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Notes and Comments

Sex Allocation in Haplodiploid Cyclical Parthenogens with Density-Dependent Proportion of Males

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The allocation of resources to male and female progeny is a major component of the reproductive strategies of all sexual plants and animals (Godfray and Werren 1996). The evolutionary theory of sex ratio developed by Fisher ([1930] 1958) predicts equal parental allocation to the two sexes. It has been shown that the principles underlying this prediction may be generalized to any situation in which organisms invest in male and female function—what Charnov (1982) called "sex allocation." An important part of the theoretical work on sex allocation evolution has focused on developing and applying models for organisms with reproductive features other than those of the model dioecious organism—that is, bisexual diploid organisms with a sex-independent parental investment per descendant (e.g., Trivers and Wilard 1973; Charnov 1982; Frank 1990; Bulmer 1994).

This note addresses theoretically the optimal sex allocation in monogonont rotifers, which are common planktonic invertebrates. They frequently inhabit temporal, or ephemeral, aquatic habitats that become unsuitable for more or less predictable periods. Diapause has evolved as the means by which populations survive harsh environmental periods (Gilbert 1974). Monogonont rotifers have a cyclical parthenogenetic life cycle (see, e.g., Birky and Gilbert 1971; Wallace and Snell 1991), which includes an asexual (amictic) and a sexual (mictic) phase, the diapausing form being the sexually produced resting egg. Habitat colonization begins when the resting eggs hatch and emerge from the sediments. With these hatchlings, the amictic phase starts, which is a repeated sequence of amictic females parthenogenetically producing amictic daughters. Once the growing season has started, the contribution of resting egg hatching to the current population is presumed to be negligible. The mictic phase starts with the production of both amictic and mictic daughters by amictic mothers in response to inducing factors such as population density (King and Snell 1980; Carmona et al. 1993). Thus, mictic female production may be sustained for some time since amictic female production does not necessarily stop after mictic phase initiation. Mictic females produce haploid eggs that develop into either haploid males or, if fertilized, resting eggs. A single copulation provides enough sperm to fertilize all the eggs of a mictic female (Snell and Childress 1987). Resting eggs are diploid, sexually produced eggs that typically have a diapause period before they hatch into a new generation of amictic females in the following growing season. Hence, the only individuals involved in zygote formation are fertilized mictic females and males.

Sex determination in monogononts differs from other haplodiploids as the proportion of fertilized eggs in rotifers may not be entirely under female control since, in at least some genera, it is controlled by male density. In the genus *Brachionus,* mictic females may only be fertilized within a few hours of birth (Snell and Childress 1987); if the female is not fertilized during the earlier hours of her life, she will produce only males. Given that the fertilization is dependent on random encounters between males and females (Snell and Garman 1986), the abundance of males is self-regulated to some extent since, if males are rare, fertilization will also be rare and male-producing mictic females will become more frequent. Thus, a built-in negative feedback system exists that affects the sex-ratio adjustment.

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Along with this density effect on sex-ratio, the age at which a mictic female loses her fertilization susceptibility (briefly, threshold age of fertilization) also affects sex ratio. This trait controls the reproductive fate of a mictic female in two ways: directly, since a shorter period of fertilization susceptibility involves a higher probability of becoming a male-producing female, and, indirectly, through the effect of this fate on male density and, so, on the rate of fertilization. Hence, the sex allocation problem in monogonont rotifers is related to the timing of reproductive receptivity. In this note, we focus on the evolution of threshold age of fertilization since it is an intrinsic trait affecting sex allocation that can undergo selection.

