

7-1-1975

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## Recommended Citation

Moore, W. S. 1975. Stability of small unisexual-bisexual populations of *Poeciliopsis* (Pisces: Poeciliidae). *Ecology* 56(4):791-808.

<http://dx.doi.org/10.2307/1936292>

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## STABILITY OF SMALL UNISEXUAL-BISEXUAL POPULATIONS OF *POECILIOPSIS* (PISCES: POECILIIDAE)<sup>1</sup>

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**Abstract.** All-female species of *Poeciliopsis* depend upon ♂♂ of closely related species for sperm. This relationship creates a competitive situation in which bisexual ♀♀ compete with unisexual ♀♀ for sperm from ♂♂ of the bisexual species. Earlier studies demonstrated a sufficient mechanism inherent in the behavior of ♂♂ for allowing coexistence in mixed unisexual-bisexual populations. Courtship preference of ♂♂ for conspecific ♀♀ is dynamically countered by social interaction among ♂♂: subordinate males mate with unisexual ♀♀ in impetuous courtships. The *Poeciliopsis monacha*-*Poeciliopsis 2 monacha-lucida* complex occurs naturally in small isolated populations where stochastic factors are not negligible. This paper evaluates the stability of small populations of this complex by laboratory population experimentation and stochastic computer simulation. Three small mixed populations persisted in the laboratory for 2 yr but extinction of the bisexual species occurred in four of nine simulated replicates of these experiments. Life tables and fitness values calculated from estimates of birth and death rates showed the all-female species to be much more fit in the laboratory populations than was the bisexual species. Additional simulations done at relative fitness values more characteristic of natural populations indicated that extinctions in small isolates would be rare in nature. Isolated demes can become confluent during the annual rainy season. It was expected that this confluence, by effectively increasing population size, might enhance stability by reducing the effect of stochastic factors; simulations of two and four demes mixed annually did not support this hypothesis.

**Key words:** Coexistence; gynogenesis; life table; model; *Poeciliopsis*; population; simulation; stochastic.

### INTRODUCTION

Several all-female "species" occur in the viviparous fish genus *Poeciliopsis*. These forms, although variable in their morphology, genetics, meiotic mechanisms, distribution, and ecology, all depend upon males of bisexual host species for sperm. This fact defines a triangular ecological interaction in which unisexual females compete with bisexual females for the sperm of the males of the bisexual species. Ecologically, the unisexual forms represent distinct species competing for a common limiting resource and although they utilize male gametes they do not share a common gene pool with the bisexual host species (Schultz 1961, 1966, 1967, 1969). The reproductive potential of unisexual females is partially or wholly realized only if they are successfully courted by males of the host species; on the other hand, if this potential were fully realized, the unisexual form would rapidly exclude the bisexual species because the unisexual's reproductive potential is approximately twice that of the bisexual since they produce only female offspring. Competitive exclusion of the bisexual would subsequently bring the demise of the sperm-dependent unisexual. Thus, the persistence of both the unisexual and bisexual components of a complex population requires a mecha-

nism for controlling sperm flow to the alternative female types.

Behavioral characteristics of males described by McKay (1971) appear to provide a sufficient regulatory mechanism. Males of two bisexual species, *Poeciliopsis lucida* and *Poeciliopsis monacha*, showed an almost absolute preference for conspecific females under conditions where they could choose between a conspecific and a unisexual form. However, groups of males tended to form dominance hierarchies in which subordinate males were denied access to conspecific females, and they therefore frequently inseminated the less preferred unisexual females. Moore and McKay (1971) translated these behavioral patterns into a mathematical function which in turn served as a submodel in a deterministic computer simulation model of a unisexual-bisexual species population of *Poeciliopsis*. The conclusion was that mate preference dynamically countered by social interaction among males was sufficient to generate equilibria in simulated populations. Further, the model generated several testable hypotheses regarding clinal variation, nature of equilibria, and the amount of sperm available to the unisexual population as a function of bisexual density. These hypotheses were tested against data on the *Poeciliopsis occidentalis*-*Poeciliopsis monacha-occidentalis* species complex; the hypotheses accurately reflected the natural populations.

<sup>1</sup> Manuscript received 5 October 1973; accepted 18 September 1974.

An unrealistic assumption of the earlier model was that population behavior was deterministic and that stochastic factors were negligible. Although accurate data is not available for natural population sizes, considerable variation in size is readily observed between populations of different unisexual-bisexual complexes and even between populations of a single complex. The purpose of this paper is to report the nature of stability in small populations where stochastic factors cannot be ignored.

The triploid unisexual species *P. 2 monacha-lucida* and its bisexual "host" species, *P. monacha*, characteristically inhabit small bedrock pools in the headwaters of the Rio Fuerte in Sonora and the Rio Sinaloa in Sinaloa, Mexico. These pools, varying in size from a few liters to several thousand liters, contain populations ranging from 10 individuals to several thousand. Throughout the 9-mo dry season (approximately early October to early July) individual pools are isolated and their volumes maintained by seepage or flowing springs. During the rainy season pools occasionally become confluent during heavy rains, thus affording the opportunity for migration and mixing of isolates. Then, as the streams recede, the small isolated population condition is quickly reestablished.

The complex involving *P. monacha* and its triploid associate is examined in some detail and an assessment made of the stability of small isolates, by means of a systems analysis approach. The focal point of the study is a computer simulation model similar to that used by Moore and McKay (1971) but different in that most deterministic functions are replaced by analogous stochastic functions. In addition, the results of laboratory population experiments and other supporting experiments are reported. The purposes of these experiments are (1) to study actual populations under control situations, (2) to fit empirically probability distributions to random variables such as brood size, number of deaths, and age at sexual maturation, and (3) to estimate values for the numerous parameters inherent in a systems model. I used the population model to simulate additional replicates and to perform additional experiments by changing the value of a single variable and observing the outcome. The total process allows some inferences to be made about long-term stability of natural populations.

#### MATERIALS AND METHODS

Three mixed populations of the triploid unisexual *P. 2 monacha-lucida* and its bisexual host species, *P. monacha*, were maintained in artificial stream pools in a greenhouse for 2 yr beginning 1 July 1969. Each pool measured 2.44 m  $\times$  0.61 m  $\times$  0.33 m and contained approximately 380 liters of water. Space

limitations prevented arranging the pools so that each received equal sunlight exposure; therefore, it was necessary to move each population to a different pool at periodic intervals. This was done every 15 days until March 1970 when a 20-day interval was adopted in conjunction with a series of experiments of 60-day duration conducted in the pools. Water temperature was kept constant at 28°C. A common water circulation system with a capacity of 290 liters per hour and a reservoir of 359 liters served the three pools. This provided conditioned water for other aquaria maintained in the laboratory and was occasionally replenished by tap water to which a mixture of salts was added to increase hardness. The reservoir typically required replenishment every 3–4 days.

One quarter of each pool was partially partitioned off by a cement block. The block was placed perpendicular to the back of the tank and supported about 5 cm above the bottom. This left an 8-cm space between the block and the front of the tank and 1–1.5 cm of water above the block. A 20-  $\times$  30-cm tray of densely planted *Valesneria* was placed along the outer edge of the block and extended across the space to the front. This arrangement provided an area of each pool which was accessible to all fish but easily defended by a few dominant females. The partition was placed at the inflow end of the pool and dry food was always introduced in this area. This created an optimal area similar to those seen in natural habitats and described by McKay (1971). In addition, the shallow water above the block and vegetation provided protective areas for young from cannibalistic females. Two additional trays of *Valesneria* were placed in each tank, one in the middle and one at the far end. The tanks were covered with glass leaving a 5-cm space above the water surface. The populations were fed dry food each morning and evening and a preparation of blended beef liver and wheat germ three times per week. Live daphnia were fed when available, usually four or five times per week. Although excess food was not available to the fish at all times, this is an abundant feeding schedule and food was not a limiting factor.

Every effort was made to accurately model natural habitats. The *P. monacha* complex is restricted to residual bedrock pools of rocky arroyos that are isolated or connected by trickles throughout the 9-mo dry season. Pools are highly variable, and the size and depth of the laboratory pools falls well within the range of that of natural pools.

Occasional population censuses were made. Generally one population was counted every 20 days in conjunction with the scheduled rotation; thus, each population was counted every 60 days. Early in the study, population size was sufficiently small to allow counting all three populations on a scheduled rota-

tion (i.e., every 20 days); on other occasions, the interval between censuses was longer.

The three experimental populations provided a data source for estimates of parameters in the several probability density functions that served as submodels in the larger simulation model. Many of the fish were marked at the onset of the study; these provided age-specific mortality data. Three or four females were removed at each census and preserved. These were subsequently dissected and the number of ova and young contained in the ovaries tabulated. Removed females were always replaced by females of comparable age. Additional marked fish were introduced during the study period to gain additional mortality data; fish equivalent in size and class were always removed when marked fish were introduced. Small numbers (1 to 10) of marked virgin unisexual and bisexual females were introduced occasionally and removed after a specified period. This allowed estimating the probability of a female becoming inseminated in a specified time interval. At the end of the 2-yr experimental period the three populations were preserved; thus, additional females were provided for fecundity data.

Disruption of the populations at censuses was unavoidable, and little can be said about the effect this might have had on the behavior of fish other than that the two species involved appear to resume normal behavior within a few minutes following their return to a familiar habitat. Removal of individuals was always done during a census to avoid additional disruptions. Fish added to the populations during the course of the study were introduced at dusk or at night when the fish were most quiescent.

