Evidence for an even sex allocation in haplodiploid cyclical parthenogens

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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; 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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