

Sex, population dynamics and resting egg production in rotifers

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Abstract

The interaction between sexual reproduction and population growth in the rotifer *Brachionus plicatilis* was examined using exponential and logistic growth models. A computer simulation was used to explore the effects of the frequency of sex and the proportion of a female's daughters reproducing sexually on population growth rate and resting egg production. Within the parameters of the simulation, the proportion of sexual daughters required for maximum resting egg production increased as the frequency of sex decreased. Adding density-dependence to the model also shifted this optimum towards a higher proportion of sexual daughters. When population growth was unconstrained by density, the optimum proportion of sexual daughters varied between 10–50%, depending on the frequency of sex. This compares to 25–64% when the greatest density restraints were applied at $K = 500$ females. As the population growth rate (r) increases, the optimum proportion of sexual daughters increases nonlinearly and these effects are exaggerated as sex becomes less frequent. A compilation of published data from laboratory populations of four *Brachionus plicatilis* strains reveals that the average proportion of sexual daughters is 21% and in close agreement with that predicted by simulation. The limitations of the simulation and its generalizability to other rotifers are discussed.

Introduction

Explaining sexual reproduction in cyclical parthenogens like cladocera and rotifers has captivated biologists for some time. The problem actually is composed of three parts: why, when, and how much sex? Several authors have developed explanations for why sex should persist in these life cycles (e.g. Williams and Mitton, 1973; Williams, 1975; Maynard-Smith, 1978; Manning and Jenkins, 1980; Bell, 1982), with the 'balance' hypothesis receiving the most widespread support. Likewise, the timing of sexual reproduction has been examined from a variety of perspectives (e.g. Williams and Mitton, 1973; Williams, 1975; Bell, 1982). In this paper, I approach the question of how much sex? by examining both the frequency of sex and the amount of sexual reproduction occurring in each generation and investigating how they interact to deter-

mine resting egg production in rotifers.

In rotifers, the products of sexual reproduction are resting eggs (reviewed by Birky and Gilbert, 1971; Pourriot and Snell, 1983). These resting eggs have a dual function: because of their sexual origins they are the products of recombination and sources of genotypic variability (King and Snell, 1977). Secondly, they permit escape from harsh environments through dormancy. With the *B. plicatilis* life cycle as a model, and using experimentally determined life history data, I examine reproduction from the point of view of an individual female capable of producing both asexual and sexual daughters. I determine through computer simulation the percentage of sexual daughters produced by females which maximizes their resting egg production. These results are then compared to the level of sexual reproduction observed in experimental populations of *B. plicatilis* and an explanation

of their correspondence is offered. The limitations of the simulation and its extension to other rotifers is also discussed.

Life cycle

In the rotifer life cycle two types of females exist which differ in their reproductive mode (reviewed by Birky & Gilbert, 1971; Pourriot & Clement, 1981; Pourriot & Snell, 1983) Amictic females produce eggs mitotically and give birth parthenogenetically to only daughters. The eggs of mictic (sexual) females are produced meiotically and develop into males if unfertilized, or resting eggs if fertilized. A rotifer population therefore consists of separate pools of amictic females, unfertilized mictic females, fertilized mictic females, males and resting eggs (Fig. 1). Shifting from asexual reproduction to sexual reproduction diverts offspring from the amictic female pool to the other pools. The consequences of this shift are considerable for the growth dynamics of the population. Once a female

enters the mictic female pool she no longer contributes to current population growth because she either produces males, or if she is fertilized, resting eggs. Her male offspring do not feed and are short lived (reviewed by Birky & Gilbert, 1971). Unless these males manage to transmit their genes by fertilizing a female and contributing to her resting eggs, the males die without contributing to the next generation. Fertilization and resting egg production is indeed a means of avoiding this genetic dead end, but it too has its cost. Resting eggs have an innate minimum period of dormancy varying from 2 to 90 days according to species (Pourriot & Snell, 1983). As a result, females participating in resting egg production are removed from the active population and cannot contribute to population growth for the duration of the dormancy period. Sexual reproduction in rotifer populations therefore represents a compromise between present population growth and resting egg production.

While the cost of producing resting eggs is substantial both energetically (Gilbert, 1980) and in the reduction of population growth, resting eggs appear to be critical for rotifer survival from one year to the next. The temporally disjunct distributions of most rotifer populations (see King, 1980) suggest that environments at certain times are unsuitable for adult rotifer survival. Dormancy is the only bridge across these unsuitable environments to the next growth period and, in monogonont rotifers, resting eggs are the sole means of dormancy (Gilbert, 1974).