Fish were marked for recapture experiments by injection of small amounts of colored latex into the caudal musculature (Moore 1971). The incidence of mortality attributable to this procedure is negligible. Occasionally a major blood vessel or the nerve cord is injected bringing on fatality or paralysis; newly marked fish either recover or show signs of imminent death within 2 days of injection. All marked fish used in experimental studies were held for at least 1 wk between marking and introduction to the study.

The *P. monacha* and *P. 2 monacha-lucida* stocks used in the experimental populations were collected in the Arroyo de los Platinos, a small bedrock arroyo that feeds the Rio Fuerte through the Arroyo Jaquari, near Guirocoba, Sonora, Mexico. This is the type locality of *P. monacha* (Miller 1960) as well as the source of the triploid unisexual *P. 2 monacha-lucida* originally described by Schultz (1969). The *P. monacha* stocks were second-generation descendants of three wild females captured in April 1968. The triploid stocks were second-generation descendants of two wild females from the same location. Additional stocks, used in various experiments, were

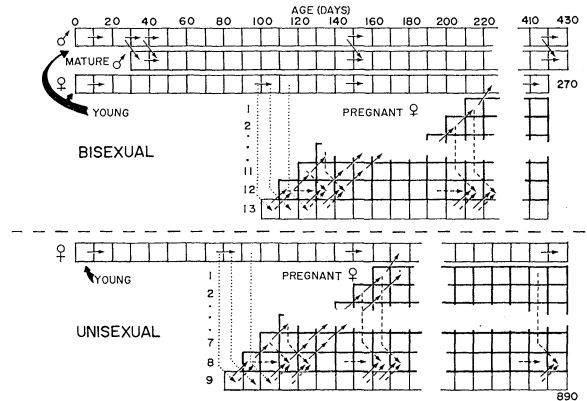


FIG. 1. Schematic diagram showing structure of a complex population of unisexual, *P. 2 monacha-lucida*, and its bisexual "host," *P. monacha*, at time  $t$ . In the passage of time from  $t$  to  $t + \Delta t$ , the numbers of individuals lost to mortality or allocated to new cells are modeled as random variables; random variables are represented by arrows in diagram. Dotted arrows indicate allocation of newly inseminated ♀♀. Dashed arrows indicate allocation of reinseminated ♀♀. Solid arrows indicate possible allocations of other types. Heavily outlined cells contain productive ♀♀; young are collected and entered into first cell of the appropriate array as indicated by heavy arrows.

maintained in aquaria with 7.6–75.8 liters capacity. Generally a density of one fish per 3.8 liters or less was maintained for rearing stocks.

Additional methods used in estimating parameters will be discussed with the presentation of the parameter.

### MODEL

The general structure of the stochastic simulation model is similar to that of the discrete time deterministic model devised by Moore and McKay (1971) for a complex population of *Poeciliopsis*. Although there are several ways to symbolize the basic model, perhaps the simplest is to visualize the population structure as several arrays of numbers (Fig. 1). Each array represents a type of fish, e.g., males, unisexual females. Each array is further divided into age intervals; e.g., the first interval of the male array represents males aged 1–10 days inclusive; the second, 11–20 days inclusive. The state of the population at time  $t$  can be represented by assigning appropriate numerical values to each of the array intervals or cells; e.g., if the population contained five immature males aged 25 days, the third cell of the immature male array would contain the number 5. The state of the population at time  $t + \Delta t$  is determined by a set of probabilities conditioned on the state of the population at time  $t$ . For convenience, the age intervals are equal to the time increment  $\Delta t$ . During an increment of time the fish in each cell

TABLE 1. Fixed values of deterministic variables

Variable	Value			
	<i>Poeciliopsis monacha</i>		<i>Poeciliopsis 2-monacha-lucida</i>	
	Estimated	Used	Estimated	Used
Brood interval (days)	12.12	10	10.53	10
Gestation ( $2 \times$ brood interval)	...	20	...	20
Age (days) at sexual maturation ( $\text{♀}$ $\text{♀}$ )	101-110	101-110	81-90	81-90
Maximum age obtainable ( $\text{♀}$ $\text{♀}$ )	270	261-270	890	881-890
	430	421-430		
Length of sperm storage (from time of insemination to day of last brood)	128	121-130	89	81-90

are subjected to age-specific mortality rates. Survivors aged  $i$  at time  $t$  are advanced to the next cell representing age  $i + \Delta t$  at time  $t + \Delta t$ . Unlike the earlier model, the number of survivors advanced to age  $i + \Delta t$  is considered a random variable and given an appropriate probability density function. Additional phenomena affect certain cells: mature unisexual and bisexual females are subject to insemination, immature males may mature, young are produced by pregnant females, and young aged zero to  $\Delta t$  are subject to cannibalism. Each of these phenomena is modeled by a random variable. The probability density function for each random variable is defined later.

Four arrays are one-dimensional while the two arrays representing pregnant females are two-dimensional. The two-dimensional arrays allow simulation of sperm storage and superfetation. Once inseminated, *Poeciliopsis* females can produce offspring at approximately 10-day intervals (following an initial gestation period) for 3-4 mo. Superfetation allows the production of broods at more frequent intervals. This species typically has ovarian broods in two developmental stages; consequently, the brood interval is one-half of the gestation period. Newly inseminated females first produce young after two brood intervals (approximately 20 days) have elapsed and at single brood intervals (approximately 10 days) thereafter. Modeling sperm storage and superfetation requires that females be classified not only as to species and age but also as to state of pregnancy: not pregnant, newly inseminated, inseminated one increment prior to  $t$ , etc. Mature, nonpregnant females aged  $i$  which are inseminated at time  $t$  are moved to the cell representing age  $i + \Delta t$  in the bottom row (Fig. 1) of the appropriate pregnant female array at time  $t + \Delta t$ . As time progresses, pregnant females move up a row for each elapsed time increment,  $\Delta t$ , if they are not re-inseminated, until they run out of sperm in the top row and re-enter the nonpregnant female array. If a female is re-inseminated during the process of decay through

the sperm storage array, she is returned to the next-to-bottom row of the array. Newly inseminated females that were placed in the bottom row do not produce offspring: production of young begins in the next row. Holding newly inseminated females for a time interval,  $\Delta t$ , which is equivalent to the length of one brood interval, simulates the initial gestation period.

#### DETERMINISTIC VARIABLES

The dimensions of the arrays are considered deterministic variables in the model. These variables are maximum age, brood interval, gestation period, length of sperm storage, and age at sexual maturation. As applied to this study, the array dimensions are assigned constant values based on estimates. Deterministic variables of the model along with the constant values estimated and actually used are summarized in Table 1.

For convenience and because of restrictions in the model, the values used as array dimensions are not equal to the estimates, although they are similar. For example, a brood interval of 10 days was used in the model when the estimates were 12.12 and 10.53 days for the two types of females. The age interval ( $\Delta t$ ) was also set at 10 days. Ideally, one would like to find an age interval such that estimates of all array dimensions were integral multiples of that value, but, since such a value does not exist for this set of estimates, 10 days was chosen because it facilitated tabulation of results. Further, the model can represent individuals in specific age intervals (e.g., 101-110 days) but not of specific ages (e.g., 106 days); therefore, age at sexual maturation, maximum ages, and length of sperm storage are represented in the model by the 10-day intervals that contain the point estimates of these parameters.

Maximum ages were set at the end of the 10-day interval in which the oldest marked individual was reported missing in a census.

Brood interval data were obtained from laboratory stocks that originated approximately 2 miles from the

source of fish used in the population studies. Brood intervals were measured in a laboratory constant temperature bath by M. Cimino (*unpubl. data*). Although the mean brood interval for unisexuals and bisexuals was computed to be 10.53 ( $n = 43$ ) and 12.12 ( $n = 59$ ), respectively, a brood interval of 10 days was assumed for both forms in the stochastic computer simulations.

Duration of sperm storage was measured from the time a female was isolated to the time of her last brood. I tested four females of *P. monacha* and nine of *P. 2 monacha-lucida* by placing them with males until young were first seen. The females were then isolated and production tabulated until at least 30 days had passed without production of offspring, at which time the females were dissected to make certain they did not contain additional embryos. The mean duration of sperm storage was 128 and 89 days for *P. monacha* and *P. 2 monacha-lucida*.

Age at sexual maturation was estimated from dissected females by means of their length-age relationships (Moore 1971). The youngest *P. monacha* females with mature ova were approximately 101–110 days old; the youngest mature *P. 2 monacha-lucida* were 81–90 days old. The range of ages within which females mature is not as variable as that of males.

RANDOM VARIABLES

In the passage of time from  $t$  to  $t + \Delta t$ , the numbers of individuals lost to mortality or allocated to new cells are modeled as random variables. The six random variables are (1) number of females inseminated, (2) number of deaths, (3) brood size, (4) number of young surviving cannibalism, (5) sex ratio, and (6) age at which males mature.