The Model, Analysis, and Simulations

We assume a continuous version of the model depicted in figure 1. Initially, we examine a steady-state model and later introduce temporal variability into the model. Mictic females are produced by amictic mothers at a constant rate B (number of mictic females born per unit of time). The set of conditions resulting in constant recruitment rate of mictic females, B, is constant amictic female density, constant amictic female fecundity, and constant ratio between mictic and amictic daughters. The mictic females change their status at two ages, the threshold age of fertilization, T, and the age at maturity, M (T is assumed equal or lower than M). They may also change their status if fertilized. The expected number of males encountered per female in dt resulting in fertilization is $eH\mathrm{d}t$ (H, number of males; e, male-female encounter rate; see also fig. 1). The per capita death rate in dt is $\mu\mathrm{d}t$ for females, assumed to be age and stage independent, and $\mu_\mathrm{h}\mathrm{d}t$ for males. From our assumptions, it follows that the proportion of mictic females, either virgin or mated, that survive from birth to the age at maturity is $\exp(-\mu M)$. If we assume that a demographic equilibrium is achieved, then at that equilibrium H will be constant (i.e., H^*), and, assuming a Poisson process, $\exp(-eTH^*)$ will be the probability that a mictic female at age T or older has not been fertilized. At demographic equilibrium, recruitment of mature virgin females ($B\exp(-eTH^*)\exp(-\mu M)$) equals deaths ($\mu F_\mathrm{h}^*$, where F_h^* is the number of mature unfertilized mictic females at equilibrium), which gives

$$F_\mathrm{h}^* = \frac{B}{\mu}\exp(-eTH^*)\exp(-\mu M). \qquad (1)$$

Consequently, for resting egg–producing mictic females (i.e., fertilized, mature females) at equilibrium (F_r^*), we obtain

$$F_\mathrm{r}^* = \frac{B}{\mu}[1-\exp(-eTH^*)]\exp(-\mu M). \qquad (2)$$

Given that the number of males (H) is constant at equilibrium, the rate of male deaths, $\mu_\mathrm{h}H^*$, equals the rate of male births, mF_h^* (m: per capita fecundity rate of male-producing mictic females assumed to be constant), $\mu_\mathrm{h}H^* = mF_\mathrm{h}^*$.

Combining with equation (1), we get

$$H^* = \frac{mB}{\mu_\mathrm{h}\mu}\exp(-eTH^*)\exp(-\mu M). \qquad (3)$$

By combining equation (2) and equation (3), we obtain

$$F_\mathrm{r}^* = \frac{B}{\mu}\exp(-\mu M) - \frac{\mu_\mathrm{h}}{m}H^*. \qquad (4)$$

From equation (4), the number of resting eggs produced would be maximized when the number of males (H^*) is minimized. To find the value of T that minimizes the number of males, note that equation (3) yields

$$T = \frac{K-\ln(H^*)}{eH^*}, \qquad (5)$$

where $K = \ln(mB/\mu_\mathrm{h}\mu) - \mu M$ is constant. On the other hand, since $T > 0$, we have $H^* < \exp(K)$. Hence, since the function $\mathrm{f}(x) = [K-\ln(x)]/ex$ is decreasing if $x \le \exp(K+1)$, the production of males is minimized when T takes on its maximum possible value, that is, M, the age at maturity. When $T = M$, the production of resting eggs is maximized.

It is well known, however, that the evolution of sex allocation does not necessarily maximize reproductive output at the population level (Zhang and Wang 1994), and, in our case, may not maximize the resting egg production. The evolution of sex allocation in monogonont rotifers was analyzed by simulating the change in frequency of a rare, nonrecessive allele that changes the threshold age of fertilization of mictic females. No other difference between the rare and the common allele was assumed. While the initial frequency of the rare allele is low, the dynamics of the corresponding homozygote was not considered. Two alleles—the rare one, A, and the common one, a—were assumed to be present such that $Aa:aa = 1:100$ in the population of resting eggs (zygotes) before the hatchlings started to colonize the habitat. This proportion was assumed to be unchanged during the parthenogenetic phase, and so it gives the genotype frequency of the mictic females eventually produced in the population. Hence, the mictic female recruitment rate from amictic females, B, is $B_{Aa} + B_{aa}$, the summation of the recruitment rates for the mictic females with different genotypes. Consequently, in our simulations, which dealt

