table 1; Fig. 2). Note that the small sample sizes and distribution of the stages of development are largely responsible for this variation in slopes. There was significant heterogeneity among these slopes ($F_{4,35} = 3.00$, $P = 0.0316$), with the one nonsignificant positive slope being responsible for the heterogeneity. The common slope is -0.016 (standard error = 0.004), with an intercept of 2.04 (standard error = 0.19). This results in an estimated loss of 41% of the dry mass during development. This statistic and the overall trend in the data indicates that the species is lecithotrophic, although there may also be variation among populations in this trait, as indicated by the one positive slope.

All of our dissections of wild-caught fish and our laboratory data indicate that this species is nonsuperfetating. In field collections, each individual contained offspring in only a single stage of development. Some of the large females from the irrigation ditch along side the Guacinal River, which contained up to 80 developing embryos, showed variation in the stage of development. This variation represented continuous

variation around some mean value, rather than discrete litters. For example, some litters had young that ranged in stage from uneyed to mid-eyed, with most of the litter being early eyed. This variation was only apparent when the litters were early in development. Thibault and Schultz (1978) illustrate similar variation in guppies (*Poecilia reticulata*), which are also non-superfetating.

The mean interbrood interval, estimated in the laboratory at 25 C, was 32.4 days (SE = 0.7, range = 27–37 days, $n = 26$) for the original seven females and 33.2 days (SE = 2.79, range = 23–40 days, $n = 52$) for their 31 offspring. One observation of 59 days and three observations of 60, 64, and 75 days were excluded from the two analyses. These longer intervals are statistical outliers and equal to approximately twice the normal interval. We have observed similar, prolonged intervals in guppies (*Poecilia reticulata*; Reznick and Endler, 1982) and interpret them as skipped litters. The mean value for the interbrood interval is typical of a nonsuperfetating species. A superfetating species could be expected to have half or less than half of this interval (Reznick and Miles, 1989). An additional female, which produced three litters at intervals of 17 and 20 days, was excluded from the second group of fish. Her mean value deviated substantially from the means of the remaining females in the group. Again, we have occasionally seen an abnormally short interval in guppies (DR, pers. obs.) and do not have any explanation for this phenomenon.

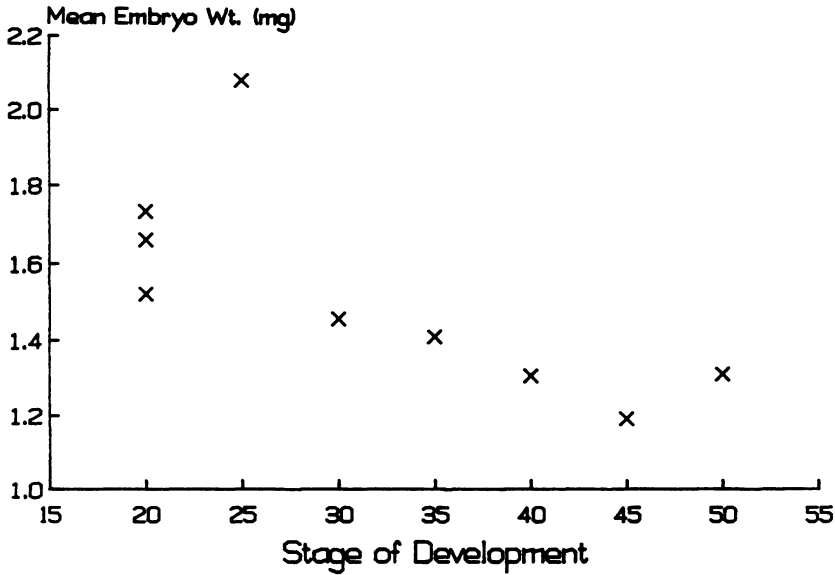


Fig. 2. The relationship between mean dry embryo weight and the stage of development of the embryos for fish from the Palo Verde.

Comparisons among populations in female life-history traits.—Fecundity was significantly correlated with female size, but there was significant heterogeneity in the slopes of the female weight-litter size regressions for both untransformed ($F_{4,44} = 3.80$, $P = 0.0114$) and log-transformed ($F_{4,44} = 4.38$, $P = 0.0056$) data. Because of this slope heterogeneity and because the covariate accounts for so much of the variation in litter size, it was not possible to perform a valid statistical comparison among localities for fecundity. The best available index of relative fecundity in these circumstances is the predicted value for the average weight female for all five collections (215 mg). These values (Table 1) range from 4.7–9.6 offspring per litter. *Brachyraphis* from the fifth locality (Palo Verde) have substantially higher fecundities, with a predicted value of 24.6 offspring per litter.