*Number of females inseminated*

Let  $X_t$  be the number of nonpregnant females of a given type (unisexual or bisexual) in the population at time  $t$ . Assume that during any short interval of time,  $t$  to  $t + h$ , each female has a probability  $\mu(y)h + o(h)$  of being impregnated;  $\mu(y)$  is a function of  $y$ , the number of males in the population; and  $o(h)$  is any function such that  $\lim [o(h)/h] = 0$  as  $h \rightarrow 0$ . Further, assume that the impregnation of one female is independent of the impregnation of other females. We are interested in the number of nonpregnant females remaining after a time interval  $(0, t)$  and the corresponding probability

$$P_{i,n}(t) = P(X_t = n | X_0 = i), \quad (i \geq n)$$

of finding  $n$  nonpregnant females at time  $t$  given there were  $i$  at time zero. This describes a “pure death process” and the Kolmogorov forward differential equation and boundary value are

$$P'_{i,n}(t) = -\mu(y)nP_{i,n}(t) + \mu(y)(n+1)P_{i,n+1}(t), \quad (i \geq n)$$

$$P_{i,n}(0) = \delta_{i,n},$$

which has the solution:

$$P_{i,n}(t) = \binom{i}{n} e^{-i\mu(y)t} [e^{\mu(y)t} - 1]^{i-n}, \quad (i \geq n)$$

$$= \binom{i}{n} e^{-n\mu(y)t} [1 - e^{-\mu(y)t}]^{i-n}$$

(Feller 1968: 478, 498).

This is the probability density function of a binomial random variable with parameters  $i$  and  $e^{-\mu(y)t}$ ;

$$E(X_t) = ie^{-\mu(y)t}$$

$$\text{Var}(X_t) = ie^{-\mu(y)t}[1 - e^{-\mu(y)t}].$$

The functional relationship between female impregnations and number of males is influenced by two factors: mate preference and social interaction among males (Moore and McKay 1971). Let

$$\mu(y) = \alpha y^2 + \beta y$$

where  $y$  = number of males,

$\alpha$  = constant (coefficient of male interaction),

$\beta$  = constant (coefficient of mate preference).

The linear term in the quadratic reflects mate preference while the quadratic term reflects social interaction among males. Although a male interaction term is not evident in the limited data reported here, an appreciably better fit of simulated impregnation-frequency data to natural data for the *P. occidentalis* complex was obtained in an earlier study by incorporating such a term into the unisexual impregnation submodel (Moore and McKay 1971). The evolutionary affinities of the several unisexual-bisexual complexes of *Poeciliopsis* make it likely that the same behavioral patterns are important to the population dynamics of all complexes, and therefore the male interaction terms is incorporated into this model as well.

The limited range of values for the number of males ( $y$ ) in the experimental populations precludes estimating both  $\alpha$  and  $\beta$  without making an additional assumption. As the sub-submodel,  $\mu(y) = \alpha y^2 + \beta y$ , applies to unisexual and bisexual impregnations, reasonable assumptions can be made that allow elimination of one term. With regard to bisexual courtship, males show a strong preference for conspecific females (McKay 1971) and there is no intuitive reason nor data to suggest that social interactions influence bisexual impregnation; therefore, assume  $\alpha = 0$ . In contrast, unisexual impregnations appear to result primarily, if not entirely, from male social interactions (McKay 1971). Therefore, it is reasonable to assume  $\beta = 0$  as the impregnation model applies to unisexual females.

A series of impregnation tests was run in the three experimental populations for the purpose of estimat-

TABLE 2. *P. 2 monacha-lucida* insemination tests

Test number	Popu- lation	No. of ♀♀ recovered	No. of ♀♀ pregnant	Length of trial (days)	No. of ♂♂			
					Initial	Mid <sup>a</sup>	Final	$\bar{x}$
1	2	6	1	60	14	17	13	14.67
2	3	5	2	60	7	..	15	11.00
3	2	10	1	62	17	13	8	12.67
4	3	9	1	67	15	..	13	14.00
5	2	5	0	68	13	..	8	10.50
6	1	5	1	76	2	..	2	2.00
7	2	10	2	82	8	8	9	8.33
8	2	6	0	75	9	..	18	13.50
9	3	7	1	81	11	..	15	13.00
10	2	8	0	89	18	..	12	15.00
11	3	9	0	77	15	..	11	13.00
12	1	10	0	95	6	..	14	10.00
13	1	9	2	66	14	..	15	14.50
Totals		99	11					
$\bar{y} = 11.7$	$\Delta\bar{t} = 7.37$	$\hat{P}_{1,1} = .889$	$a = 10^{-4}$					

<sup>a</sup> If a census happened to fall during the course of a test, the number of ♂♂ was included in the average for that test.

ing impregnation parameters. Each test consisted of releasing a small group (10 or less) of marked virgin females into a population for 60–75 days. At the end of the period the females were recaptured and preserved and their ovaries examined for pregnancy.

Under the assumptions made and the data from Tables 2 and 3, estimates of the social-interaction coefficient ( $\alpha$ ) and the mate-preference coefficient ( $\beta$ ) for the respective unisexual and bisexual impregnation sub-submodels can be made. For unisexuals, the probability,  $P_{1,1}$  that a female is not impregnated in a time interval of length  $t$  in the presence of  $y$  males is

$$P_{1,1} = \exp[-\mu(y)t] = \exp(-\alpha y^2 t).$$

Now, substituting the average time interval ( $\bar{t}$ ), average number of males ( $\bar{y}$ ), and the frequency of impregnated females ( $P_{1,1}$ ) totaled over all tests from Table 2 into this equation and solving for the estimate ( $a$ ) of  $\alpha$  yields  $a = 10^{-4}$ . Thus, given a cell representing the number ( $i$ ) of unisexual females of a particular age and pregnancy state at time  $t$ , the number which remain nonpregnant (or not re-impregnated), at time  $t + \Delta t$  is a random variable with the binomial distribution with parameters  $i$ , and

$$P_{1,1} = \exp(-10^{-4} y^2 \Delta t).$$

A similar argument and the data from Table 3 yield an estimate of  $\beta$  for the bisexual impregnation sub-submodel of  $b = 0.0137$ . Correspondingly the number of bisexual females ( $i$ ) of a particular state which remain nonpregnant (or not re-impregnated) has the binomial distribution with parameters  $i$ , and  $P_{1,1} = \exp[-(0.0137 y \Delta t)]$ .

*Numbers of deaths*

*Poeciliopsis* has overlapping generations; therefore, age specific death rates must be considered in a model of its population dynamics. Let  $L_x$  be the number of individuals of age  $x$  alive at the beginning of a time interval  $dt$  and  $L_{x+dt}$  be the number surviving the interval to reach age  $x + dt$ . Intuitively, the random variable  $L_{x+dt}$  has a binomial distribution with parameters  $L_x$ ;  $p_x =$  (probability of a fish surviving the interval  $dt$ ). This intuitive notion can be confirmed and the explicit form of  $p_x$  derived by the “pure death process” (Chiang 1960a).

The importance of life tables in medical and actuarial studies has stimulated several investigations into the stochastic variables of life tables (Chiang, 1960a, b, 1961) and, in particular, the estimation of the age-specific survival probabilities  $p_x$  (Cutler and Ederer 1958, Chiang 1961, Kuzma 1967). Frequently in studies of mortality rates under a specific risk (e.g., following diagnosis of cancer, attainment of a certain age), some individuals under study are lost to observation and, in the idiom of life table analysts, are “lost-to-follow-up.” Other individuals, the “withdrawn-alive” cases, may have entered the study interval after the beginning of the study and have not experienced the risk for the full length of the interval. Although these cases could be discarded in estimating  $p_x$ , valuable data may be lost. Chiang (1961) derived the maximum likelihood estimate for  $p_x$  assuming no cases were lost-to-follow-up. Cutler and Ederer (1958) suggested a more intuitive estimator that considers both cases withdrawn-alive and lost-to-follow-up. Their estimator is defined as

$$p_{*i} = 1 - q_{*i} = 1 - d_i/L'_i$$

TABLE 3. *P. monacha* impregnation tests

Test number	Popu- lation	No. of ♀ ♀ recovered	No. of ♀ ♀ pregnant	Length of trial (days)	No. of ♂ ♂			
					Initial	Mid <sup>a</sup>	Final	$\bar{x}$
1	2	2	1	68	13	8	8	9.67
2	1	2	0	76	2	..	2	2.00
3	2	3	1	80	8	8	9	8.33
4	2	3	3	76	9	..	18	13.50
5	3	1	1	83	11	..	15	13.00
6	1	3	3	66	14	..	15	14.50
Totals		14	9					
$\bar{y} = 10.17$		$\Delta \bar{t} = 7.48$	$\hat{P}_{1,1} = .357$	$b = .0135$				

<sup>a</sup> If a census happened to fall during the course of a test, the number of ♂ ♂ was included in the average for that test.

where

- $q_{*i}$  = estimate of the proportion dying during the  $i$ th interval,
- $p_{*i}$  = estimate of the proportion surviving during the  $i$ th interval,
- $d_i$  = number that died in the interval,
- $V_i = l_i - \frac{1}{2}(f_i + w_i)$   
= "effective" number exposed to the risk of dying,
- $l_i$  = number alive at the beginning of the interval,
- $f_i$  = number lost-to-follow-up during the interval,
- $w_i$  = number withdrawn-alive during the interval.

Kuzma (1967) compared the estimators of Chiang and of Cutler and Ederer and found the discrepancy to be negligible when the withdrawing rates were  $\leq 30\%$  and the lost-to-follow-up rate  $\leq 40\%$ .

