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COEXISTENCE IN UNISEXUAL-BISEXUAL SPECIES COMPLEXES OF *POECILIOPSIS* (PISCES: POECILIIDAE)[1]

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Abstract. All-female forms of *Poeciliopsis* rely on males of closely related bisexual species for sperm. The natural habitat of *Poeciliopsis* in Sonora, Mexico, consists of a variety of small ponds connected by intermittent watercourses. Optimal areas, containing mixed female aggregates, are defended by territorial males. Social structure in natural populations very closely resembles that of laboratory experiments, wherein subordinant males show reduced mate discrimination and inseminate unisexuals.

An equation relating male density to unisexual inseminations is used in a computer simulation model of a population. A stable equilibrium is inherent in unisexual-bisexual species complexes but the level of equilibrium is affected by the environment. Coexistence does not require niche separation. The simulations predict the percentage of unisexuals pregnant in natural populations and explain their distribution pattern. The strength of the mechanism is demonstrated by a natural population in which the percentage of unisexuals pregnant responded strongly to a modest change in unisexual-bisexual composition.

The population ecology of all-female forms in the genus *Poeciliopsis* is complicated by the fact that sperm is necessary for embryonic development. This requires the coexistence of two closely related "species," one a unisexual and one a bisexual, in a limited habitat. If the two forms are ecologically distinct to the extent that the population growth of each is limited by different factors, there is no problem since competition will not exist. Although evidence suggests slight differences in niche requirements between the elements of at least one complex (Moore, Miller, and Schultz 1970), strong niche separation has not been reported. It appears that in the sperm-dependent type of unisexual-bisexual complex, mechanisms exist which allow the two forms to coexist.

In laboratory experiments McKay (1971) showed that the amount of sperm available to the unisexual population is limited by a strong preference of males for conspecific females. However, social interaction in groups of males leads to the formation of monarchistic hierarchies in which a dominant male prevents subordinates from courting conspecific females. Unisexual inseminations result from subordinate males seeking alternatives for their sexual drive. This suggests an equilibrium system in which the advantage of producing only female offspring is dynamically countered by the amount of sperm available.

This paper relates the social structure observed in the laboratory to natural populations and habitats; it tests the sufficiency of male density, social structure, and mate selection as a control system in regulating the composition of unisexual-bisexual complexes of *Poeciliopsis;* and it examines some properties of this mechanism that are fundamental to understanding the population ecology of these complexes.

METHODS

During October and November of 1969, *Poeciliopsis* was studied in the upper tributaries of the Rio Fuerte in Sonora, Mexico. Since laboratory experiments had indicated that social structure was an important parameter in the population dynamics of these complexes, emphasis was placed on male social hierarchies, distribution of age groups, and aggressive behavior.

The ovarian contents of samples of 20 adult unisexual females from eight collections preserved at the University of Michigan Museum of Zoology were examined for pregnancy. The collections were from the *P. occidentalis–P. monacha-occidentalis* complex. Females were chosen at random and were included in the sample only if their ovaries contained mature ova. A female was considered pregnant if late primitive streak or more advanced embryos were clearly discernible.

A digital computer simulation for a *Poeciliopsis* complex was devised with particular interest given to an equation relating the number of males in the population to the number of unisexuals inseminated.

STRUCTURE OF NATURAL POPULATIONS AND HABITATS

Since the distribution, competitive interactions, and social structure of *Poeciliopsis* are critical in understanding unisexual-bisexual population dynamics, the physiognomy of natural habitats is described here. The headwaters of the Río Fuerte in Sonora, Mexico, were selected for this description since a majority of the behavioral and social structure observations were made there.

During the dry season, which extends from Octo-

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ber to July, water movement in these streams is confined to the central portions of the rock and gravel bed. This results in a variety of small pools, shallow regions, and broader flows. Small bedrock watercourses or arroyos with steeper gradients feed these streams and provide a habitat for *P. monacha,* the only species of *Poeciliopsis* found there. Such arroyos consist of isolated or connected pools of various sizes which after heavy rains become joined by torrents of water. The distribution of *P. monacha* and its unisexual associate is limited to those arroyos and to several miles of stream where they overlap in a short region with *P. lucida* and its unisexual forms.

As is true of most animals in natural communities, individuals are not distributed randomly throughout the habitats described. Optimal areas exist where they congregate, compete, and select mates. Optimal areas for all forms of *Poeciliopsis* included here consist of small shallow pools seldom deeper than 0.5 m, although deeper bedrock pools with depths of up to several meters are utilized when they are available. Since these deeper bedrock pools contain predacious cichlids, *Cichlasoma beani,* and since algal growth is limited to the rocky margins, only the edges constitute optimal regions. Rooted vegetation is almost totally absent but algal growth occurs on submerged rocks and the gravel bottom. Algae are not abundant in these narrow headwater streams but sometimes form large floating mats in the wider and slower portions down river. Optimal pools have sufficient inflow of water to wash in small invertebrates and other food materials.