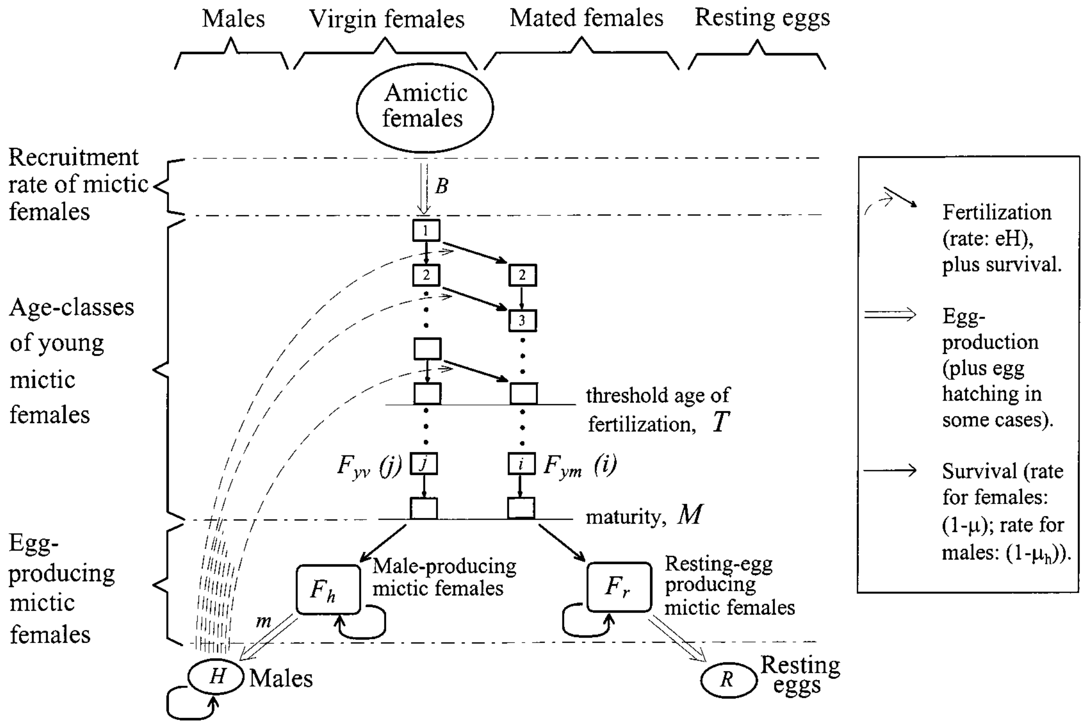

Figure 1: Sexual (mictic) phase of the reproductive cycle of monogonont rotifers as assumed in our model. Variables: young virgin mictic females, j aged $[F_{\mathrm{yv}}(j)]$; young mated mictic females, i aged $[F_{\mathrm{ym}}(i)]$; males (H, for haploids); male-producing mictic females (F_{h}); resting egg–producing mictic females (F_{r}); resting eggs (R). Parameters (assumed to be age and time independent): recruitment rate of mictic females from amictic females (B); per capita female mortality rate (μ); per capita male mortality rate (μ_{h}); per capita fecundity rate of male-producing mictic females (m); male-female encounter rate (e); threshold age of fertilization (T); the age at maturity (M, $T \leq M$).

only with the mictic phase (fig. 1), we assumed that B_{Aa}: $B_{aa} = 1{:}100$. The variation through time in the numbers of fertilized and unfertilized young mictic females at each age, the numbers of fertilized and unfertilized mature mictic females, and the numbers of males were computed using the model described above (see fig. 1), with all these numbers initially set at 0 (i.e., mixis initiation). The simulations were run until demographic equilibrium was achieved (i.e., when there was no change in the number of individuals in each class) and, then, allele frequencies in the resting eggs produced were computed. These frequencies are considered representative of the sum total of resting egg production because the prevalence of the demographic equilibrium during the mictic phase was assumed. By comparing these frequencies to those before mixis, we found which allele can invade but cannot be invaded, so defining an evolutionarily stable strategy (ESS).