I used two methods to obtain data for estimating  $p_x$  in laboratory populations. Adult unisexual females, bisexual females, and males were marked with colored latex and entered into the populations. When a marked fish was missing from a census, it was scored as a death in the 10-day interval containing the age of the fish on the census date. Since a method of marking fish  $< 26$  mm long was not available, I used an alternative method to obtain

TABLE 4. Life tables for laboratory-reared *P. monacha* and *P. 2 monacha-lucida*

	Age Interval <sup>a</sup> (Days)	$l_x$	$d_x$	$f_x$	$w_x$	"Effective" no. exposed to risk of dying: $l_x - \frac{1}{2}(f_x + w_x)$	Esti- mated propor- tion dying $q_{*x}$	Esti- mated propor- tion surviv- ing $p_{*x}$	Length of interval $\times 10 =$ days	Esti- mated <sup>b</sup> propor- tion ( $\hat{p}'$ ) surviv- ing a single 10-day interval	Cumu- lative propor- tion surviv- ing to end of inter- val
<i>P. monacha</i>	Young 1-90	105	38	0	0	105	.362	.638	9	.951	.638
	♂ ♂ 91-170	22	6	0	0	22	.273	.727	8	.961	.464
	171-250	20	9	0	0	20	.450	.550	8	.928	.255
	251-330	11	2	0	0	11	.182	.818	8	.975	.209
	331-430	9	8	1	0	8.5	.941	.059	10	.753	.012
	♀ ♀ 91-140	26	4	0	0	26	.154	.846	5	.967	.540
	141-190	29	8	8	0	25	.320	.680	5	.926	.367
	191-240	10	2	1	0	9.5	.211	.789	5	.954	.290
	241-270	7	4	0	0	7	.571	.429	3	.754	.124
	<i>P. 2 monacha-lucida</i>	Young 1-90	92	6	0	0	92	.065	.935	9	.993
♀ ♀ 91-290		128	14	88	0	84	.167	.833	20	.991	.779
291-490		47	11	10	0	42	.262	.738	20	.985	.575
491-690		26	15	5	0	23.5	.638	.362	20	.950	.208
691-890		6	5	0	0	6	.833	.167	20	.914	.035

<sup>a</sup> Age intervals are inclusive; i.e., fish aged zero through 90 days are included in the interval designated 1-90.

<sup>b</sup> Assuming the probability of survival is the same for each of the 10-day subintervals of the larger designated interval.



TABLE 5. Brood sizes of *Poeciliopsis 2 monacha-lucida* \* =  $p < .05$ ; \*\* =  $p < .025$ ; \*\*\* =  $p < .01$ ; \*\*\*\* =  $p < .005$

Age interval (days) <sup>a</sup>	No. of broods	Sample <sup>c</sup>			Pooled			$\chi^2$ (df) Poisson <sup>d</sup>	$\chi^2$ (df) negative binomial <sup>d</sup>
		$\bar{X}$	$S^2$	$k$	$\bar{X}$	$S^2$			
101-110 <sup>b</sup>	14	1.57	1.10	$S^2 < \bar{X}$					
111-120	8	3.25	1.94						
121-130	39	4.44	5.79	22.93	4.21	5.03	1.71(4)	2.38(2)	
131-140	9	4.11	3.43						
141-150	18	4.72***	8.53						
151-160	25	4.28	5.16	7.35	4.63	7.06	7.34(5)	2.25(4)	
161-170	17	4.88	7.75						
171-180	3	5.33	8.22						
181-190	8	6.50	11.25	4.592					
191-200	8	8.88****	29.86	2.154					
201-210	18	12.17****	26.58	10.104					
211-220	18	7.83****	17.47	4.416					
221-230	20	10.35****	48.93	2.914					
231-240	5	7.20****	28.56	1.056					
241-250	7	8.43****	25.96	2.550					
251-260	21	10.38****	36.52						
261-270	23	8.91****	29.12						
271-280	4	12.00****	40.50	2.27	9.39****	39.84	...	20.50(9)**	
281-290	9	11.11****	30.54						
291-300	21	9.00****	40.29						
301-310	18	9.17****	55.7						
311-320	44	10.61****	68.65						
321-330	26	13.12****	79.33	1.49	11.90****	78.93	...	15.72(9)	
331-340	13	13.85****	100.59						
341-350	15	14.53****	67.05	2.012					
351-360	6	13.50****	125.58	.950					
361-370	14	21.5****	151.96	2.346					
371-410	10	16.3****	102.95	1.076					

<sup>a</sup> Age intervals are inclusive.  
<sup>b</sup> Includes 2 broods from 81-90 interval.  
 Tests: (Table 5 & 6)  
<sup>c</sup>  $H_0: \mu = \sigma^2$  Statistic:  $nS^2/\bar{X} \sim \chi^2(n)$ , Bliss (1953).  
 $H_1: \mu \neq \sigma^2$   
<sup>d</sup> Fit to appropriate probability distribution. Statistic:  $\chi^2(df)$ .

mortality data for immature fish. Newborn fish were placed in aquaria at a density less than or equal to one fish per 3.8 liters. At the end of 90 days the number of survivors was scored. The life tables for *P. monacha* males and females and *P. 2 monacha-lucida* were constructed from these experiments by means of the Cutler-Ederer estimator (Table 4). For use in the simulations, a survivorship probability was needed for each 10-day interval; thus, an additional assumption was made: the probability of surviving a 10-day subinterval,  $p'$ , of the longer interval,  $t$ , is the same in each 10-day subinterval of  $t$ . Thus,  $p' = p^{1/t}$  (where  $p$  is the probability of surviving the longer interval  $t$ ). The mortality data are summarized in Table 4.

Brood size

Two probability distribution functions defined on the non-negative integers were considered in describing the distribution of brood sizes: the Poisson and the negative binomial. The probability density function of the Poisson is

$$P(X = x) = \mu^x e^{-\mu} \div x! \quad (x = 0, 1, 2, \dots),$$

and is completely defined by the single parameter  $\mu = E(X) = \text{Var}(X)$ . The probability density function for the negative binomial is

$$P(X = x) = \frac{(k + x - 1)!}{x!(k - 1)!} \cdot \frac{R^x}{q^k}$$

where  $k > 0$   
 $q = 1 + p$   
 $p = \mu/k$   
 $\mu = E(x)$   
 $R = p/q = \mu/(k + \mu)$  Bliss (1953).

Both distributions have wide application in biology for modeling such diverse phenomena as spatial distribution of organisms (Pielou 1969), evolutionary events (Uzzell and Corbin 1971), and parasite attacks (Griffiths and Holling 1969). Usually the Poisson distribution can be used to model data composed of the non-negative integers when the sample variance ( $S^2$ ) is not significantly different from the sample mean ( $\bar{X}$ ). The negative binomial is characterized by over-dispersion and is usually a better model when  $S^2 > \bar{X}$ . As the variance of the negative binomial approaches the mean,  $k \rightarrow \infty$  and  $p \rightarrow 0$

TABLE 6. Brood sizes of *Poeciliopsis monacha*

Age interval (days)	Broods (N)	$\bar{X}$	Sample <sup>a</sup> $S^2$	k
101-120	9	1.78	2.17	3.78
121-140	10	2.50*	4.85	1.55
141-160	9	2.44*	5.14	0.76
161-180	12	3.75*	6.69	2.82
181-200	19	4.32**	7.69	5.06
201-220	10	8.10	4.76	$S^2$
221-240	10	10.6	9.24	$S^2$
241-260	18	11.00****	32.00	5.449
261-280	4	15.5	34.25	10.738

<sup>a</sup> See footnote c of Table 5.

and its distribution converges to that of the Poisson (Bliss 1953).

I measured 542 brood sizes by dissecting the ovaries of 244 females preserved during and at the termination of the experimental study. Since these specimens were withdrawn from the population it was necessary to calculate their ages from an age-length relationship which was also determined during the study (Moore 1971). Females superfetate but ova and embryos can be readily grouped into distinct developmental stages; thus, more than one brood size can usually be determined for a single female. As expected, average brood size increased with increasing age (length) in both *P. 2 monacha-lucida* and *P. monacha*; therefore, age-specific parameters for populations of brood sizes were estimated by grouping females into age intervals, and the sample means and variances were calculated for each (Tables 5 and 6). Broods of *P. 2 monacha-lucida* were put in 10-day intervals ranging from ages 101 to 410 days inclusive. Because less data were available, broods of *P. monacha* were put in 20-day intervals ranging from 101 to 280 days inclusive. Since sufficiently large samples from each age interval were not available, data for age groups with similar means and variances of brood sizes were pooled. Four large pools were obtained for *P. 2 monacha-lucida* and compared to the Poisson and negative binomial distributions. Good fits to both distributions were obtained in the two "youngest" pools where the sample mean and variance of each group were generally not significantly different (Table 5). The sample means and variances of all of the age groups comprising the two "oldest" pools were significantly different and, since the mean and variance of the Poisson distribution are identical, it was inferred that the Poisson distribution was an inappropriate model for brood sizes of older females. A good fit to the negative binomial obtained for the *P. 2 monacha-lucida* females aged 311-340 days while the pool of broods from females aged 251-310 days had a  $\chi^2(9) = 20.50$  ( $0.1 > p > .025$ ). Since this value is not highly significant, i.e.,  $p < .01$ , and good fits

obtained in the other five tests, it was assumed for the purpose of simulation that the brood sizes for all age groups of both *P. 2 monacha-lucida* and *P. monacha* had either a Poisson or a negative binomial distribution. The Poisson was used for age groups where the sample variance was not significantly different from the sample mean and the negative binomial where the sample variance was greater than the sample mean ( $\alpha = 0.1$ ).