Size classes are not equally distributed throughout the stream. As is true of other poeciliid fishes, smaller individuals are found in the shallow areas and larger fish in the deeper pools (Kilby 1955, Haskins et al. 1961, Baird 1968). Intraspecific aggression, predation, and cannibalism determine this distribution. Since many forms of *Poeciliopsis* are cannibalistic (Schultz 1960), escape behavior forces the smaller size classes into shallow regions. Aggressive interactions between individuals of the same sex disperse individuals into size groups because size is important in determining the outcome of such encounters. Small cichlids are sometimes found in the shallow optimal pools where they capture or drive out the small size classes of *Poeciliopsis.*

Some degree of male interaction was observed in each of 12 shallow optimal pools, but social and sexual behavior varied according to the physical parameters. Territoriality was strong if the size and shape of the pool provided a confined area for female aggregations. In the region of sympatry of *P. monacha* and *P. lucida,* a typical pool with a territorial *monacha* male was approximately 0.3 m deep, 6 m long, and 2.4 m wide. *P. monacha* and its unisexual associate were most frequent in this community as determined by capturing both the dominant male and a number of females. One large black male defended a portion of this pool delineated by submerged rocks. Large females in the area formed a loose aggregation which occasionally dispersed while females browsed on the algae on rocks. During these feeding periods females maintained an individual distance that distributed them evenly over the feeding area. Aggression appears important in maintaining distance since if one individual moved too close to another it was threatened. The dominant male drove the subordinant males out of the area into shallow, suboptimal regions; some attempted to re-enter and mate with females before they were again driven out. Occasionally, a subordinant male would remain unchallenged and apparently unnoticed on the periphery of the pool and attempt to mate.

Mouth contact, a prelude to copulation, was performed by the dominant male as he moved from female to female (this behavior has been implicated as having a species recognition function with the involvement of olfactory cues, McKay 1971). Occasionally he vigorously pursued and thrust at particular females, 13 of which were captured and identified as *P. monacha.* During the period of observation the mixed species population resembled that of the low male-density situations of the laboratory (see below). Fish in other stream pools in this region, particularly those downstream, had similar social organizations but were dominated by *P. lucida* and its associated unisexual forms; *P. lucida* males defended such pools in a manner similar to that of *P. monacha.*

The bedrock tributaries which support *P. monacha* and its associated triploid were generally low in nutrients and lacked organic complexity; most populations appeared to be semistarved. Several atypical pools of the 10 to 15 examined in these arroyos contained large populations in excellent condition; sufficient nutrients were available to support a complex community including submergent and emergent vegetation. One such pool was 0.9 m at its greatest depth, 15 m long, and 6 m wide. Size classes were distributed as in the stream, with young and juveniles in shallow regions and adults in deeper areas. The optimal feeding regions were patches of submerged vegetation. The segregation maintained by the mechanism of individual distances, which was observed in the stream habitat, was also pronounced in bedrock pools. In the nutrient-rich pools that supported healthier populations, rocks and plants delimited small areas about 15 cm in diameter that both sexes defended; numerous aggressive displays occurred there between members of the same sex. Individual feeding territories were not rigidly maintained; individuals occasionally moved to new areas and defended them with the same tenacity. The intensity of aggression was directly related to the density of the feeding population. It was most pronounced in the optimal bedrock pools that contained numerous individuals and limited feeding areas. Large mature individuals always selected and defended the choice feeding areas, and aggressive interactions resulted in the typical distribution of size classes.

In the laboratory, insemination of unisexuals occurred in mixed populations only when circumstances allowed the formation of monarchistic hierarchies among males (McKay 1971). In these situations a single dominant male emerges who constantly attempts to deny all other males access to female aggregates. Subordinate males frequently swim toward and thrust at the closest female, often a unisexual, before they are driven away. Other laboratory experiments, initiated with larger numbers of immature males, resulted in unisexual pregnancies as the male population passed through an ephemeral monarchistic hierarchy stage when only a few males had matured. Once all males had matured, the monarchistic hierarchy was replaced by a less-rigid dominant-subordinate relationship in which all males could discriminate and no unisexual pregnancies resulted. McKay (1971) states that the latter situation is probably an artifact of the laboratory.

The technical difficulties in marking and observing individual *Poeciliopsis* and controlling the numerous variables during field studies has made it difficult to visually confirm insemination of unisexuals by subordinant males. The behavior of dominant and subordinant males in natural populations and the overall social organization described above strongly suggest that the same interaction exists there as in the laboratory.