Model

In the following simulation I examine the quantitative effects of sexual reproduction on population growth using both density-independent and density-dependent population growth models. The integrated forms of the common exponential and logistic equations were used:

$$NP_t = NP_o e^{rt}$$

$$NP_t = NP_o [Ke^{rt}/K - NP_o(1 - e^{-rt})]$$

Where NP_t = number of parthenogenetic females in generation t , r = the intrinsic rate of population increase (Birch, 1948), and K = equilibrium population size. Since males do not feed, equilibrium

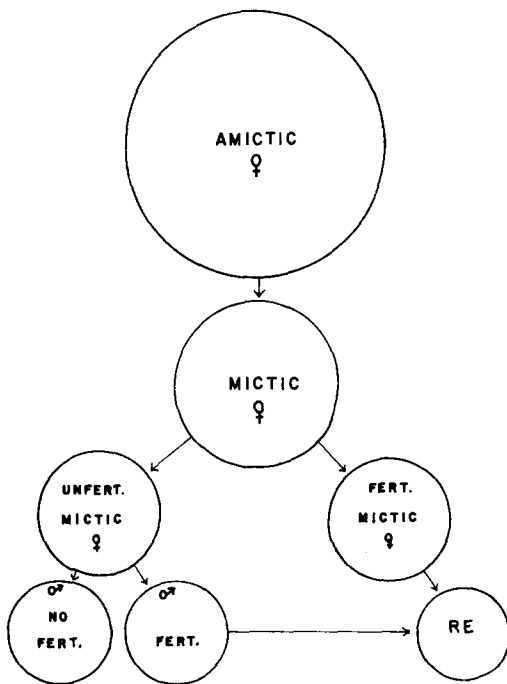


Fig. 1. Rotifer life history stages consisting of amictic female, unfertilized mictic female, fertilized mictic female, male and resting egg pools.

population size here is determined by females exclusively. The effects of mictic female production can be added to the exponential model by determining NS_t , the number of sexual females produced in generation t , where: $NS_t = M_t NP_{t-1} e^r$. M_t is the mictic rate and equals the proportion of progeny from amictic females that is sexual in generation t . NS_t is then subtracted so that $NP_t = NP_{t-1} e^r - NS_t$. In the logistic model $NP_t = NP_{t-1} [Ke^r/K - NP_{t-1}(1 - e^r)] - NS_t$.

The number of resting eggs produced by the population each generation is calculated as $RE_t = NS_t F_t Y_t$, where F_t is the percent of sexual females that are fertilized and Y_t is the number of resting eggs produced per fertilized female.

Since a rotifer female can produce some daughters that reproduce asexually and others that reproduce sexually, it is important to determine how various mixtures of asexual and sexual daughters affect population growth and the number of resting eggs produced by a female's descendants. I will first consider the consequences of the extremes of a continuum ranging from all daughters asexual to all daughters sexual. Females producing daughters that all reproduce parthenogenetically will experience rapid population growth, but will produce no resting eggs and not experience the benefits of recombination (Williams, 1975; Maynard-Smith, 1978). In contrast, females producing daughters that all reproduce sexually will experience a cessation of population growth because they either produce males, or resting eggs which become dormant. While some resting egg production is likely to occur in this case, because of the severe constraints on population growth that this level of sexuality imposes, population size will never be very large. Consequently, there will never be large numbers of females to participate in resting egg production. An obvious solution is a compromise in the level of sex, with females producing some daughters that will continue to reproduce asexually, contribute to population growth and remain available for future resting egg production. Other daughters reproduce sexually and contribute to the resting egg pool whenever adequate time, nutrition and population density is available (Gilbert, 1980; Snell, 1986).

In the following simulation I determine the optimal mix of asexual and sexual daughters that maximizes resting egg production and assume that the amount of resting egg production by a geno-

type is highly correlated with fitness. I explore these relationships using realistic values for r , M , F , and Y determined from laboratory populations of *B. plicatilis*. Estimates of r have been reported for 13 geographically isolated strains of *B. plicatilis* (Snell and Carillo, 1984). The mean for these strains was 0.87 ± 0.05 ; however, I used a somewhat more conservative value of 0.75, which was assumed to be constant. The level of sexual reproduction (M) was the independent variable and varied from 0 to 75%. The percent of sexual females that are fertilized each generation (F) was assumed to be a constant 25%. F is dependent on the probability of male-female encounter (Snell and Garman, 1986) and the probability of copulation (Snell and Hawkinson, 1983). Encounter probabilities are clearly dependent on population density, but the model does not take into account this density-dependence. The number of resting eggs produced per fertilized female (Y) is constant at 3 resting eggs, a value determined from my own laboratory observations.