The parameter *k* was estimated iteratively by Fisher's (1953) maximum likelihood method.

*Number of young surviving cannibalism*

The role of cannibalism in regulating the carrying capacity of the laboratory populations was detected early in the study. Additional experiments conducted for the purpose of defining the functional relationship between cannibalism and carrying capacity and estimating voracity parameters did little more than reveal the complexity of the relationship. Rose (1959) postulated the existence of a "water-born product" that induced cannibalism at high population densities of guppies. Further, this mechanism was thought to regulate the carrying capacity of guppy populations in aquaria. It is doubtful that such a product induces cannibalism in *Poeciliopsis* (Moore 1971), although cannibalism appeared to be the major factor controlling the carrying capacity of experimental populations. Other factors appear to interact so as to manifest a relationship between adult density and cannibalism similar to that seen in guppies. These factors include contagious feeding behavior, hunger thresholds, levels of hunger satiation, and perhaps other factors, but these factors and their interactions are not sufficiently understood to warrant further development here (Moore 1971 gives experimental data).

Surprisingly, the simplistic exponential model,  $s = \exp(-\alpha x)$ , where *s* is the probability of a young surviving cannibalism, *x* is the number of adult females, and  $\alpha$  is a "voracity" constant, in conjunction with this simulation model, appears to be an adequate submodel for cannibalism inasmuch as it generates carrying capacities in simulations very similar to those in experimental populations (Results).

The voracity constant,  $\alpha$ , was estimated by a least-squares fit of the cannibalism submodel to data derived from experimental populations. At each census, I estimated the proportion of young surviving cannibalism by estimating the potential recruitment for the population during the 60 days preceding the census and counting the actual number of individuals less than 60 days old (determined by age-length relationship) at that census (Moore 1971). The estimated proportion surviving was plotted against number of adult females (cannibals) at each census and a least-squares estimate of  $\alpha$  made. Converted

to a 10-day period, the least-squares estimate of  $\alpha$  was  $a = .049$ .

For the purpose of simulation, the number of newborn young surviving cannibalism in each 10-day period is assumed to be a random variable with the binomial distribution. The probability of each young surviving is  $s = \exp(-0.049x)$ .

#### Sex ratio

A binomial random variable with parameter  $p =$  (probability of becoming a male) is used as a submodel for sex-ratio for the bisexual species. The value of  $p = 0.5$  was used for all simulations in this study.

#### Male maturation

At the beginning of the population experiments, the importance of variation in the age at which males mature was not fully realized. The relatively large numbers of immature males at censuses and the consistently small numbers of mature males suggested that maturation in males might be delayed beyond the maturation age of females. The suggestion was confirmed by maturation ages of males marked and introduced into populations for mortality studies and of males reared in aquaria. The earliest age of maturation (as judged by the appearance of the gonopodial hook) was recorded for an aquarium-raised male at 40 days, whereas the latest age was between 283 and 343 days, for a marked male in an experimental population.

For the purpose of simulation, it was assumed that beginning at age 40 days, an immature male had a probability,  $m_{10}$  of not maturing during each successive 10-day interval and that  $m_{10}$  remained constant throughout the life span. This simplifying assumption is frequently made in discrete time, pure birth and death models and is equivalent to assuming that the age at which males mature has a geometric distribution with parameter  $1 - m_{10}$  (Feller 1968). Further, the probability of remaining immature for any 10-day interval within the interval 41–90 days is  $m_{10} = m_{50}^{1/5}$  (where  $m_{50}$  = probability of not maturing in a 50-day interval). Of 70 *P. monacha* males surviving to age 90 days in aquaria, 18 matured and 52 remained immature during the interval 41–90 days; thus,  $m_{10} = (52/70)^{1/5} = 0.942$  is the probability of an immature male remaining immature in any 10-day interval throughout its life from age 40 days on. For the purpose of simulation, the number of males ( $n$ ) in a given age interval which mature at that age has the binomial distribution with parameters  $n$  and  $p = 1 - 0.942$ .

#### Generation of random variates

Random variates from three probability distribution functions were needed in stochastic simulations: binomial, Poisson, and negative binomial.

For binomial random variates when the number of trials ( $n$ ) was less than 100,  $n$  successive Bernoulli trials were reproduced via the rejection technique (Naylor et al. 1966). For  $n \geq 100$  the Poisson approximation or the normal approximation were used; the Poisson was used when  $np < 10$  ( $p$  = probability of a "success"), otherwise, the normal was used. Normal and Poisson random variates were generated by established methods (Naylor et al. 1966:92–93, 111–114). The proportion of successes in 1,000 generated Bernoulli trials was compared with the parameter  $p$  for three different combinations of  $n$  and  $p$  by each of the three methods; all were not significantly different from  $p$  (Z-test;  $\alpha = 0.1$ ).

Negative binomial random variates were generated by a method that can be used to approximate any discrete probability distribution (Naylor et al. 1966). The method involves partitioning the interval  $[0,1]$  into subintervals corresponding to the values that the random variable can assume; the length of each subinterval is equal to the probability that the random variable will assume a given value. A random variate with the uniform distribution over the interval  $[0,1]$  is then generated and compared with the partitioned interval; the variate generated is the value of the discrete random variable associated with the subinterval containing the uniform variate (Naylor et al. 1966). The accuracy of the subroutine written to generate negative binomial random variates was tested at two combinations of parameters ( $k = 2.27$ ,  $\mu = 9.39$ ;  $k = 1.49$ ,  $\mu = 11.90$ ) representative of the range of parameters for which brood sizes were simulated; the distributions of generated random variates were not significantly different from the corresponding negative binomial distribution ( $\chi^2$ -test,  $\alpha = 0.1$ ).

## RESULTS

### Laboratory populations

The histories of the three laboratory populations are graphed in Fig. 2, 3, and 4 along with three simulated replicates of each laboratory population.

Laboratory population I, initiated with a high unisexual:bisexual ratio, did not undergo the early rapid growth seen in populations II and III. This difference was due to cannibalism by females. Males of *Poeciliopsis* are not known to cannibalize young whereas females do; therefore, the unisexual:bisexual ratio interacts not only with recruitment but with the carrying capacity of the population which is governed by cannibalism. In population I, not only was recruitment depressed by a lack of pregnant unisexuals, but the young produced by both types of females had low probabilities of avoiding cannibalism. After approximately 1 yr the number of bisexual females in population I increased significantly coincident with a decline in the number of unisexual females. After

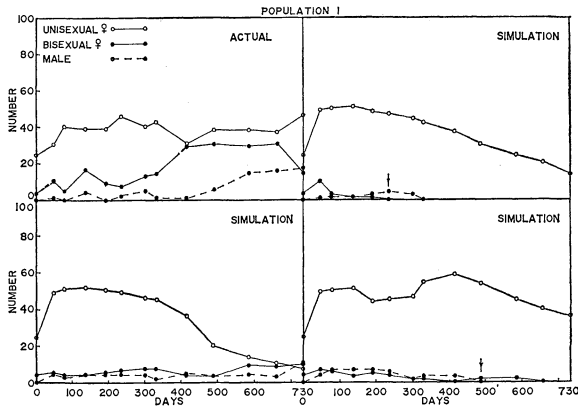


FIG. 2. History of laboratory population I and three simulated replicates (↓ denotes extinction; only mature individuals are represented).

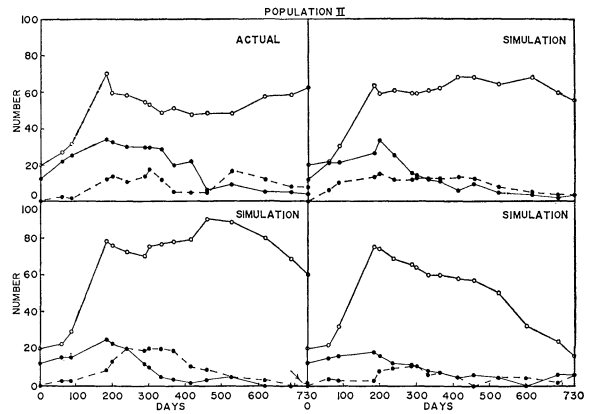


FIG. 3. History of laboratory population II and three simulated replicates (↓ denotes extinction; only mature individuals are represented).

a lag this trend was followed by a period of increase in the number of mature males present; this in turn increased the probability of unisexual inseminations, reflected by the increase in unisexual recruitment near the end of the experiment.

Laboratory populations II and III underwent an initial period of rapid growth to a carrying capacity of about 50–105 adult females. Although population II was initiated with a unisexual:bisexual ratio near unity and population III with a ratio favoring bisexuals, unexpected mortality of bisexual females in the latter caused the state of population III at 90 days to be similar to that of II at zero days; therefore, these two populations are more properly considered as replicates of the same experiment than distinct experiments. In population II both unisexual and bisexual female numbers increased markedly up to approximately 175 days followed by a leveling off and gradual decline of both classes. The greater growth rate of the unisexual population can be attributed to two factors: (1) unisexuals produce only female offspring and (2) mortality rates are higher for bisexual females. At approximately 525 days, the unisexual element of population II began a second sustained period of growth which appeared to result from a concurrent period of high mature male abundance (18 on the 525th day). Although population III had nearly as many mature males during the same period (15 on the 557th day), the unisexuals continued a gradual decline to the end of the experiment. Although chance may cause this difference, the probability, from the insemination model, of a unisexual's becoming pregnant during a 10-day period is 0.201 for 15 males and 0.277 for 18 males; i.e., a 37.8% increase in unisexual insemination probability accompanies a 20% increase in number of males for this range of male densities.

