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SEX RATIO COMPENSATION IN ANT POPULATIONS¹

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Forsyth (1981) has studied the sex ratio in colonies of the hymenopteran ant, *Apterostigma dentigerum*. Mating, colony initiation, and sexual production occur throughout the year, so that, at any time, a sample should reveal a typical cross-section of the population. Colonies are started by a queen who produces workers and reproductives. If the queen dies or fails to function, at least one worker will develop ovaries and lay (unfertilized) male eggs. Forsyth found that queens produced reproductives with a female-biased sex ratio. He suggested that this bias might have evolved to compensate for the all male production of workers in colonies which had lost their queen. My purpose is to build a simple model to see how such sex ratio compensation might work.

Forsyth ascertained that male and female alates had the same dry weight, hence assumed that they were equally expensive to make, and that ratios of investment in the two sexes could be calculated by counting individuals. Of 53 colonies sampled containing sexual alates, 35 had a functional queen and had produced 269 female and 164 male alates, and the remaining 18 had no functional queen and had produced 121 males. The observed sex ratio of queen production is $164/433 = .38$ males/total giving an overall population sex ratio of $285/554 = .51$.

To construct a simple model for this situation, let β denote the ratio of worker reproductive output to queen reproductive output in the population. Forsyth's estimate of β would be $121/433 = .279$. Denote by r the equilibrium sex ratio (proportion of males) of queen produced offspring. In a steady state situation each queen expects to contribute to the next generation, 1 daughter, $r/(1 - r)$ sons and $\beta(1 + r/(1 - r)) = \beta/(1 - r)$ grandsons (by a worker), and each male expects to mate with $(1 - r)/(\beta + r)$ queens.

Following the standard ESS argument, we suppose the sex ratio r is controlled by an allele t which is expressed in the queen. We postulate a rare mutant allele T , dominant over t , which codes for an alternative ratio s . Then r is the equilibrium value if for every $s \neq r$, the allele T has no selective advantage over t . The rarity of T allows us to ignore matings between Tt females and T males, and hence ignore the existence of TT females. If we denote by x and y the numbers of Tt queens and T males, respec-

tively, in one generation, the numbers x' and y' in the next generation are linearly related to x and y by the equation $\begin{bmatrix} x' \\ y' \end{bmatrix} = A(s) \begin{bmatrix} x \\ y \end{bmatrix}$ where A is the 2×2 transition matrix. We calculate the entries of $A(s)$ by assuming a constant population size so that each tt queen contributes one reproductive daughter to the next generation and $r/(1 - r)$ sons. Thus each Tt queen contributes $(1 - s)/(1 - r)$ queens, half of which have Tt , $s/(1 - r)$ sons, half of which have T , and $\beta/(1 - r)$ grandsons by her workers, one quarter of which have T . Similarly each T male expects to mate with $(1 - r)/(\beta + r)$ queens and through each such queen get one reproductive daughter who has Tt , and $\beta/(1 - r)$ grandsons, half of whom have T . Thus

$$A(s) = \begin{bmatrix} \frac{1-s}{2(1-r)} & \frac{1-r}{\beta+r} \\ \frac{s}{2(1-r)} + \frac{\beta}{4(1-r)} & \frac{1-r}{\beta+r} \cdot \frac{\beta}{2(1-r)} \end{bmatrix}$$

The condition that T have no selective advantage is that the eigenvalues of the transition matrix be, in absolute value, less than or equal to unity. As expected, $A(r)$ has dominant eigenvalue 1 with right eigenvector $(2(1 - r), \beta + r)$. A necessary condition that the dominant eigenvalue of $A(s)$ be ≤ 1 for all s is that

$$\frac{d}{ds} \det[A(s) - I] = 0$$

at $s = r$ (Taylor and Bulmer, 1980). This condition gives

$$r = (1/2) - (\beta/4). \tag{1}$$

The overall population sex ratio in this case is

$$\frac{r + \beta}{r + \beta + 1 - r} = \frac{2 + 3\beta}{4 + 4\beta} \tag{2}$$

which is somewhat greater than $1/2$. Thus the equilibrium sex ratio of the queen is female biased, but the bias is not sufficient to produce an unbiased population sex ratio. Notice that a population sex ratio of $1/2$ would be produced by a queen sex ratio of $r = (1/2) - (\beta/2)$. Her equilibrium ratio (1) splits the difference between this value of r and her preferred ratio of $1/2$ for the case of no laying workers ($\beta = 0$). Thus the extent of her sex ratio compensation is to "go half-way" toward a population sex ratio of $1/2$.

If we use Forsyth's estimate $\beta = .279$, then (1)

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gives $r = .430$ and (2) gives an overall ratio of .555. This compares with the observed ratios of $r = 164/433 = .379$ and an overall ratio of $285/554 = .514$. The observed ratios are somewhat more female biased than our model predicts. There are at least two explanations that could account for this, partial control of sex ratio by workers (Trivers and Hare, 1976), and local mate competition (Hamilton, 1967; Alexander and Sherman, 1977; Taylor and Bulmer, 1980).

DISCUSSION

An intuitive analysis of the situation might lead to the prediction that the equilibrium sex ratio should be that value $r = (1/2) - (\beta/2)$ which gives a population ratio of $1/2$. This assumption turns out to be incorrect, but it is not immediately clear why, because a fairly sophisticated technique is needed to obtain the correct result.

It is tempting to suppose that the complications arising from haplodiploidy have led our intuition astray. We can check this by looking at the analogous diploid situation, except that we must provide mates for our workers if they are to produce sons. If we suppose, for example, that they mate with their

father or indeed with any male of his generation, and then produce diploid sons, the analogous calculations give the same equilibrium ratio as (1). Thus it appears that haplodiploidy has little to do with the result.

The result certainly underscores the need for careful models in genetically complicated situations.

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