Poeciliopsis males, denied access to females, demonstrate weaker mate selection when subsequently given a choice of females. This has been shown in both artificial isolation tests and in larger population experiments and interpreted as an indication of the males' heightened sex drive due to isolation (McKay 1971). If conspecific females are not readily available to subordinant males as shown in the laboratory and as implicated in natural populations, some of their sperm is contributed to unisexuals each generation. Clark, Aronson, and Gordon (1954) reviewed the evidence from fish and other vertebrate studies showing that males of most animal species accept heterospecific mates if conspecifics are unavailable. Hubbs (1964) made the general statement that "males of every fish I know will attempt to court females of related species if homospecific females are unavailable." To ignore the role of social organization and competition among males in the population ecology of unisexual-bisexual complexes is untenable.

Social interactions in natural populations may be modified by predation on males. The jet black dominant males are conspicuous against the generally light gravel stream beds, and the wariness normally found in females is often lacking in these individuals. Males were easily approached and captured in a small dip net. Avian predators (kingfishers, herons) and cichlids may take such males with greater frequency. This differential predation would preclude the high male-density situation described in the laboratory. In any case, the relationship between frequency of bisexuals and percentage of unisexuals pregnant monotonously increases in natural populations.

In this paper we are interested in the potential for regulation of unisexual-bisexual *Poeciliopsis* complexes within a single stream pool or bedrock pool. If regulation can be understood at this level, particularly the problem of coexistence, it can be understood for entire drainage systems.

In the development of the submodel for unisexual inseminations, a single pool is envisioned with a capacity of 500–1,000 liters. The habitat is stable in time with a fixed number of optimal areas. At very low male densities each male would be effectively isolated and would court only conspecifics. As male density increases, greater numbers of males would be denied free access to mixed female aggregates which are generally found browsing in optimal areas defended by dominant males. This in turn increases the frequency of impetuous courtships and unisexual inseminations.

A POPULATION MODEL FOR A *Poeciliopsis* COMPLEX

A deterministic, discrete time model was devised which is generally applicable to unisexual-bisexual species complexes in the genus *Poeciliopsis*. The model includes most of the biological attributes of species of *Poeciliopsis* relevant to their population dynamics. Some of these features are: age structure, age-specific birth and death rates, superfetation, sperm storage, continuous reproduction, cannibalism, competition, mate selection, and social interaction among males. Results are from numerical analysis by digital computer.

The model is presented here as four arrays of values (Fig. 1). The arrays represent: males of the bisexual species, young and females of the bisexual species, young and virgin females of the unisexual form, and pregnant unisexual females. The first three arrays are one-dimensional; the fourth is two-dimensional. The ability of both unisexual and bisexual females to store sperm is an important factor in the dynamics of these complexes; the two-dimensional pregnant-unisexual array simulates this phenomenon.

Each array is divided into age intervals equal to the length of the brood interval of the fish under consideration. A brood interval of 11 days was used