The similarity between simulated replicates and

actual population histories is not as great as one might hope. Extinction did not occur in any of the three actual populations, whereas extinction occurred in 4 of the 9 simulated replicates. It is likely that this result reflects an inadequacy in the simulation model although it could be due to chance. If it is assumed that number of extinctions in  $n$  populations has the binomial distribution, and the probability of an extinction in a given trial is  $4/9$ , the probability of no extinctions in 3 trials (e.g., the 3 laboratory populations) is 0.171. In other words this probability is not sufficiently remote to discount chance as the cause of the difference in number of extinctions.

Empirically population III deviated most from the simulated replicates, and, as mentioned, this was apparently due to an exceptionally high bisexual female mortality at the onset of the experiment which affected the population for the remaining 2 yr.

The predictive power of the model is further

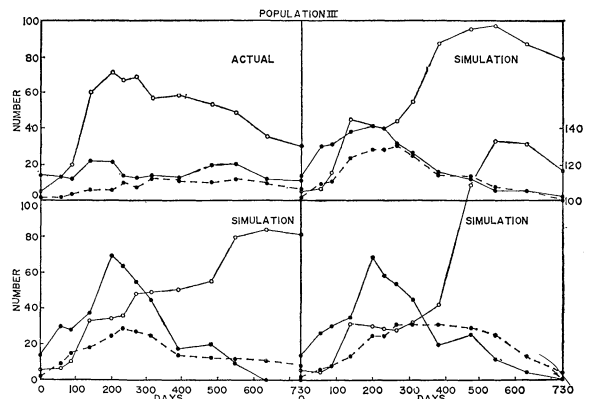


FIG. 4. History of laboratory population III and three simulated replicates (↓ denotes extinction; only mature individuals are represented).

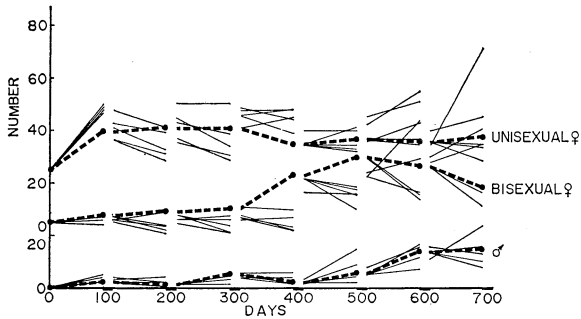


FIG. 5. 100-day prediction intervals for population I.

examined by means of data derived from the original simulations plus some additional simulations (Fig. 5, 6, and 7). The history of each population is divided into seven 100-day prediction intervals. The heavy dashed lines represent the progress of different types of fish in the actual populations. The lighter solid lines represent simulated populations which were in a state similar to that of the actual population at the beginning of the interval. The original computer simulations were set up so that the complete state of the population was printed out every 100 days. Initial states for 100-day prediction simulations were chosen from these data by the following method: The printouts of the nine original simulations were searched for states similar to that of an actual population at the beginning of a given 100-day prediction period. States judged similar to that of the actual state were collected, and from these the five most closely resembling the actual state were chosen by an index of similarity similar to the chi-squared statistic. In instances where five "similar" states were not found, additional simulations were done. The initial states for these were established by population states chosen from previous simulations in which the three types of fish considered were in excess of that in the actual population. Excess fish

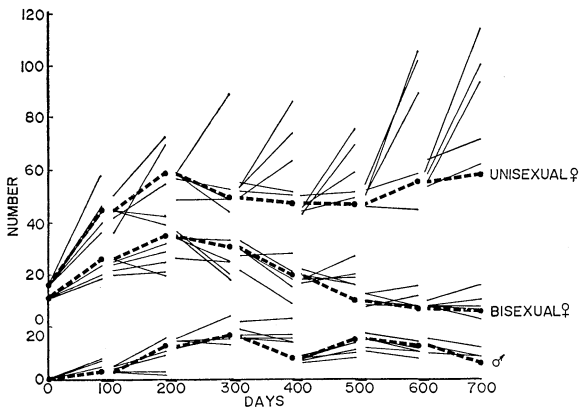


FIG. 6. 100-day prediction intervals for population II.

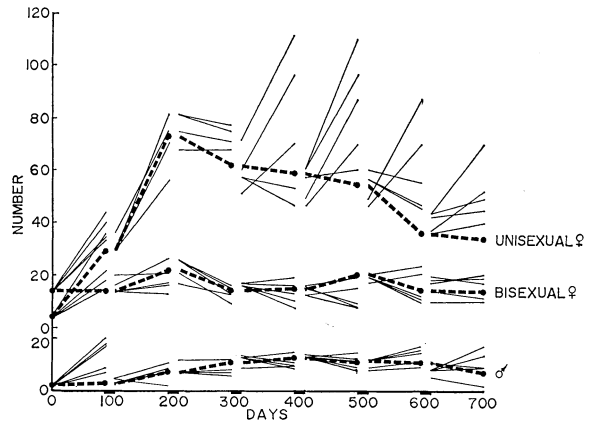


FIG. 7. 100-day prediction intervals for population III.

were then eliminated by a random process of assigning a number to each cell in a given array that contained fish; numbers were then chosen at random with replacement and one fish was eliminated from a cell each time the cell's number was drawn. The process was repeated for each array until the population state was identical to an actual state in terms of adult females, males, and young. The result of this process was to create five initial population states similar or in some cases identical to the actual population state for each of the 100-day prediction intervals. However, the states created this way probably differed in detail from the actual states because it was impossible to tell exact ages of individuals or, in the case of adult females, their state of pregnancy in actual populations. From this set of initial states, the sets of five 100-day simulations were done for each of the 100-day prediction intervals.

Some inferences regarding the predictive power of the model can be made from Fig. 2-7. Generally, agreement between the simulated and actual results was quite good for the 100-day prediction intervals. The most consistent type of deviation was for greater numbers of unisexual females to enter the simulated populations than the actual populations when the overall population was near its carrying capacity. This was evident in populations II and III in the 2nd yr of growth. A second, less obvious, deviation occurred in the population I prediction intervals beginning at 300 days and 400 days: a significant recruitment of bisexual females occurred in the actual populations but not in simulations.

The continuous history simulation graphs of population III (Fig. 4) differ from the actual population for a reason noted above. In populations I and II the greatest deviation between the actual populations and simulated replicates is that the numbers of bisexual females at times was greater in both the actual than any of the simulated replicates.

Several explanations can be given for apparent deviations. First, it is possible that deviations were due to chance and do not represent trends. In each of the instances where recruitment of unisexuals seemed high in the simulated prediction intervals, there is at least one replicate that followed the actual trend rather closely. Similarly, the two prediction intervals with evident differences between actual and simulated numbers of bisexual females recruited are followed by a third interval with a similar initial state in which a significant amount of recruitment did occur. Thus, in those instances where simulations deviated most noticeably from reality, the simulation at least had a reasonable probability of following the actual trend. Second, better empirical fits were obtained by deliberately perturbing model parameters. For example, slightly decreasing the mortality rates for the bisexual species tended to increase the number of bisexuals in the populations, to diminish the tendency for excessive unisexual recruitment, and to produce a better fit overall. However, increasing unisexual mortality slightly, shifting the sex ratio to favor females, or delaying male maturation had similar effects. Thus, a small error in the estimation of any one of these parameters could, in itself, account for the deviations. Although deliberately perturbing parameters in a systems model can provide useful insights, and this method is used subsequently, it does not seem to be a useful method of identifying an inadequacy of a submodel or estimate here because so many distinct changes give similar results. Finally, there is the possibility that some unidentified factor contributes to the dynamics of real populations which, of course, is not in the model.

*Decreasing the unisexual:bisexual fitness ratio*

The term "fitness" is generally used to express the ability of a species or phenotype to contribute genetically to the next generation, but its specific meanings are so varied that some contextual definition is needed. To model the population biology of unisexual-bisexual complexes, Moore (1975) partitioned fitness into three components: (1) probability of a given offspring being female, (2) probability of a given female being impregnated, and (3) primary fitness. The first two components are of peculiar interest in studies of unisexual-bisexual populations and are incorporated into the sex ratio and insemination submodels respectively. Primary fitness includes all components usually considered in fitness measures: birth rates, death rates, etc., and is a measure of an organism's potential for success in a given environment. Primary fitness is constant for a given environment, whereas the impregnation probability is a dynamic component of the population.

Moore and McKay (1971) and Moore (1975)

TABLE 7. The effect of reducing unisexual primary fitness on average extinction time  $r$  = intrinsic rate of increase (Birch 1948);  $R_0$  = net reproductive rate (Birch 1948)

	( $r$ )	$R_0$	Unisexual: bisexual $R_0$ -ratio	Coexistence time (days) <sup>a</sup>
Bisexual female				
1	.01457 <sup>b</sup>	15.62	...	...
Unisexual female				
1	.02720 <sup>b</sup>	452.32	28.0	560
2	.02713	300.01	19.2	1,070 <sup>c</sup>
3	.02707	203.51	13.0	1,600 <sup>c</sup>
4	.02700	141.02	9.0	1,560
5	.02693	99.69	6.4	1,800
6	.02685	71.78	4.6	2,000
7	.02678	52.56	3.4	2,000
8	.02670	39.08	2.5	2,000
9	.02663	29.46	1.9	2,000
10	.02656	22.48	1.4	2,000
11	.02649	17.34	1.1	1,700 <sup>d</sup>

<sup>a</sup> Kruskal-Wallis test for homogeneity of the population of extinction times:  $H = 19.42$ ,  $df = 10$ ,  $p < .005$ .