Results

The effects of various levels of sexual reproduction on population growth rates can be seen in Fig. 2. In this exponential model I alternated periods of exclusively asexual reproduction with periods of mixed asexual and sexual reproduction because this seems to be the pattern typical for many rotifers (see King, 1980). It is clear that as the level of sexuality in the population rises, the rate of population growth is correspondingly diminished. At 75% mixis, population growth is so constrained that the population does not increase in number at all, but oscillates around mean of about 10 individuals. Other patterns of sexual reproduction were also examined and they support the above result of decreased population growth with increased level of sex. Including density-dependence by using the logistic model likewise yielded similar results.

The effects of various levels of sexual reproduction on resting egg production are not quite so predictable. In this simulation, females could produce from 0 to 75% sexual daughters in each generation, except the first three generations which were always exclusively asexual. The patterns of sexual reproduction ranged from continuous sexuality – 6 generations of asexual + sexual reproduction

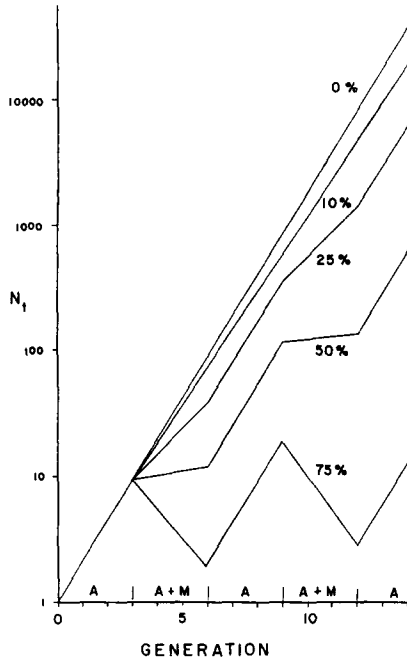


Fig. 2. The effects of different levels of sexual reproduction on density-independent population growth. The percentages represent the percent of a female's daughters that reproduce sexually. N_t is the total number of females in the population. The pattern of sexual reproduction is 3 generations of exclusively asexual reproduction (A) followed by 3 generations of asexual + sexual reproduction (A + M).

and none of the exclusively asexual reproduction (6 A + M/OA), to 1 generation asexual + sexual and 5 exclusively asexual (1 A + M/5A). Each pattern was repeated twice in every run for a total of 15 generations per run, abbreviated 3A/2(1A + M/5A). This specifies 3 generations of exclusively asexual reproduction followed by 1 generation of asexual + sexual reproduction, then 5 generations of exclusively asexual reproduction. The 1 A + M/5A pattern is then repeated to give a total of 15 generations. All simulations were begun with a single asexual female and the total number of resting eggs produced was calculated after 15 generations. Resting eggs produced were assumed to remain dormant for the duration of the simulation. This approach facilitated comparison of resting egg production in clones differing in frequency of sexual reproduction and in the percentage of sexual daughters produced in each generation.

The results of these comparisons using the exponential model of population growth are presented in Fig. 3. It is clear that for all patterns of sexual reproduction, resting egg production is maximized by producing intermediate percentages of sexual daughters. For example, when sexuality is continuous (6 A + M/O A), a female maximizes her resting egg production if, on average, 10% of her daughters reproduce sexually. More or less sexual reproduction than this will diminish the female's resting egg output. For other reproductive patterns, the levels of sexuality for maximum resting egg production are: 5/1, 11%; 4/2, 14%; 3/3, 19%; 2/4, 28% and 1/5, 50%.

It is important to note that all curves except the 1/5 pattern are strongly skewed left. This means that lower levels of sexuality will actually yield greater numbers of resting eggs. When sex occurs in less than about 20% of the generations, the curves approach a more normal distribution. Moreover, it is clear that the highest levels of resting egg production occur when sex is frequent (5/1, 83% of generations) and only a low percentage of a female's daughters reproduce sexually (11%).