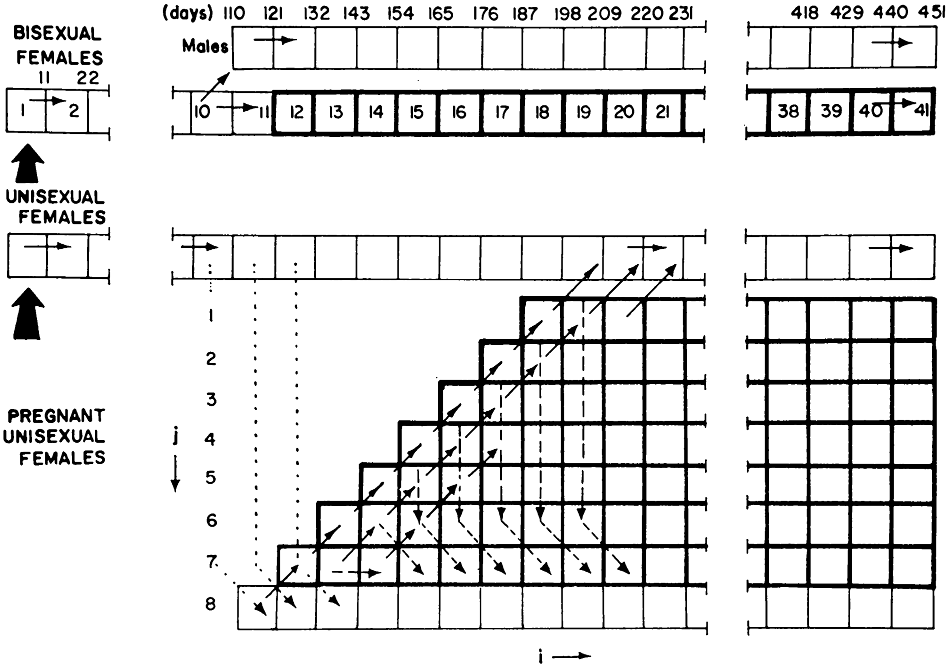

FIG. 1. Schematic diagram of a computer simulation for a unisexual-bisexual species population in the genus *Poeciliopsis*. Dashed arrows indicate movement of unisexual females reinseminated in the current time interval. Dotted arrows indicate movement of newly inseminated unisexual females. Solid arrows indicate possible movements of other types. Not all arrows are shown; a representative few show the general pattern. See text for a full explanation. Heavily outlined cells contain productive females; young are collected and entered into the first cell of the appropriate array as indicated by the heavy arrows.

for all fish in this analysis. Thus, the first cell in each array represents fish aged 0–11 days; the second, fish aged 12–22 days, etc. The last interval contains fish in the last 11 days of life. It is assumed that no fish live beyond the maximum age defined (451 days).

Time is divided into increments equal to one age interval. During an increment of time the fish in each cell are subjected to the birth and death rates characteristic of that age and type of fish. Additional parameters act upon certain cells: The fish aged 0–11 days are subjected to cannibalism; sexual maturity occurs in bisexuals in the 10th age interval; some proportion of the fish in the two unisexual arrays from cells 10–41 are impregnated. In the two bisexual arrays, after the fish have been subjected to the life functions at time t, the fish in the ith cell are advanced to cell $i + 1$ and time becomes $t + 11$ days. The number of fish in cell 10 of the bisexual array is divided according to a fixed sex ratio and a proportion allocated to cell 11 of the male array.

The events in the two unisexual arrays are similar except that a proportion of the mature females in the two are inseminated or reinseminated and moved into temporary holding arrays. The noninseminated fish remaining are advanced as follows: the fish in the virgin-unisexual array from cell i to cell $i + 1$ and the fish in the pregnant-unisexual array from cell (i,j) to cell $(i + 1,\ j - 1)$. The fish from the (i,j)th cell of the pregnant-unisexual array which were reinseminated are now moved to the $(i + 1,7)$th cell of the same array. Newly inseminated fish from the ith cell of the virgin-unisexual array go to cell $i + 1,8)$ of the pregnant-unisexual array where they remain for one time increment without producing young. At time $t + 22$ days these fish go to cell $(i + 2,7)$ where they begin production of young.

The net result of the operations on the two unisexual arrays is the simulation of sperm storage and superfetation in the unisexual form. Pregnant unisexuals begin production in the cells of the seventh row and continue production through the first row. If a female in the first row of this array is not reinseminated she is moved to cell $(i + 1)$ of the virgin-unisexual (nonproductive) array at time $t + 11$ days. Females in the pregnant-unisexual array which are reinseminated are again moved to the seventh row and begin the "decay" through the "sperm storage" rows until the last of their sperm is used in row one.

All members of the genus exhibit superfetation. Typically, two distinct stages of embryos are apparent in ovary dissections (Schultz 1961), the develop-

TABLE 1. Values of fixed parameters

Parameter	Value	Parameter	Value
Brood interval	11 days	Age at first brood production	121–132 days
Gestation period	22 days		
Age at onset of maturity	110 days	Length of sperm storage (from time of first brood to last)	77 days
Maximum age obtainable	451 days	Age specific birth rate, $y = 0.0617\,\Upsilon x - 6.18$, $x = (115.5, 126.5, 137.5, 148.5, \ldots, 445.5)$ where: y = expected number of young/brood x = age (days) $\Upsilon = \begin{cases} 1 \text{ for pregnant unisexuals in rows 3–7}^{a} \\ 0.616 \text{ for pregnant unisexuals in row 2} \\ 0.321 \text{ for pregnant unisexuals in row 1} \end{cases}$	
Increment of time	11 days		
"Voracity" coefficient cannibalism (α)	.015		

[a] In the laboratory a decline in brood size is noticeable in the last two broods produced as a female runs out of sperm. Multiplying row 1 and 2 of the pregnant unisexual array by an appropriate fraction simulates this decline.

mental time between states being equal to the length of a single brood interval. The gestation period then must be twice the brood interval. It would be expected, and borne out by laboratory observations, that a minimum of two times the expected brood interval should elapse between the time a nonpregnant female is inseminated and her first brood appears. Subsequent broods would be spaced by a single brood interval. Because newly inseminated females are held in the eighth row, where reproduction does not occur, the elapsed time before the female first reproduces is two brood intervals, thus simulating the initial gestation period.

It is assumed that the sexual vigor of males and their preference for conspecific mates renders all bisexual females pregnant at all times. Thus, the sperm "decay" phenomenon is not simulated for bisexuals.

