SEX ALLOCATION STRATEGIES OF PSEUDO-ARRHENOTOKOUS PHYTOSEIID MITES

by

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SUMMARY

In arrhenotokous arthropods males arise from unfertilized eggs. Hence, by controlling the fertilization process mothers can adjust the sex ratio in their offspring. In pseudo-arrhenotokous phytoseiid mites, however, males are haploid, but arise from fertilized eggs. The haploid state is achieved through elimination of the paternal chromosome set during embryonic development. It is shown in this paper that phytoseiid females can control the sex ratio in their offspring and that this control seems as flexible as in arrhenotokous arthropods. As predicted by current evolutionary theory of sex allocation, sex ratios approached half males, half females under random mating, whereas a female bias was observed under sub-mating.

The importance of these results for understanding the adaptive significance of pseudo-arrhenotoky are discussed. It is suggested that arrhenotoky is selected for when there is a substantial risk to the females of remaining unmated. When this risk of becoming a wall flower is low, pseudo-arrhenotoky may evolve because it retains the possibility to reinsert lost genetic information in the maternally derived chromosome by using the paternal chromosome as a template for DNA-repair. The retention of the diploid state in males during embryonic development may thus have certain advantages. It is argued that pseudo-arrhenotoky may be an adaptive genetic system under certain conditions and not an instable system that readily reverts to diploidy or evolves towards arrhenotoky or thelytoky.

INTRODUCTION

In an outstanding book on the evolution of sex determining mechanisms Bull (1983) devoted several chapters to the selective advantages of producing uniparental males. Despite many variations among uniparental male systems each shares the property that males are effectively haploid and transmit the maternal genome only. Such systems include arrhenotoky where males arise from unfertilized eggs, and pseudo-arrhenotoky where males arise from fertilized eggs but become haploids after inactivation (heterochromatization) and/or elimination of the paternal chromosome set. Exactly when the loss of...

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the paternal chromosomes occurs, depends on the organism under study. In some scale insects somatic tissues retain the paternal chromosome in an active state whereas it is eliminated in the germ line just before or during spermatogenesis. In phytoseid mites chromosome loss or inactivation occurs early in embryogenesis but not until after some mitotic divisions have taken place (Nelson-Rees et al., 1980). As far as we know now, pseudo-arrhenotoky is a relatively rare phenomenon when compared to arrhenotoky. However it has evolved independently at least three times in the arthropods and because it is much less easy to detect than arrhenotoky and because it has not been investigated systematically, it might be much more widespread than currently thought.

According to Bull (1979, 1983) the selective advantage for the evolution of male haploidy stems from a two-fold representation of maternal genes in gametes of haploid sons in comparison to diploid sons of biparental origin. The probability of gene identity-by-descent between grandmother and grandchild through uniparental sons is therefore double the probability through biparental sons. This two-fold advantage of producing uniparental sons may overcome the potential lower fitness of these sons and may therefore be the key to our understanding of the advantage of male haploidy. As noted by Bull (1979, 1983) the two-fold advantage provides a selective basis not only for male haploidy but also for the evolution of any genetic system in which the genes of one parent are excluded from gametes in the offspring of one sex. Bull (1979, 1983) therefore considered four different systems with two sexes in which offspring of one sex transmit only the genome inherited from one parent. His preliminary conclusion was that systems with males transmitting only the maternal genome are more stable compared to the other three systems which have lack of recombination (and may thus go extinct), and/or which are more likely to revert to diploidy or to evolve towards thelytoky. Bull (1979) also provided an argument why pseudo-arrhenotoky may be more rare than arrhenotoky. Because uniparental males increase the transmission of maternal genes at the expense of the would-be-father, there is selection in the most extreme form of genes that when transmitted through sperm avoid this elimination. Under arrhenotoky sperm do not enter the eggs destined to become males; hence, there is no opportunity for paternal gene expression in sons. However, under pseudo-arrhenotoky sperm penetrates all eggs and any paternal mutant that avoids loss once in the egg of a son is favoured. Thus, there is this extra factor that may render pseudo-arrhenotoky somewhat more susceptible than arrhenotoky to revert to diploidy. This argument may hold especially soon after the origin of pseudo-