Following this procedure, we found the evolutionarily stable threshold age of fertilization by testing several, realistic arrays of values for the parameters in the model. In all the cases analyzed, an ESS for T (T_{opt}) was found, which was strictly lower than M and dependent on the values assigned to the parameters. An example of our results is shown in figure 2. An allele determining the threshold age of fertilization (T) of about 40% the age at maturity can invade a population that includes any resident allele, but such an allele cannot be invaded when resident.

Looking for a regularity in our simulation results, we explored the relationships between the classes of individuals considered in our model. We found that a condition for the ESS was that the frequency of male-producing females equals the frequency of resting egg–producing females at the equilibrium ($F^{*}_{\mathrm{h}} = F^{*}_{\mathrm{r}}$), a result analogous to the even allocation to male and female function predicted by the sex allocation theory.

From the assumption of a stage-independent mortality rate for the females, it follows that the proportion F^{*}_{h}: F^{*}_{r} is determined at T since fertilization is not possible afterward (fig. 1). Hence, our finding of $F^{*}_{\mathrm{h}} = F^{*}_{\mathrm{r}}$ at the evolutionary equilibrium might be a by-product of selection of an equal number of x-aged fertilized and unfertilized mictic females for a given $x \geq T$. In order to explore this possibility, we modified our model, relaxing our assumption of a stage-independent mortality rate. We performed a set of simulations assuming that μ changes for the mated mictic females at one of three different critical

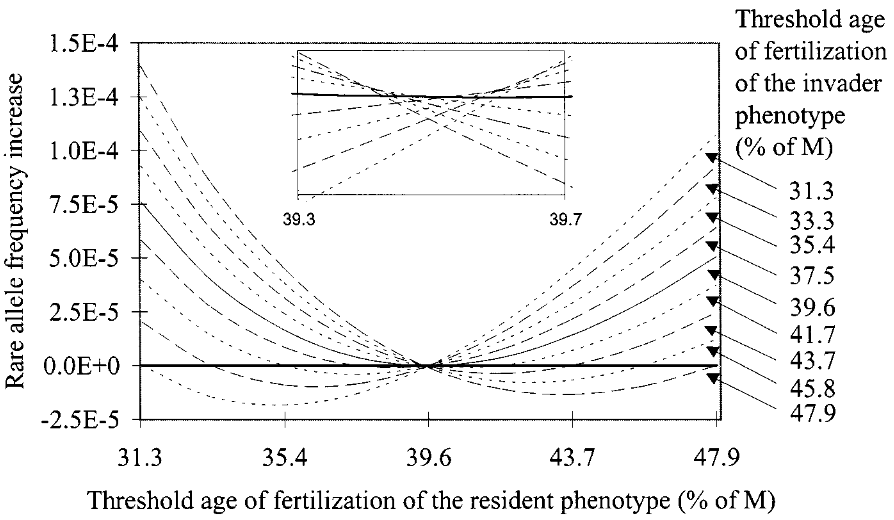

Figure 2: Selection for rare alleles (invaders) affecting the threshold age of fertilization (T) as evaluated by computer simulation. Each curve indicates the increase of the frequency of a rare allele in relation to the phenotype determined by the common (resident) allele in homozygotes (abscises). The phenotypes of the heterozygotes bearing the rare alleles are shown on the right side (M, age at maturity). The increase of the frequency of the rare allele was computed by comparing frequencies before and after mixis. If the curve is above 0, the rare allele is therefore positively selected. The inset shows a detail of selection when the resident allele determines T values close to 39.6% of age at maturity. Assumed values for parameters were: $B = 24$ and 0.24 females M^{-1} for *aa* and *Aa* genotypes, respectively (*a*, common allele; *A*, rare allele), $\mu = 0.4\ M^{-1}$, $e = 0.04$ male^{-1} M^{-1}, $\mu_h = 0.7\ M^{-1}$, $m = 1.5$ male female^{-1} M^{-1} (M is the unit of time). These values are consistent with observations if the number of individuals is per liter and M (the age at maturity) is about one day.

