Evidence for an even sex allocation in haplodiploid cyclical parthenogens

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Abstract

Recent theoretical work has shown that haplodiploid cyclical parthenogens, such as rotifers, are expected to have an equal frequency of male-producing and resting-egg producing females during their sexual phase. We tested this prediction by following sexual reproduction dynamics in two laboratory populations and one field population of the rotifer *Brachionus plicatilis* through two growing seasons. We recorded population density, proportion of sexual females, and sex allocation (the proportion of male-producing sexual females as a fraction of total sexual females). We found this sex allocation ratio to vary from 0.3 to 1.0 in single sampling events. However, when we computed sex allocation by using the integrated densities of both male-producing sexual females and resting-egg producing sexual females over time, the two laboratory populations and one of the two field growing seasons showed sex allocation ratios that did not significantly differ from the expected value of 0.5.

Introduction

Since Fisher (1930/1958) first discussed the effect of sex ratio on parental fitness, a number of extensions of the basic theory have been made by altering several of its implicit assumptions (MacArthur, 1965; Hamilton, 1967; Trivers & Willard, 1973; Trivers & Hare, 1976; Charnov & Bull, 1977; Charnov, 1982, 1993; Werren, 1987; Werren *et al*., 1988; Wrensch & Ebbert, 1993). Theoretical work on sex-ratio evolution has focused on providing a formal population genetics derivation of the theory (e.g. Bodmer & Edwards, 1960; Eshel & Feldman, 1982; Karlin & Lessard, 1986) and on developing the theory for organisms with particular reproductive features (e.g. Trivers & Willard, 1973; Charnov, 1982; Frank, 1990; Bulmer, 1994). In this context, the cyclically parthenogenetic life cycle provides a valuable model for the study of the evolution of sex allocation (Barker & Hebert, 1986). Sexual haplodiploids have been used in a number of sex allocation theory tests (Charnov, 1982), and much of the empirical work on sex ratios (e.g. Hamilton, 1972; Trivers & Hare, 1976; Charnov, 1978; Oster & Wilson, 1978; Boomsma & Grafen, 1991) concerns sexually reproducing haplodiploid organisms, because they can easily adjust their sex ratio (Bulmer, 1994; Varndell & Godfray, 1996). Until recently (Aparici *et al*., 1998), sex allocation theory has not been applied to cyclically parthenogenetic haplodiploids (i.e. to monogonont rotifers, a group common in the zooplankton; see, e.g. Birky & Gilbert, 1971; Wallace & Snell, 1991). This was perhaps because of their complicated life cycle: the occurrence of asexual females, density dependence of male production, and the fact that sexual individuals (males and resting-egg producing sexual females) constitute distinct generations.

In the rotifer life cycle (Fig. 1), ameiotic parthenogenesis in the absence of males producing clonal females is mixed with occasional bouts of male production and sexual recombination producing resting eggs. In addition

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