Reproductive allotment was not correlated with either female size or the stage of devel-

opment of the offspring. There were significant differences among localities (Table 2), with the largest difference being between the two samples from the Guacimal River (Table 1). Because these sites are adjacent to one another and there is a continuous possibility of gene flow between them, we assume that the differences are attributable to differences in local environment. This was during the rainy season, and the water level in the river (Guacimal B) was very high. Because *B. rhabdophora* appear to feed either on algae or on invertebrates caught in the water column, the high discharge in the rainy season may limit feeding opportunities. The flow rate was low in the irrigation canal (Guacimal A), and it had abundant emergent vegetation.

There were also substantial differences among localities in offspring size (Table 1, 2). The population from Palo Verde produced the smallest offspring. This is the site that also had the highest size-specific fecundity. Next, the two samples

TABLE 2. COMPARISONS AMONG POPULATIONS FOR FEMALE LIFE-HISTORY TRAITS.

Variable	Source of variation	F	Degrees of freedom	r^2	Significance level
RA	Locale	5.94	4,40	0.37	**
MnEmb ^a	Locale	28.67	4,40	0.74	**
MnEmb ^b	St. Dev. (covariate)	13.57	1,39	—	**
	Locale	34.75	4,39	0.81	**
% fat—female	Locale	25.67	4,41	0.71	**
% fat—offspring	Locale	1.25	4,40	0.11	ns

** $P < 0.01$.

ns = not significant.

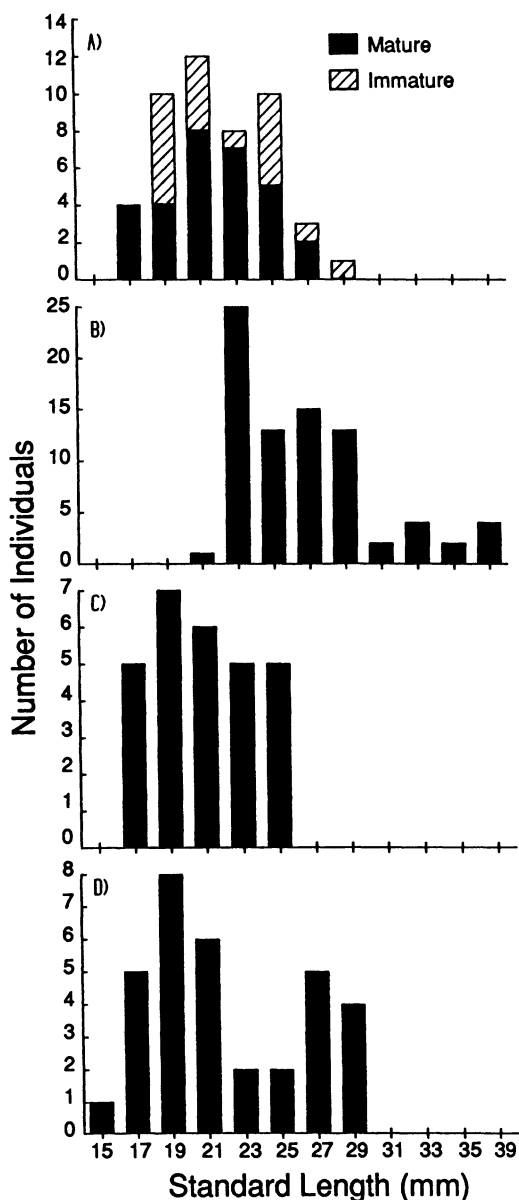


Fig. 3. The size distribution of mature and immature males from four localities. A = Rio Piedras; B = Colon; C = Quebrado 36, Puntarenas; D = Corcovado.

from the Rio Piedras drainage did not differ significantly and produced intermediate sized offspring. The largest offspring, from the Guacimal River, were more than twice as large as those from Palo Verde. There were also significant differences among the two Guacimal samples, with the River population producing significantly larger offspring than the fish from the irrigation canal.