The model requires a detailed set of numerical values for all parameters. We are primarily interested in the interaction of three factors and the resultant dynamics of *Poeciliopsis* complexes. The factors are: (i) increased reproductive potential of unisexuals; (ii) mate selection; and (iii) social interaction among males. All other parameters are fixed at equal values for the two forms and the effects of the parameters of interest deduced from the numerical results. The fixed parameters used in this analysis are presented in Table 1 and Fig. 1. Values were estimated from unpublished laboratory and field data accumulated on *Poeciliopsis lucida* and associated unisexual forms and another unisexual form associated with *P. monacha*. Generally these data reflect the physiological capabilities of the genus with respect to longevity, fecundity, age at maturity, brood interval, gestation period, length of sperm storage, and so forth.

In the model, overall population size was controlled by cannibalism. Cannibalism has been observed in the laboratory for several species of *Poeciliopsis* and definitely operates as a density-dependent regulating factor in experimental populations (*unpublished data*). In addition, remains of young have been noted in stomachs of field-collected females (R. Thibault, *personal communication*). Since males are small and probably not important as cannibals, the carrying capacity of the population is affected by the unisexual:bisexual ratio. When the population is predominantly unisexual, there are more females in the population and thus more cannibals. When bisexuals dominate, a large segment of the population is composed of males which are not active in regulating the carrying capacity; thus, the overall population must increase to achieve an equivalent amount of cannibalism.

Rose (1959) demonstrated reduced recruitment in laboratory populations of guppies as population density increased and ascribed this totally to cannibalism. His data suggest that the number of young surviving is an exponential function of adult density. In the application of this model, the number of young surviving cannibalism in each time interval is given by

$$p = {}^{-ax}$$

where: p = proportion of young surviving
x = number of adult females (cannibals)
α = a constant.

A general age-specific mortality rate of 0.1 was leveled on all age groups of both the bisexual and unisexual forms.

Submodel for unisexual inseminations

Since all-female forms require sperm as a stimulus for embryonic development, unisexual recruitment depends upon the number of unisexuals inseminated. Mate preference limits unisexual inseminations; however, social interaction prevents some males from courting conspecifics and unisexual inseminations result. In this study the numbers of males and females are considered to be continuous variables; thus the number of unisexuals inseminated with respect to the number of males can be expressed as the differential equation

$$\frac{\mathrm{d}Y}{\mathrm{d}m} = (im + c)(L - Y) \qquad (1)$$

$$Y(0) = 0 \qquad (2)$$

where: Y = the number of unisexuals inseminated
L = the number of unisexuals in the population
m = the number of males in the population
i = constant (coefficient of male interaction)
c = constant (coefficient of mate selection).

Equation (1) is an expression of social interaction. The infinitesimal change in unisexuals inseminated as a result of an infinitesimal increase in the number of males is greater at high male densities than low. However, the number of unisexuals inseminated cannot exceed the number of unisexuals present; the second quantity on the right of equation (1) causes the derivative to approach zero as this occurs. Equation (2) is a side condition and states that the number of unisexuals inseminated is zero when the number of males in the population is zero.

The solution of this initial value problem is

$$Y = L - \exp\{-[im^2/2 + cm - \ln(L)]\}. \qquad (3)$$

The proportion of unisexuals inseminated is

$$p = \frac{Y}{L} = 1 - \frac{\exp\{-[im^2/2 + cm - \ln(L)]\}}{L}. \qquad (4)$$

Equations (1), (3), and (4) contain two constants, i and c, which are characteristic of the males of the species under consideration. The constant c, representing the incremental increase in unisexual inseminations delivered in the absence of social interaction, is sufficiently small to be difficult to detect. In trials where a single male was allowed to mate with either a unisexual or bisexual female, no unisexual inseminations occurred. In additional trials where response times of single males to both types of females were recorded, conspecific females were strongly preferred and the little attention unisexual females did receive was due to initial identification by males (McKay 1971). For the purposes of this study it is sufficient to assign c a small positive value, say, 10^{-3}.

The coefficient i, representing the increase in unisexual inseminations due to social interaction, is more complex. It depends not only on a species characteristic interaction, but also on the volume and structure of the population container. This paper is primarily concerned with the existence of social interaction, and thus with the existence of the coefficient i rather than its actual value. Nonetheless, numerical analysis demands that a value for i be supplied. It is reasonable to suppose that in a population containing 100 unisexual females (L), 40 bisexual females, and 40 males, 0.5 of the unisexuals would be inseminated in an 11-day period. This supposition is based upon laboratory experience. Solving equation (4) gives the value $i = 8.165 \times 10^{-4}$. This value is assumed in all simulations where male interaction is assumed to exist. Fig. 2 is the graph of equation (4) for the parameters given.