steps (at the moment in which female becomes fertilized, at T, and at M). We found that the ESS satisfied

$$F^{*}_{yv}(T) = F^{*}_{ym}(T), \tag{6}$$

where $F_{yv}(T)$ and $F_{ym}(T)$ are respectively the numbers of virgin and mated young mictic females T aged. It follows from this result and equations (1) and (2) that $\exp(-eH^{*}T_{opt}) = 1/2$.

Combining with equation (3), it follows that

$$T_{opt} = \frac{\mu_h \mu \ln 4}{emB \exp(-\mu M)}. \tag{7}$$

Putting it into words, the evolutionarily stable value of T is that which equalizes the number of the two mictic female types—virgin mictic females and mated mictic females—at the moment at which young mictic females lose their fertilization susceptibility. This value of T is dependent on the other demographic parameters and will be lower in better conditions (i.e., higher recruitment, encounter rate, and fecundity, lower mortality, and earlier maturity).

The above conclusion is critically dependent upon the assumption that the demographic equilibrium was prevalent in the mictic phase, requiring constant B and a relatively long mixis period. These conditions may be expected in the "spanned mictic pattern" (Carmona et al. 1995) where mixis—initiated early at relatively low population density—spans most of the rotifer growth season, but these conditions are unlikely if the mixis pattern is "punctuated," with mixis starting at high population density at the end of the growth season (Carmona et al. 1995).

We addressed the effects of relaxing our assumption that B is constant, following a simulation procedure similar to that used above. Several linearly increasing and decreasing functions were used for B variation or it was allowed to switch from a given constant value to a markedly different one. In order to limit exploration time, B was assumed to become 0 after a given time, and dynamics were simulated until extinction of mictic females and males. With these conditions, a demographic equilibrium does not exist until population extinction. We found (table 1) that the ESS of T in most cases was the one satisfying approximately the equation $\int F_{yv}(T, t)dt = \int F_{ym}(T, t)dt$, which is a straightforward extension of equation (6) when the abundance of classes of individuals varied. This result indicates that an even total allocation in male and resting egg–producing mictic females should evolve. The exception found, when B decreased sharply (fourth row in table 1), seems to be related to the fact that, unlike the other cases, the numbers of each type of mictic female both waved during most of the dynamics and showed a short period of monotonous, quasi-linear variation—correlated to B changes. How this fea-

Table 1: Optimal (evolutionarily stable) threshold age for fertilization (T_{opt}) with time-dependent recruitment rate and corresponding total numbers of unfertilized and fertilized mictic females at T_{opt}

Time-dependent recruitment rate, B(t) (*females per unit of time*)	T*opt* (*% age at maturity*)	*Mictic females*	
		*Unfertilized**	*Fertilized†*
$B(t) = 24 + 1.70\ t$	14.2	1,586	1,578
$B(t) = 24 + 0.48\ t$	28.8	802	806
$B(t) = 96 - 1.92\ t$	18.3	1,109	1,096
$B(t) = 96 - 4.80\ t$, if $t \leq 20$; $B(t) = 0$, if $t > 20$	29.2	372	464
$B(t) = 24$, if $t \leq 25$; $B(t) = 72$, if $t > 25$	17.5	666	676

Note: Results from simulations were obtained assuming the conditions reported in the legend of figure 2, except that B was time dependent, and the integration over time of the resting egg production was used to determine the selection of rare alleles. $B(t) = 0$ for $t > 50$.

* Total number of unfertilized mictic females is $\int F_{yv}(T_{opt}, t)dt$.