<sup>b</sup> Actual values measured in the laboratory.

<sup>c</sup> Sample size = 5.

<sup>d</sup> Extinction of unisexual.

suggested that when the fitness of the unisexual is equal to that of the bisexual in all components except the ability of the former to produce all-female offspring and to obtain sperm, greater than 80% of the females in mixed populations will be of the unisexual type at equilibrium. Although unisexual frequency is sometimes higher than 80% in nature, numerous populations are known where unisexuals are less frequent (Moore et al. 1970 for the *P. occidentalis* complex, McKay 1971 for the *P. lucida* complex, R. J. Schultz, *pers. comm.* for the *P. monacha* complex). In fact the high primary fitness of *P. 2 monacha-lucida* relative to *P. monacha* reported here for laboratory populations would result in unisexual equilibrium frequencies in excess of 0.98, a level rarely obtained in any natural population by unisexual forms of *Poeciliopsis*. Therefore, to better understand the stability of small natural populations, I did a series of simulation experiments in which the relative primary fitnesses were adjusted to more realistic values by progressively increasing the age-specific mortality rates of the unisexual (Table 7).

Three or five replicates for each of 11 unisexual fitness values were simulated. Each of the 37 total replicates was initiated with the same population (this starting state was not identical to any of the initial states of the laboratory populations) and the simulation ran for 2,000 days or until one of the species became extinct. In Table 7, rows 1-11 under Unisexual female show the average coexistence times for 2,000 days of simulation, Birch's (1948) intrinsic

TABLE 8. The effect of increasing the number of isolated demes on extinction time. Asterisk indicates extinction time in days

Replicate no.	One deme		Two demes $R_o$ -ratio		Four demes	
	19.2	28.0	19.2	28.0	19.2	28.0
1	950*	600	1,880	560	720	430
2	630	520	1,480	890	800	770
3	2,000	410	870	510		
4	890	480	670	560		
5	870	800	640	480		
$\bar{X}$	1,068	562	1,108	600	760	600

insic rate of increase ( $r$ ), net reproductive rate ( $R_o$ ) for the unisexual, and ratio of  $R_o$  for the unisexual to  $R_o$  for the bisexual for each of the 11 life tables used in this series of experiments. For the fitness ratio found in the laboratory, the stability of small isolated demes is not great and, in fact, for this starting state are expected to persist less than 2 yr. As unisexual fitness decreased however, the stability of the demes increased markedly and no extinctions occurred in 15 replicates in the interval of  $R_o$  ratios of 1.4–4.6.

Three additional simulation experiments were conducted with values identical to line 9 of Table 7 but with starting states corresponding to that of each of the three laboratory populations. After 2,000 simulated days extinction was not imminent in any of the three populations.

For use in the Discussion, a note is needed on the use of  $R_o$  as a measure of primary fitness. Crow and Kimura (1970) pointed out that the term  $\exp(rt)$  in the exponential growth model,  $N_t = N_o \exp(rt)$ , is analogous to the "Wrightian fitness" coefficient,  $w$ , in discrete generation growth and selection models ( $r$  = intrinsic ratio of increase,  $t$  = time,  $N_o$  = initial population size,  $N_t$  = population size at time  $t$ ). In fact, when  $t$  is chosen so that  $t-0$  is equal to the length of one generation,  $w$  and  $\exp(rt)$  are equivalent measures of fitness. Moore (1975) used a ratio of primary fitness equivalent to Wrightian fitness in a discrete generation model to evaluate the relationship between relative fitness and the frequencies of unisexual and bisexual forms of *Poeciliopsis*. To compare results obtained in the overlapping generation model developed here and the discrete generation model used by Moore (1975), it is necessary to have a comparative measure of fitness ratios for the two models. The ratio  $R_o^{(Q)}/R_o^{(P)}$ , roughly equivalent to  $W_P/W_Q$  for the discrete generation model, will be used for comparisons in this paper ( $R_o^{(Q)}$  and  $R_o^{(P)}$  are the net reproductive rates for the unisexual and bisexual females respectively;  $W_Q$  and  $W_P$  are primary fitnesses for the respective females in the discrete generation model).

The fitnesses for the two female types can be

written as  $\exp(r_Q T_Q)$  and  $\exp(r_P T_P)$  where  $r_Q$  and  $r_P$  are the intrinsic rates of increase for unisexual and bisexual females respectively, and  $T_Q$  and  $T_P$  are the mean generation lengths. An approximate measure of  $W_Q/W_P$  based on an overlapping generation model is  $W_Q/W_P = \exp(r_Q T_Q)/\exp(r_P T_P)$ . According to Birch (1948),  $T = 1n(R_o)/r$ . Now, substituting  $1n(R_o^{(Q)})/r_Q$  and  $1n(R_o^{(P)})/r_P$  for  $T_Q$  and  $T_P$ , the previous expression, after simplification, becomes  $W_Q/W_P = R_o^{(Q)}/R_o^{(P)}$ .

Table 7 gives  $R_o^{(Q)}/R_o^{(P)}$  for each of the 11 experimental life tables.

#### Increasing population size

Increasing population size should decrease the effect that chance events have on populational history. The structure of this model and experimental study does not allow population size to be increased without the possibility of destroying the realism of the model. However, a similar situation which might be important in understanding natural populations can be simulated; specifically, simulating several demes simultaneously and allowing migration between demes during an annual rainy season. To determine whether increasing population size in this way diminished the effects of chance events, I conducted two additional sets of simulations, one with two demes and one with four demes. At the end of each year of simulation, the demes were pooled and individuals redistributed by a series of binomial or tetranomial trials. Results of these trials are presented in Table 8. For one and two demes 10 trials were done: 5 at the fitness values measured in the laboratory ( $R_o$ -ratio) and 5 for a slightly reduced ratio. For the set involving four demes only 2 replicates for each fitness ratio were done.

No differences in mean time to extinction were detected in this analysis nor was there a significant linear regression of extinction time on number of demes for either  $R_o$ -ratio. The deterministic equilibria of populations under these fitness conditions would be non-trivial but with a very high unisexual: bisexual ratio. The average time to extinction due to stochastic factors was no different for a single deme, two demes mixed annually, or four demes mixed annually.

#### DISCUSSION

Results of laboratory population studies and stochastic computer simulation studies presented here are most meaningful in context of deterministic models presented elsewhere (Moore and McKay 1971, Moore 1975). A fundamental question about the population ecology of sperm-dependent all-female species is what allows the two forms to coexist. Moore and McKay (1971) suggested that the behavior of males provided a mechanism sufficient to

allow coexistence; viz, mate preference and a tendency to form dominance hierarchies.

A mixed unisexual-bisexual population of *Poeciliopsis* appears to be a controlled system with a steady state where both unisexual and bisexual species persist (Moore and McKay 1971, Moore 1975). The output of the system, the frequency of unisexuals in the population, controls input of the system, recruitment of unisexuals, by regulating the amount of sperm available to the unisexual component of the population (Moore and McKay 1971, Moore 1974). When the bisexual species predominates, the presumably abundant males interact behaviorally and male dominance hierarchies result; subordinate males are denied access to the preferred conspecific females and mate with unisexuals in impetuous courtships (McKay 1971, Moore and McKay 1971). Consequently, the unisexual component of the population increases and competitively diminishes the bisexual component. However, as the bisexual component decreases, the number of subordinate males decreases and hence the sperm flow to the unisexual component decreases. The frequency of unisexual females is sensed by the system through a negative feedback loop resulting from the courtship behavior of males. As long as the primary fitness of the unisexual is roughly greater than one-half that of the bisexual, the two forms will coexist, provided stochastic factors are not of sufficient magnitude to cause a fortuitous extinction (Moore 1975).

Results presented here demonstrate that the postulated negative feedback loop is strong enough to offset endogenous chance perturbances that might cause chance extinctions in a small population. This conclusion is weakly based on the fact that coexistence obtained in three out of three laboratory populations for a 2-yr experimental period; the conclusion is greatly strengthened by the several simulation experiments where coexistence occurred repeatedly for 2,000 days of simulation.

Probably the most important result of this study is that for primary fitness ratios similar to those which appear to exist in nature, small isolated populations should be highly resistant to extinction. This conclusion is based on data in Table 7 and earlier inferences (Moore and McKay 1971, Moore 1975) regarding the relative primary fitness of the unisexual and bisexual forms of the more northerly *P. occidentalis* complex. In the *P. occidentalis* studies we concluded that when the primary fitnesses of the unisexual and bisexual were equal, approximately 85% of the females in a population would be unisexual. As the unisexual:bisexual ratio increases beyond unity, the percentage of unisexual females becomes even greater. Judging by the *P. occidentalis* complex, the ratio of net reproductive rates ( $R_0$ ) measured in the laboratory populations of *P. 2 monacha-lucida*

and *P. monacha* would generate a deterministic equilibrium of approximately 98% unisexuals, assuming the parameters for unisexual inseminations are similar for the two complexes. Since unisexual females are rarely this successful in nature, it appears that the high primary fitness ratio measured in the laboratory is deceptive and lower ratios are the rule for natural populations.

