

## 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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