Finally, there was significant variation among

localities in the fat content of the females (Tables 1, 2). Fish from both Guacimal sites had significantly higher fat reserves than those from the other three localities. These differences were not attributable to differences in body size, because the slopes of the body size-fat content regressions varied from significantly positive to significantly negative. The differences in fat reserves were not represented in the fat content of the offspring (Tables 1, 2). In this case, there were no differences among the five localities. It, therefore, appears that the fat content of the offspring is regulated independently of the fat reserves of the mothers.

Male life history.—Our plots of the size distribution of mature males reveals, first, that there is a very large size range in all samples, as observed by Turner for *Brachyrhaphis episcopi* (Fig. 3). These samples included one northern population (Rio Piedras A) and three southern populations (Colon, Corcovado, and Puntarenas). Mature males ranged from extremes of 15–38 mm, and generally covered a range of 15 mm within each collection (Plate 1, Fig. 3). For example, the range within the Corcovado sample was from 16–35 mm. We observed similar range in body sizes in most of our smaller collections (not illustrated).

The size distribution differs significantly from normality in two of the four localities and approaches significance in a third locality. The way in which the distribution deviates from normality is of interest. For example, bimodal distributions have been observed in some *Xiphophorus* species (Kallman, 1989) and, in some cases, have been found to represent genetic polymorphisms for the age and size at maturity (e.g., Kallman and Schreibman, 1973). A polymodal distribution would be expressed as a large negative value for kurtosis (a platykurtic distribution). However, a similar deviation could also be expressed in terms of large values for skewness if there is a large inequality the abundance of large versus small males. Two of our samples had large negative values for kurtosis (Table 3), whereas a third had a relative large positive value for skewness. The Corcovado sample is distinctly bimodal, whereas the Colon sample appears bimodal but is skewed to the right in the statistical analysis because of the greater abundance of small versus large males. The fourth sample (Rio Piedras) has a normal distribution but still has a broad size range of mature males (17–27 mm). There was a similar range in the size distribution of immature males so that there was broad overlap between the sizes of mature and immature individuals (Fig.



Plate 1. Extremes in the size distribution of mature males from the Colon collection.

3). This variation in the size of mature males, therefore, cannot be attributed solely to post-maturational growth (which is generally minor in the Poeciliidae; e.g., Snelson, 1982).

DISCUSSION

Female life history.—Our recent review of life histories in this family revealed that, with one exception, all species of Poeciliidae were either nonsuperfetating and lecithotrophic or superfetating and matrotrophic. All species within the tribe Gambusiini, with the exception of questionable reports by Scrimshaw (1944, 1945), are nonsuperfetating and lecithotrophic. We, therefore, expected and found a similar reproductive pattern for *B. rhabdophora*. We conclude that *B. rhabdophora* is nonsuperfetating because

there is only one stage of developing embryos in all wild-caught females, and the interbrood interval in the laboratory averaged 33.1 days. We conclude that this species is lecithotrophic because there was an average loss of 41% of the dry weight of eggs between fertilization and birth. There is some hint of variation in this trait (Rio Piedras B, Table 1), but larger sample sizes and repeated observations would be necessary to document this. Trexler (1985) reports possible variation in maternal provisioning among populations of *Poecilia latipinna*.

All other well-investigated species of the tribe Gambusiini (genera *Brachyrhaphis*, *Gambusia*, and *Belonesox*) also have similar values for size-specific fecundity and offspring size. This overall similarity in female life histories is illustrated by plotting the discriminant function score for

TABLE 3. COMPARISONS OF THE LENGTH FOR FREQUENCY DISTRIBUTION OF MATURE MALES WITH A NORMAL DISTRIBUTION. "Pr normal" equals the probability that the size distribution represents a sample drawn from a normal distribution. See Materials and Methods for details.

Locality	n	Pr normal	Skewness	Kurtosis
Rio Piedras A	30	0.494 ns	0.124	-0.621
Colon	58	0.036*	0.694	0.020
Quebrada 36, Puntarenas	27	0.091†	-0.118	-1.222
Corcovado	33	<0.01*	0.483	-1.204

* $P < 0.05$.

† $0.05 < P < 0.10$.

ns = not significant.