Table 7 shows that the average coexistence time increased from 560 to 2,000 days as the ratio of net reproductive rates was decreased from 28 to 4.6, and in a total of 18 replicates over the range of ratios from 1.4 to 4.6 no extinctions occurred in the 2,000 simulated days of any replicate. Thus, for fitness ratios that are realistic in terms of natural populations, local extinctions of demes are expected to be infrequent.

The result that annual confluence of demes would not increase the stability of populations was somewhat surprising. In fact, the series of simulations where two and four demes were mixed at yearly intervals was motivated by the hypothesis that extinctions in small isolates were common but a periodic mixing would replenish local demes. I believed that the annual mixing might, in effect, act to enlarge the population size and reduce the significance of stochastic factors. This hypothesis can be unequivocally rejected because local extinctions are probably rare, and mixing did not significantly change extinction time.

In summary, the unisexual-bisexual species complex of *P. 2 monacha-lucida* and *P. monacha* appears to have the potential for long-term stability in spite of small population sizes where one might expect stochastic factors to cause extinction of one form or the other. Local extinctions in nature are probably rare. The annual mixing of demes is not a factor in reducing the probability of extinction.

Since the elements of a theoretical explanation of the population ecology of unisexual-bisexual species are contained in this and three additional papers (McKay 1971, Moore and McKay 1971, Moore 1975) a collecting of the elements and synthesis of the theory is appropriate. The following is a brief sketch of the population ecology of these complexes as I believe it to exist. Stable equilibria exist between the unisexual and bisexual elements of complex populations of *Poeciliopsis*. The equilibria are nontrivial provided the population is in an environment where the primary fitness of the unisexual is at least in very slight excess of one-half of that of the bisexual (primary fitness consists of all fitness components except the abilities of the unisexual to produce only female offspring and to obtain sperm). The slight amount depends on the efficiency of males to discriminate between female types; for the one complex for which data is available, the slight excess is less than  $10^{-7}$ .



Each primary fitness ratio generates a unique unisexual:bisexual ratio at equilibrium provided it is a nontrivial equilibrium. Regulation of complex populations results from the discrimination by males against unisexual females dynamically countered by social interaction manifested in hierarchy formation among males (McKay 1971): subordinate males frequently court the less preferred females. This mechanism allows the two types, which are distinct species, to coexist even though they compete for a common limiting resource. The unisexual:bisexual ratio in natural populations depends on the primary fitness ratio of the two forms in a given environment and thus should vary clinally over an environmental gradient. Clinal variation should be nonlinear with a threshold-like change from a preponderance of unisexuals to a preponderance of bisexuals. The variance in frequency of unisexuals should be great in the transition zone and small in the extremities of the range. Other factors, such as differences in the onset and termination of the reproductive season, aberrant sex ratios, and interactions with other species, may modulate population behavior or introduce spurious oscillations; but the behavioral patterns of mate selection and hierarchy formation manifest in the males of the host species are at least sufficient conditions, and mate selection is probably a necessary condition to the persistence of unisexual-bisexual species complexes of *Poeciliopsis*.

The applicability of this theory to sperm-dependent unisexual-bisexual species complexes in general has yet to be resolved. It certainly applies to three species of *Poeciliopsis*—*P. lucida*, *P. monacha*, and *P. occidentalis*—and their several unisexual parasites. Two other species, *Poeciliopsis latidens* and *Poeciliopsis viriosa*, also support unisexual species, but insufficient data are available to make an inference about their population ecology. In addition to the unisexual forms of *Poeciliopsis*, triploid gynogenetic populations of goldfish occur in Russia (Cherfas 1966), and both diploid and triploid forms of gynogenetic *Poecilia formosa* occur in southeastern Texas and northeastern Mexico (Hubbs 1964, Darnell and Abramoff 1968, Rasch et al. 1970). No information is available on the population biology of gynogenetic goldfish. It is likely that the mechanism which allows unisexual forms of *Poeciliopsis* to persist also sustains populations of *P. formosa*. *Poecilia formosa* maintains a sperm-dependent relationship with one or the other of its parental bisexual species (*Poecilia latipinna* or *Poecilia sphenops*) analogous to that in *Poeciliopsis*. In an extensive analysis of the fecundity of mixed populations of *P. formosa* and *P. latipinna*, Hubbs (1964) found patterns similar to if not identical with those in *Poeciliopsis*. Briefly, the reproductive potential of *P. formosa* was slightly greater than that of *P. latipinna* but this, plus the advantage of producing only

female offspring, was countered by a low frequency of pregnancies in the unisexuals. Further, the frequency of pregnant unisexuals increased as bisexual density increased. In terms of behavior, *P. latipinna* males showed a strong mate preference for conspecifics and, in natural populations, were territorial. McKay (1971) reported territoriality in males of *Poeciliopsis* and concluded that this was a manifestation of social interaction among males. Hubbs noticed that large *P. latipinna* females were most frequently pregnant, followed by small *P. latipinna* females, then small *P. formosa* females and finally large *P. formosa* females.

The mechanism postulated by Hubbs (1964) to explain these data is quite different from that presented here and by McKay (1971). Hubbs believed *P. latipinna* males first courted all *P. latipinna* females in their territory, beginning with the largest and working toward the smallest. "Sail fin (*P. latipinna*) males that had inseminated all the female sailfins in their territory would then court and inseminate amazons." As McKay (1971) pointed out, the existence of such a mechanism is unlikely because the requisite behavior simply does not exist. In addition, this mechanism would seem to have an effect opposite to that of stabilizing populations: i.e., it would decrease stability. According to Hubbs, at low bisexual densities males would court the comparatively few *P. latipinna* females in their territories and then turn to the more numerous unisexual *P. formosa* females. At the other extreme when bisexual density was high, more time would be spent courting conspecifics and less courting unisexuals; this in turn would increase bisexual density and subsequently further decrease unisexual inseminations. Such a system would soon lead to the demise of one form or the other.

McKay interpreted Hubbs' data in terms of mate preference and social structure as seen in *Poeciliopsis* and obtained a better fit. Baird (1968) studied aggressive behavior and social organization in *P. latipinna*; as in *Poeciliopsis* social organization was largely a function of male density, and the behavioral elements necessary to sustain unisexual-bisexual complexes were evident. Thus, it is likely that the mechanism which sustains and regulates unisexual-bisexual species complexes of *Poeciliopsis* obtains in complexes involving *P. formosa*.

The *Ambystoma jeffersonianum* complex (Amphibia, Caudata) contains two gynogenetic triploid species, but comparatively little is known about the relationship between fertility of triploids and bisexual density in these complexes. Wilbur (1971) demonstrated a significant competitive interaction between larvae of the bisexual species, *Ambystoma laterale*, and its all-female associate *Ambystoma tremblayi* and reviewed evidence suggesting the existence of a

mechanism that stabilized local populations. Too little is known about the courtship behavior and reproductive biology of *Ambystoma* to develop an inclusive hypothesis regarding the stabilizing mechanism. Nonetheless, some facts have emerged: the fecundity of the triploid *A. tremblayi* is slightly greater than one-half that of its bisexual host *A. laterale* (Clanton 1934); males strongly discriminate against triploid females in courtship (Uzzell 1964, 1969); and triploid eggs are mostly unfertilized in natural populations (Wilbur 1971). Thus, it appears that the control system in *Ambystoma* complexes also operates through regulation of the amount of sperm available to the unisexual population and that mate preference is involved. An analogue to social interaction in *Poeciliopsis* which would increase unisexual courtships at high bisexual densities however has not been reported. Uzzell (1969) reported inhibitions of spermatophore production in aquaria containing several males as a result of social interactions but this would appear to be of no benefit to unisexuals. It is possible that the interaction component of the stabilizing mechanism in *Ambystoma* complexes is absent. Reproduction in *Ambystoma* occurs for a period of several nights during the early spring (Goin and Goin 1971). Males, which usually predominate in bisexual populations, migrate to the breeding ponds prior to the females. Although "supporting evidence is scant," Uzzell (1969) suggested triploid females arrive at the breeding ponds along with the first males and prior to the bisexual females. Females of *Ambystoma* have a more active role in courtship bouts than do females of *Poeciliopsis*; spermatophores are deposited on a substrate by males and the seminal fluid is subsequently taken up by aroused females. Uzzell (1969) presented evidence that suggests the arousal threshold for removal of seminal fluid is actually lower in triploids. Certainly, selection would favor such females. As pointed out, mate selection alone could account for the frequency of pregnant unisexuals in *Poeciliopsis* if it were only moderately developed. In *Ambystoma*, early migration of triploids to the breeding ponds combined with the more active role of females in courtship could counterbalance mate preference as a suppressant of unisexual inseminations. A study of the relationship between the frequency of fertilized egg masses and the relative frequencies of unisexual and bisexual females, and the development of a mathematical model for the competitive interactions within *Ambystoma* complexes could resolve this question.

#### ACKNOWLEDGMENTS

This study was supported in part by National Science Foundation grants: GB-20686 (R. J. Schultz, Principal Investigator), GB-35949 (W. S. Moore, Principal Investi-

gator), and GJ-9 to the University of Connecticut. Recognition is also due to R. J. Schultz who, with the statement: "Why don't you throw some of these unisexuals in a box and measure their fitness?" initiated my interest in population biology.

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