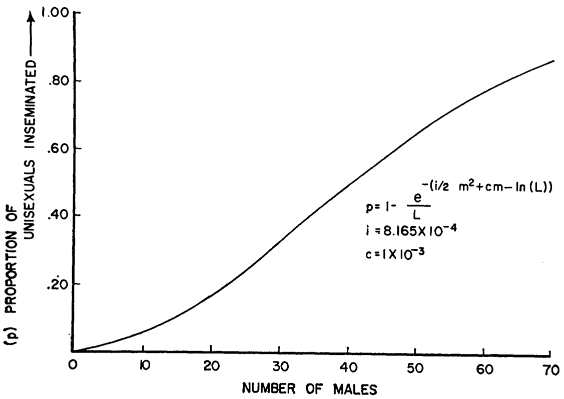

FIG. 2. Graph of equation (4) for selected parameters ($L = 100$).

THE BASIS OF EQUILIBRIUM

A simulation was run to test the sufficiency of three factors (unisexuality, mate preference, and social interaction among males) in causing an equilibrium in a unisexual-bisexual complex. Thus, the elements of the complex are assumed to be identical in all aspects except that the unisexual produces only female offspring and the proportion of unisexuals inseminated is governed by equation (4). Initially, 25 bisexuals (12.5 males and 12.5 females) were introduced. The population grew for 1,100 simulated days as a single-species population, at which time 10 adult unisexual females were introduced (Fig. 3). After an initial lag, the unisexual population grew rapidly, encroaching upon the bisexual species. However, exclusion of the bisexual does not occur; an equilibrium is established with a female composition of 88% unisexuals.

An implicit assumption of this simulation is that the unisexual and bisexual elements of the complex occupy identical fundamental niches. Thus, coexistence does not require niche separation and, since the elements of a complex are two distinct species, the system is an exception to the Gause axiom of competitive exclusion.

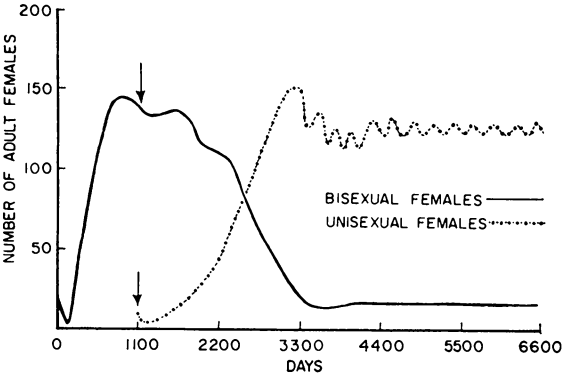

FIG. 3. Graphic result of simulation 1. The arrows indicate the point when unisexual females invaded the bisexual population.

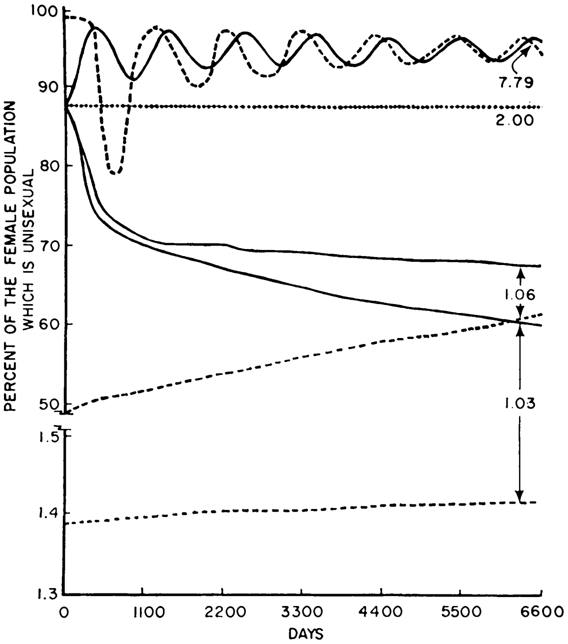

FIG. 4. Graphic results of simulations 2, 3, and 4. Each simulation consists of a pair of curves. The solid lines represent the initial simulations, the dashed line a test for convergence. The ratio of R_0 for the unisexual to R_0 for the bisexual is given for each simulation. The dotted line is the equilibrium value of the population, assuming the two forms are in the same niche. The vertical scale for the lowest curve has been expanded to show its increasing trend.

COMPLEXES IN EVIRONMENTAL GRADIENTS

That the unisexual and bisexual elements of a complex could coexist in the same niche is of theoretical interest but little else. The hybrid origin of unisexuals (Schultz 1969, 1971) guarantees that the two niches are not identical, although undoubtedly great overlap exists and possibly the inclusion of one niche within the other. In any case, competition for a common limiting factor is likely in natural populations.