When density-dependence is added to the model in the form of the logistic population growth equa-

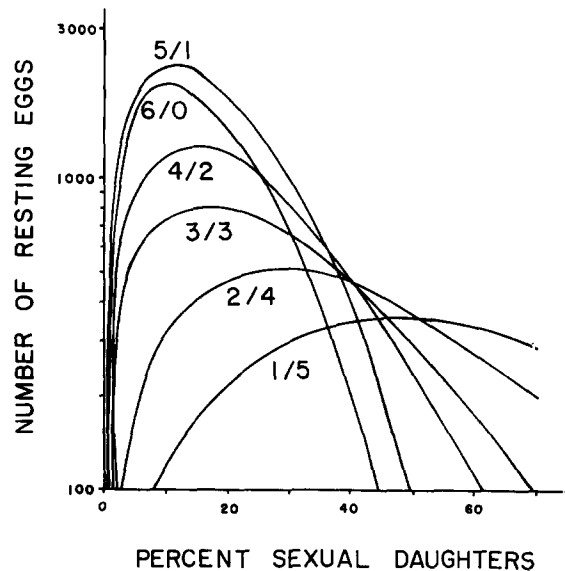


Fig. 3. Density-independent population growth and the effect of different patterns and levels of sexual reproduction on resting egg production. The ordinate is the number of resting eggs produced after 15 generations; the abscissa is the percent of a female's daughters that reproduce sexually.

tion, the results are only slightly modified (Fig. 4). Increasing density-dependence tends to shift the curves toward a more normal distribution and reduces resting egg production. The percentage of sexual daughters for maximal resting egg production are presented in Table 1 and ranges from 10 to 64% for all the mictic patterns investigated and five levels of density-dependence. These results clearly indicate that as sex becomes more frequent and population growth becomes less constrained by

density, females with between 10–30% of their daughters reproducing sexually will experience greater resting egg production.

The effect of r , the intrinsic rate of population increase, on the level of sexuality necessary for maximal resting egg production was also investigated. The relationship between r and the percent sexual daughters is non-linear with positive slope (Fig. 5). The three patterns plotted are for density-dependent growth when $K = 6000$. While the effect

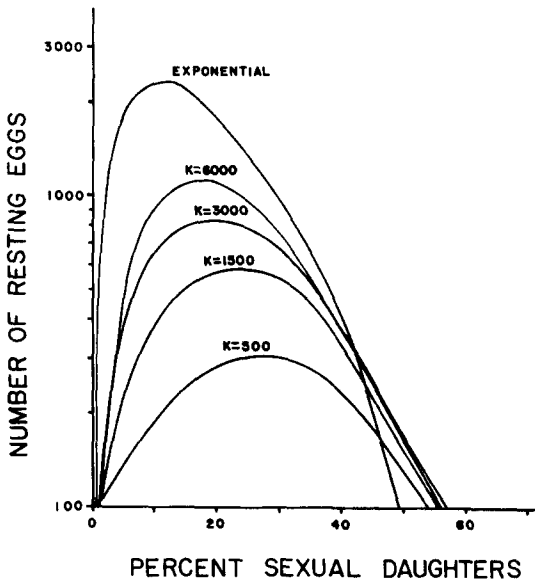


Fig. 4. Density-dependent growth and its effects on resting egg production. The ordinate is the number of resting eggs produced after 15 generations; the abscissa is the percent of a female's daughters reproducing sexually. The 5A + M/1A pattern of sexual reproduction is utilized.

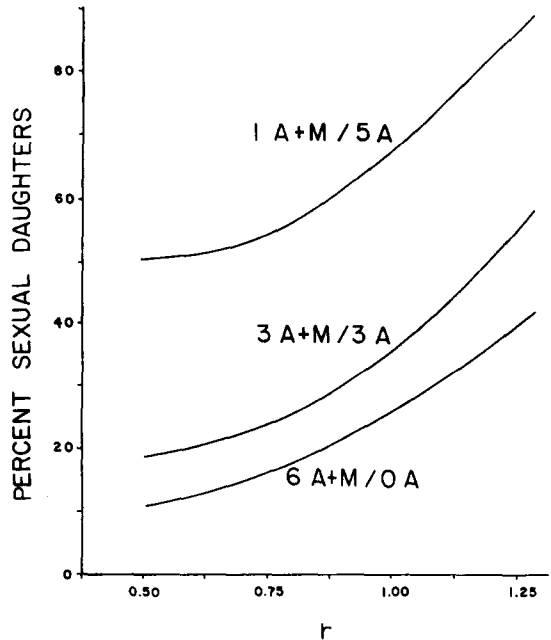


Fig. 5. The effects of the intrinsic rate of population increase (r) on the percent sexual daughters that yield maximal resting egg production.

