

Evolutionary ecology

Benevolent sisterhood

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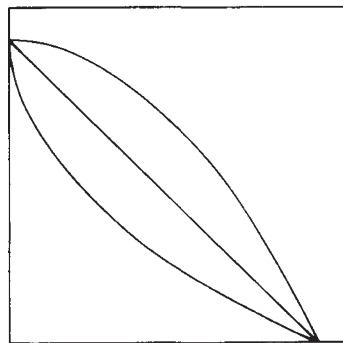
A PRINCIPLE of diminishing returns was first applied to sex-ratio evolution by Hamilton¹, who pointed out that if females usually mate with their brothers, parents should produce the minimum number of sons required to guarantee insemination of their daughters. The reason is that brothers are genetically equivalent from a parent's point of view, so that nothing is gained by having them compete among themselves for matings. This situation is referred to as local mate competition (LMC). It is common in various groups of insects that delight theoreticians by producing female-biased sex ratios remarkably like those predicted on the basis of fairly simple models^{2,3}. (For a recent example published in *Nature*⁴, see Herre's comparative study of facultative sex-ratio variation in fig wasps.) On page 346 of this issue⁵, Schwarz describes what may turn out to be a case of simultaneously diminishing and increasing returns.

LMC is a particular case of what can be called 'differentially nonlinear returns' on investment. Several different ecological causes of nonlinearity have been identified, each with different consequences for the sex ratio, depending on the way in which male and female offspring are affected². In each case the expected fitness of offspring belonging to one sex depends more strongly on the number of individuals of that sex in a brood, than does the fitness of members of the other sex. Under such conditions the equilibrium ratio of investment over the population as a whole may be far from 1 : 1, and the sex ratios of individual broods may vary dramatically with brood size^{2-4, 6-8}.

In his paper in this issue⁵, Schwarz describes a situation in which female fitness appears to increase with the number of female offspring in broods of the primitively social allodapine bee *Exoneura bicolor*. All broods are female-biased, small ones most of all, in agreement with the idea that female nest mates experience local resource enhancement (LRE). Here the interaction among siblings of like sex is cooperative rather than competitive, but otherwise LRE looks very much like an inverted form of its competitive analogue local resource competition (LRC), which is expected to produce a male bias where female siblings compete more strongly for resources than do males. This apparent symmetry is deceptive, however, because cooperative interactions among siblings can lead to outcomes of sex ratios that differ qualitatively from those produced by competitive interactions.

To see why, consider the following

simple model. Suppose that all broods are of the same size, but that parents can vary the proportion (r) of sons. If there are no sex-specific interactions among siblings, all of whom simply disperse to reproduce within the population at large, then a parent's total expected fitness through sons would be directly proportional to r , and its fitness through daughters would be proportional to $1-r$. But suppose instead that sisters interact with each other, such that their summed fitness is proportional to $(1-r)^g$. Then we can represent competitive interactions such as LRC by setting $g < 1$, so that the expected fitness of each individual female decreases as the



Fitness through sons (ordinate) versus fitness through daughters (abscissa). Top curve, $g = 1/2$; middle curve, $g = 1$; bottom curve, $g = 2$.

number of females in the brood increases. Conversely, we can represent cooperative interactions such as LRE by setting $g > 1$, so that a parent realizes increasing returns to scale on its investment in daughters.

The graph shows the combinations of fitness through daughters and fitness through sons that a parent can realize by varying r between zero (all daughters) and one (all sons), for $g = 1/2, 1$ and 2 . Because the curve for $g = 1/2$ (competition among daughters) is bowed out, a parent will achieve its greatest total fitness through daughters and sons combined by producing a mixture of both sexes; the evolutionary equilibrium (ESS) turns out to be $r = 2/3$ ($1/3$ daughters, $2/3$ sons). For $g = 1$ the curve is flat, so all brood sex ratios are equally fit if the population is in equilibrium, with overall equal investment in daughters and sons. But for $g = 2$ (cooperation among daughters) the curve is bowed in, so a parent would do better to make all daughters or all sons than it would to make a mixture of the two. Technically there is a female-biased equilibrium at $r = 1/3$ ($2/3$ daughters, $1/3$ sons), which corresponds to the male-biased equilibrium seen in the competitive case^{9,10}. But this equilibrium is dynamically unstable to

invasion by a 'split' strategy, in which with probability $1/2$ a parent makes all daughters, and with probability $1/2$ it makes all sons. If this split strategy is feasible, then the sex ratio of the whole population will be biased only slightly or not at all (depending on details of the model), and there will be a sharp division between male-biased and female-biased broods.

This is not what Schwarz finds⁵ in *E. bicolor*, which shows a strong overall female bias, with males well distributed, at least among the larger broods. If females interact cooperatively with their nest mates only during reproduction, then this distribution of brood sex ratios is puzzling. But if male offspring also benefit from being in broods that contain large numbers of females, then the problem disappears. In effect, total fitness through sons will then scale as r^h , where $h < 1$ (competitive interaction); this can easily bend the daughter-son tradeoff curve back into the bowed-out shape that favours mixed-sex broods and overall female bias. Allodapine bees develop directly into adults, rather than overwintering as larvae¹¹, so pre-reproductive females could have many opportunities to help their pre-reproductive male nest mates. Schwarz emphasizes the advantage of group defence against ants and parasites during reproduction, so it seems likely that such defence is also important before dispersal. If so, all-male broods would be at an obvious disadvantage, and the ESS could well be a brood sex-ratio distribution similar to the one actually seen in *E. bicolor*.

Nonlinear returns on investment arise in many kinds of sex-allocation problems. Why are some plants and animals hermaphrodites, whereas others are dioecious (with separate sexes)? This question seems far removed from the sex ratios of bees, and the models^{10, 12-14} proposed have not often used the language of LMC, LRC, LRE and so on. But the principles involved are seen increasingly as the same: some ecological conditions generate economies of scale in the production of one sex or kind of gamete (leading to specialization), whereas other conditions do the opposite. □

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