In the next series of simulations, nonidentical niches and a common limiting factor were assumed. The results illustrate a fundamental principle of the population ecology of these complexes and explain the distribution pattern of the *P. occidentalis* complex reported by Moore et al. (1970).

If two species with different niche requirements were exposed to a gradient of environments, their fitnesses would change differentially. This result is simulated in the computer by changing a component of fitness of one species relative to the other. To demonstrate the effect of niche separation on unisexual-bisexual species complexes a series of simulations was run, changing the age-specific mortality rates for the two elements for each simulation. The net reproduction rate, R_0 given by Birch (1948), was used as an index of fitness. R_0 is simple to calculate and is a valid comparison when the generation times of the compared species are identical, which was the case in the computer simulations.

In each case the ratio of unisexuals to bisexuals moved toward a new equilibrium value (Fig. 4). Two runs were made for each R_0. The first was begun at the population level established by the initial simulation where mortality rates were identical for the unisexual and bisexual forms. The purpose of the second run was to determine if the proportion of unisexuals was converging to a value greater than zero or less than one. This was done by initiating the second simulation at a proportion below or above the equilibrium point suggested by the first run. If the values generated by the second simulation tended toward the estimated equilibrium point, this was taken to mean that the equilibrium point was nontrivial. Thus, we do not know the precise equilibrium value for each R_0 but an interval containing this value. This is sufficient for this paper, since we are most interested in the mere existence of equilibrium.

As the values of R_0 for the two forms approach identity the number of unisexuals at equilibrium approaches zero. As R_0 for the unisexual increases, the ratio shifts favoring unisexuals at equilibrium.

In the initial simulation (equal mortality rates) R_0 for the unisexual is precisely twice R_0 for the bisexual. This simply reflects the property of producing only female offspring. Under this circumstance unisexual females constitute 88% of the female population at equilibrium. Increasing R_0 for the unisexual form 7.8 times that of the bisexual form produces an equilibrium in a neighborhood of 95% unisexual females.

In the *P. occidentalis* complex, regulation of the unisexual:bisexual ratio was apparent within each drainage, although the actual mechanism of regulation was not evident, and the ratio responded to a

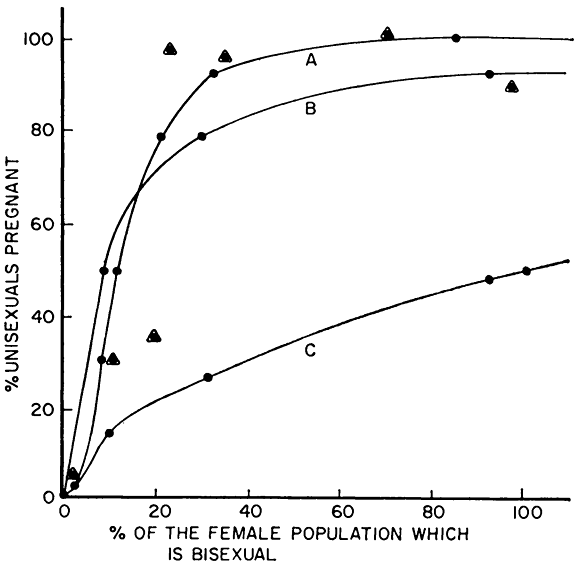

FIG. 5. Percentage of the unisexuals pregnant plotted against percentage of the female population which is bisexual in natural and simulated populations. Triangles represent natural populations. Curves A, B, and C are drawn through simulated populations (see text).

north-south environmental gradient and to localized environmental heterogeneity (Moore et al. 1970).

This model predicts a distribution similar to that seen in this complex. Existence of a stable equilibrium is solely a result of factors inherent in the biology of a complex, but localized environments determine equilibrium frequencies.

If the hypothesized regulating mechanism is operational in natural populations, the percentage of unisexual females pregnant should increase as the number of bisexuals in the population increases. The *P. occidentalis* complex has populations with a wide spectrum of unisexual:bisexual ratios. The viviparous nature of *Poeciliopsis* makes it possible to determine whether or not sperm were available to fertilize a female's ova. Samples throughout the spectrum of ratios were dissected.

There is a nonlinear, monotonically increasing relationship between the percentage of the female population that is bisexual and the percentage of unisexuals pregnant (Fig. 5, Table 2). In this study we assumed that the percentage of bisexual females is an indicator of the number of males present. Although this may be tenuous, it is undoubtedly better than assuming that the preserved collections are unbiased with respect to sex ratio. *Poeciliopsis* males are smaller than females and more likely to escape capture through a ¼-inch mesh seine. On the other hand, there is no reason to suspect a differential capture of female types.