Table 1. The effect of density-dependent population growth on the percent sexual daughters that maximize resting egg production. EXP is exponential population growth and K refers to 4 different equilibrium population sizes. Mictic pattern is number of asexual and sexual generations/number of exclusively asexual generations. % generations is the percent of generations where sexual reproduction occurs.

mictic pattern	% sexual generations	EXP	K			
			6000	3000	1500	500
6/0	100	10%	16%	18%	20%	25%
5/1	83	11	17	20	22	27
4/2	67	14	19	22	24	29
3/3	50	19	23	26	28	33
2/4	33	28	32	35	37	42
1/5	20	50	54	57	59	64

of r is clear, it does not appear excessively large over the range of r values reported for most rotifers (Allan, 1976).

Discussion

This simulation is limited by the simplifying assumptions of the population growth models. For example, generations in real rotifer populations are overlapping rather than discrete and rotifer populations have age structure. The assumption that the proportion of mictic daughters (M) is constant over a female's lifespan is true for *B. plicatilis*, but age-dependent changes in the mictic rate have been observed in *B. rubens* and *B. calyciflorus* (Pourriot and Rougier, 1976, 1977; Rougier and Pourriot, 1977) and in *Notommata copeus* (Pourriot and Clement, 1977). The percent sexual females fertilized (F) is likewise not constant, but varies with environmental conditions (Snell and Hoff, in press). Because of these differences between biological reality and the simulation, it is important to compare simulation results with experimental data.

I have compiled some data published by others and added some of my own in an attempt to determine the actual level of sexuality that occurs in laboratory populations of one of the most thoroughly investigated rotifer species, *B. plicatilis*. It should also be noted that not all environments permit the development of sexual reproduction. I have included in my analysis only those environments where sexuality was observed to occur and was not inhibited by inadequate nutrition or temperature or salinity stress. In other words, I am interested in the level of sexuality that occurs when environmental limitations are removed.

As seen in Table 2, the percentage of a female's

daughters that reproduce sexually ranges from 0 to 50%. If we examine the means of the four strains, however, we find that they range from 12.6 to 32.8% with relatively small standard errors. The grand mean for all strains is $21.2\% \pm 3.84$. This pattern of sexual reproduction suggests that, at least in *B. plicatilis*, females are striking a compromise between population growth and resting egg production. This trade-off is accomplished by producing a low percentage of sexual daughters so that population growth is not greatly reduced, but enough sexual daughters so that substantial resting egg production can occur.

The effects of sexual reproduction on population growth in rotifers have not been widely explored, but Gibert (1983) has made some preliminary inquiries. He was interested in the observation that females hatching from resting eggs appear to be less responsive to mictic-inducing conditions than females hatching from amictic eggs. Gilbert argued that the adaptive significance of this endogenous block to sexual reproduction is that it would promote more rapid initial population growth. Blocking of sexual reproduction in the early stages of population growth therefore allows the growth advantages of parthenogenesis to be more fully realized. Comparing growth rates of populations in which there is no blocking to those where blocking exists for one or two generations, Gilbert showed that during exponential population growth the increased growth rates due to blocking can be substantial.

One feature of sexuality in rotifer populations is that it occurs simultaneously with parthenogenetic reproduction (see King, 1980). In *B. plicatilis* the percentage of daughters reproducing sexually is usually substantially lower than those reproducing parthenogenetically. The results of the simulation

Table 2. Comparison of the percent sexual daughters in laboratory populations of *B. plicatilis*. The Japanese data are for 25 different clones tested in a common environment, the French are for the same strain tested in two different environments, the Israel data are for two replicate experiments and Tampa Bay is a single strain in one environment.

Strain	N	% sexual daughters	range	reference
Japanese	25	12.6 ± 1.66	0–29%	Hino & Hirano (1977)
French	19	12.6 ± 0.10	0–44%	Pourriot & Rougier (1979)
French	17	32.8 ± 0.03	7–50%	Pourriot & Rougier (1979)
Israel-Dor	85	22.1 ± 2.17	–	Lubzens, personal communication
Israel-Dor	29	23.6 ± 9.36	–	Lubzens, personal communication
Tampa Bay – MCK8	7	14.0 ± 3.49	6–31%	Snell, personal observations

provide a rationale for why the percentage of sexual daughters is lower. Sexuality diminishes population growth making the level of sexuality for maximal resting egg production a trade-off. Stabilizing selection determines the optimal level of sex in this compromise so that resting egg production is maximized. In *B. plicatilis*, this level appears to be when the proportion of a female's daughters that reproduce sexually is between 10–30%.

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