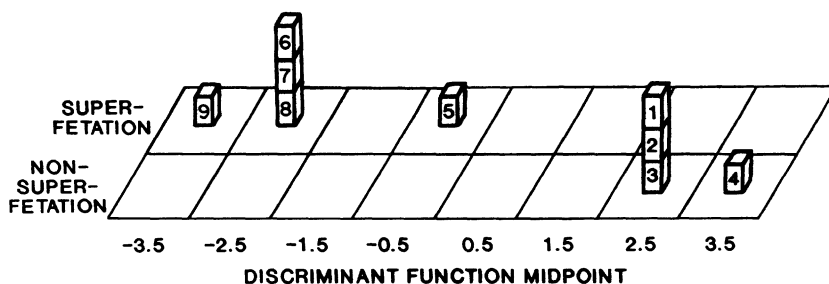


Fig. 4. Discriminant function scores for the nine species of Poeciliidae for which we have estimates of interbrood interval, mean female size, mean fecundity, and offspring size. The nonsuperfeting species included *Poecilia latipinna* (1), *Gambusia affinis* (2) [both grouped with *B. rhabdophora* (3)], and *Belonesox belizianus* (4). The superfetating species included *Poeciliopsis occidentalis* (5), *P. monacha* (6), *P. lucida* (7), *P. turneri* (8), and *H. formosa*.

the *B. rhabdophora* females, including our laboratory value for interbrood interval, with the similar data fore the other Poeciliidae (Fig. 4). The female life-history score clusters alongside the life-history scores of *Gambusia affinis* and *Poecilia latipinna* and close to the life history for *Belonesox belizianus* (data summarized from Reznick and Miles, 1989).

Because all of the samples in Table 1 were from the northern populations which may be reclassified as *B. olomina*, the observed diversity in life histories is best interpreted as a combination of intraspecific genetic differences and environmental effects, with the relative contribution of the two factors remaining unknown.

Male life history.—One typically sees a normal distribution for the size of mature males in other species of Gambusiini (e.g., Krumholz, 1948; Turner and Snelson, 1984). In contrast, the size distribution for *B. rhabdophora* is often bimodal or platykurtic. These size distributions are consistent with those reported by Turner (1938) for *Brachyrhaphis episcopi* from Panama.

The multimodality in size distribution suggests a polymorphism for male size and age at maturity (Kallman, 1989). Such polymorphisms are well described for members of the genus *Xiphophorus* and have been named p-alleles because of their apparent association with the pituitary-gonadal axis (Kallman and Schreibman, 1973; Schreibman and Kallman, 1977; Bao and Kallman, 1982). The importance of this observation is that, if *B. rhabdophora* turns out to also have a p-allele, it represents the first time that this phenomenon has been observed outside of the tribe Poeciliini, all previous observations having been in the genera *Xiphophorus* and *Poecilia* (Travis et al., 1992). The similarity in the observations on *B. rhabdophora* and *B. episcopi* suggest that genetic variation in age and size at maturity may be more widespread within this

genus. The possible genetic basis for this variation is currently being investigated by one of us (DR).

Additional data (Reznick, unpubl.) suggest that such genetic variation in male size at maturity may also be present in members of the tribe Heterandriini. If such genetic polymorphisms are found throughout the family, this would suggest that p-alleles are a primitive trait to the family, or a trait present in the common ancestor of a number of tribes, rather than a derived trait of the tribe Poeciliini. Alternatively, it suggests that the trait has evolved independently in the different tribes.

Brachyrhaphis rhabdophora is a widespread species in central and north Costa Rica and is found on the Atlantic and Pacific slopes. This distribution, in combination with possible differences among populations in the variation in the size of mature males (e.g., a bimodal size distribution in the Corcovado sample versus a normal distribution in the Rio Piedras samples) suggests that this may be an ideal species for investigating the factors that maintain genetic polymorphism in the age and size at maturity. This comparison is confounded by the possible differences between *B. olomina* (Rio Piedras) and *B. rhabdophora* (remaining three samples); however, the apparent differences in size distributions among the *B. rhabdophora* samples (e.g., Puntarenas vs Colon) suggest that, even if the new classification holds, there will remain variation within the *B. rhabdophora*. If so, then this would be an ideal species for investigating those factors that are responsible for selecting for a given age at maturity, a key component of any organisms life history.

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LITERATURE CITED

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