To investigate the factors determining the distribution of points in Fig. 5 several "collections" were simulated using this model. As discussed above, changing a component of fitness of the unisexual form relative to the bisexual establishes a new equilibrium composition. Mortality rates were chosen to generate a desired unisexual:bisexual ratio. When this had been achieved the simulation was terminated and the ovarian contents of the females read out. Three sets of simulations were made. In the first set (curve A, Fig. 5), the values of all parameters except unisexual mortality rates are as before, specifically: $i = 8.165 \times 10^{-4}$, $c = 10^{-3}$; in the second set (curve B), $i = 0$, $c = 10^{-2}$; in the third set (curve C), $i = 0$, $c = 10^{-3}$. Equating i to zero tests the dynamics of a simulated complex in the absence of male interaction.

Curves A and B give empirically close fits to the natural collections while curve C deviates considerably. Thus, if the mate preference coefficient (c) is of the order of 10^{-3} as originally postulated, then some form of male interaction appears necessary to explain the distribution of natural collections in Fig. 5. However, if c is 10^{-2} or more, then the relationship between unisexual pregnancy and bisexual frequency can be explained by mate preference alone.

In laboratory insemination tests, in which single *P. lucida* males remained in aquaria with conspecific and unisexual females for 19 days, no unisexual inseminations resulted (McKay 1971). In other tests with both complexes, groups of seven or eight ma-

TABLE 2. Relationship of unisexual inseminations to the ratio of unisexual:bisexual females in the *P. occidentalis* complex

Collection date	Percentage of female population which is bisexual	Percentage of unisexual females preganat	Sample size	Drainage
3/9/41	96.7	90.6	32	Rio Altar
3/18/41	88.7	100.0	20	Rio Matape
1/26/51	70.4	100.0	20	Rio Sonora
4/16/68	34.8	95.0	20	Rio Mayo
11/4/69	22.4	95.0	20	Rio Mayo
2/15/57	19.2	35.0	20	Rio Mayo
3/27/59	9.6	30.0	20	Rio Mayo
2/2/55	2.7	5.0	20	Rio Mayo

ture males were reared with mature unisexual and bisexual females. Those experiments yielded only bisexual pregnancies, although several continued for 5½ months; no monarchistic hierarchies existed in these tests. Additional tests measured the sexual response time of single males to pairs of females consisting of one unisexual and one bisexual. In one such series of tests utilizing both diploid and triploid unisexuals, *P. lucida* males directed 5.5% of their time to the all-female forms. When only diploid unisexuals were utilized in female pairs, that parameter was 4.4%. In the *P. monacha* complex, males directed only 2.4% of their sexual response time to unisexuals. No gonopodial thrusts at unisexuals occurred, in contrast to the *P. lucida* trials where a low number of thrusts were made. In all tests, thrusts directed at unisexuals occurred at the beginning of trials and apparently resulted from a heightened sex drive due to isolation of males prior to trials. Further, response time directed at unisexuals was predominantly mouth contact behavior, which appears important in distinguishing female types. A value of the mate preference coefficient of 10^{-2} implies a male would, on the average, inseminate 1/100 unisexual females per 11-day period. In view of the strong mate preference shown by males in the laboratory and the fact that the male's ability to discriminate between female types improves with experience (McKay 1970), it seems unlikely that c would be as large as 10^{-2}.

Finally, the strength of the male-density mechanism in regulating unisexual-bisexual species complexes, of *Poeciliopsis* is dramatically illustrated in the temporal series of collections of the complex from the Rio Mayo at Navajoa. Four collections made at the same location in 1955, 1959, 1968, and 1969 contained 97.3%, 90.4%, 65.2%, and 77.6% unisexual females, respectively (Table 2). When the unisexual females constituted 97.3% of the female population only 5% were pregnant, thus greatly diminishing their effective fitness and preventing competitive exclusion of their bisexual host species. At the other extreme for this population (65.2% unisexuals), 95% of the unisexuals were pregnant, driving the population composition back toward some point between the two extremes.

This paper has considered regulation of unisexual-bisexual *Poeciliopsis* complexes at their most basic level of organization, that of a mixed population of a few hundred individuals in an isolated pool. Many factors affecting natural populations have been explicitly or implicitly controlled or eliminated so that the effects of a few variables could be focused upon. Of particular importance would be stochastic factors acting on a small population and the heterogeneous nature of *Poeciliopsis* habitats in both time and space. A small random change in the number of males in a pool could produce a drastic shift in the insemination of unisexuals; if either the unisexual or bisexual is at a low frequency, local extinction would be likely. However, this may be offset by the 3- to 4-month rainy season in which isolated pools become temporarily confluent. The more complex stochastic variables are presently under investigation by the authors.

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