† Total number of fertilized mictic females is $\int F_{ym}(T_{opt}, t)dt$.

ture causes the uneven optimal sex allocation remains, however, unclear and deserves further analysis.

Discussion

Our simulations predict that the threshold age of fertilization should evolve to values determining a probability of fertilization equal to 0.5, which is an ESS. This implies that male-producing mictic females would tend to balance out resting egg–producing mictic females and that the evolutionarily stable threshold age of fertilization does not necessarily correspond with the threshold age that maximizes resting egg production (i.e., the age at maturity). In fact, using parameter values consistent with observations, our model predicts that the evolutionarily stable threshold age of fertilization is much earlier than the age at maturity. This prediction is consistent with empirical data in rotifers since fertilization only takes place in very young, immature mictic females (Buchner et al. 1967; Pilarska 1972; Snell and Childress 1987; Hagiwara et al. 1988). Thus, optimization of sex allocation may prevent maximization of population growth rate, a result similar to that of Zhang and Wang (1994).

Only the study by King and Snell (1980) provides empirical data on the numbers of male-producing mictic females and resting egg-producing mictic females in natural populations of rotifers. *Asplanchna girodi* populations were monitored in 1977 during two sexual reproduction periods (April and May). Population growth conditions were better in April, as pointed out by the much higher population densities. We computed integrated numbers over time of both types of mictic females from their data. The sex allocation ratio (estimated as the proportion of male-producing mictic females to the total number of mictic females) was 0.4 in April and 0.6 in May. These values were close to 0.5, the expected one, although statistical significance cannot be tested, as absolute frequencies were not reported. Moreover, deviations may be expected if T is a phenotypically fixed trait. Optimal T over long periods would be suboptimal in better than average conditions (see eq. [7], e.g., for a high recruitment), causing a deficit of male-producing females. Conversely, an excess of male-producing females is expected in the worse conditions. These expectations are qualitatively consistent with the deficit at high population density and the excess at low population density of male-producing females observed in the *Asplanchna* populations monitored by King and Snell (1980). Nevertheless, given the scarce empirical evidence available, further experimental studies providing more direct evidence are required.

The prediction that evolution favors equal frequencies of male-producing mictic females and resting egg–producing mictic females can be interpreted as a particular application of the sex allocation theory (Fisher [1930] 1958; Charnov 1982, 1993). Hartl and Brown (1970; see also Bulmer 1994) showed that frequency-dependent selection acting on the sex ratio in the diploid situation also holds for bisexual haplodiploids, predicting an even allocation to male and female function. Our results show that an even sex allocation is also expected in haplodiploid cyclical parthenogens, despite two important complications of their life cycle: the negative feedback (density dependence) that affects sex-ratio adjustment mechanistically and the fact that the sexual organisms—males and fertilized mictic females—constitute distinct generations. Despite these complexities, the Fisherian argument holds. When an amictic female (stem mother) parthenogenetically produces mictic daughters, some of these will in turn produce parthenogenetic males of their own, whereas others will become fertilized and produce recombinant resting eggs. Sex allocation symmetry (Charnov 1993) would be achieved by investing half the resources available for reproduction into male offspring and half into fertilized mictic female offspring. Since males are not directly produced by the stem mother and provided that both types of mictic daughters have equal cost for the mother, this means that half her mictic daughters should be male-producing mictic females and the other half should be resting egg–producing mictic females. The reproductive fate of mictic daughters becomes fixed at the end of the fertilization susceptibility period (T), and thus the prediction of an even sex allocation would yield equal frequencies of both types of mictic females at time T, which is precisely the result found in our simulations. Hence, in monogonont rotifers the Fisherian prediction of an even number of males and females takes the form of an even number of male-producing mictic females (accounting indirectly for male allocation) and resting egg–producing mictic females (accounting by themselves for female allocation) at the end of the period of reproductive receptivity.

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