SEX-RATIO IN AUTOPARASITIC HYMENOPTERA

Sex-ratio theory predicts that ability to control the sex of offspring will often be advantageous. Genetic, physiological, and temporal constraints may make the evolution of very fine control unattainable in many species, but in at least one hymenopteran family, the Aphelinidae, control of offspring sex is highly evolved. The consequent relevance of this group to sex-ratio theory was early appreciated by Haskins (1951) who, in discussing the aphelinid *Coccophagus scutellaris,* pointed out that "the calculation of the optimum sex ratio would present a nice problem in biological statistics" (p. 67). The sex-ratio model we present here is based on the reproductive pattern of *Coccophagus scutellaris.* We hope it will stimulate more detailed study of this phenomenon.

The key to offspring sex control in this species is its haplodiploidy (unfertilized [haploid] eggs develop into males and fertilized [diploid] eggs develop into females). In some haplodiploid species a certain coarse control of offspring sex-ratio is obtained from the timing of mating: Eggs laid before mating are haploid, after mating are diploid. *Coccophagus scutellaris* employs a more advanced mechanism, involving control of the spermathecal gland, which secretes sperm-activating fluids, and discharge of sperm through the sperm duct, enabling determination of the sex of each offspring egg (Flanders 1967). In *Coccophagus scutellaris*, the female develops as a primary endoparasite of the scale insect *Coccus hesperidum* while the male develops as a secondary endoparasite of first and second larval instars of its own species. A haploid egg aberrantly laid in the body of the scale insect fails to develop. The extensive probing of the body of the host during oviposition has been detailed by Jarraya (1975), and whether a haploid or diploid egg is laid depends on whether a larva is located or not. In addition females have been observed to parasitize their own (female) offspring (Flanders 1969).

Our model is based on the observations that a female can determine the sex of each offspring, that there is some probability that a female may parasitize her own (female) larvae, and that laying a haploid egg successfully is more difficult than laying a diploid egg. This difficulty may stem from the rarity of previously parasitized hosts or the difficulty in locating the female larva in such a host. Assume that a female lays a total of N eggs, a proportion r of which are male, and that the costs (in time and energy) of laying male and female eggs are c_1 and c_2, respectively. The ovipositing behavior suggests that $c_1 > c_2$. Let p_2 be the probability that a female egg develops to the larval stage at which point it is vulnerable to parasitism by a male egg, p_1 the probability that a male egg develops and hence kills the larva it parasitizes, and q the probability that a female, when laying a male egg, parasitizes one of her own larvae.

Fisher (1930) produced the first reasonable argument that, at equilibrium, the sex-ratio should be such that total investment in male and female offspring is the same. This principle provides a simple derivation of the equilibrium sex-ratio for our model. Investment in male offspring is of two kinds: direct investment in laying male eggs (at c_1 units per egg) and indirect investment in supplying some

daughter larvae to host sons (at c_2/p_2 units per larva supplied). Since each male egg has the probability p_1 of developing, the total male investment is

$$rNc_1 + \frac{qp_1rNc_2}{p_2}. \tag{1}$$

Since the total energy invested is $rNc_1 + (1 - r)Nc_2$, the female investment is

$$(1 - r)Nc_2 - \frac{qp_1rNc_2}{p_2}. \tag{2}$$

Equating (1) and (2) we get the equilibrium proportion

$$r = \frac{1}{c + 2pq + 1} \tag{3}$$

where $c = c_1/c_2$ and $p = p_1/p_2$ are the relative cost of laying, and probability of surviving to the larval stage, respectively, for the two sexes. If a female virtually never parasitizes her own daughters, so that $q \approx 0$, then $r = 1/(c + 1)$, and the ratio of male/female eggs laid is

$$\frac{r}{1 - r} = \frac{1}{c} = \frac{c_2}{c_1} \tag{4}$$

which is the female/male unit cost ratio, as expected. As q increases, the ratio moves, as expected, in the direction of more female investment. (In this regard, self-parasitism has the same effect as inbreeding.) The finding that "the male is relatively rare under field conditions" (Flanders 1967, p. 423) may suggest either that q is large (a female is likely to parasitize her own daughters) or that c is large (it is much more difficult to lay a male egg than a female egg).

Hamilton (1964, 1972) and Trivers and Hare (1976) were among the first to observe that Fisher's equilibrium principle must be used very carefully in the presence of complications such as haplodiploidy, eusocial behavior, meiotic drive, and inbreeding. Oster et al. (1977), Charnov (1978), Benford (1978), and Taylor and Bulmer (1980) have provided rigorous arguments using transition matrices which keep track of gene-frequency changes to handle some of these complications. We have used these methods to verify that our equilibrium ratio (3) is indeed correct.

The case of autoparasitic hymenoptera which can control the sex of their offspring is a particularly intriguing one for sex-ratio theory. We hope that students of this group will be stimulated to gather data to test the validity of our model.

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