Biology 494 <u>*Handout #68*</u> **On Sex Ratio Selection** *9 Dec 92*

2 pages...

Consider a large population that is outbred in a way that makes mate competition population-wide, which means that the offspring of any parent are unlikely to compete with their same-sex siblings for mates, and also that any individual that finds itself in a local subpopulation in which the sex ratio is skewed unfavorably for itself can move elsewhere and try again. This is the kind of population meant by Fisher (1930) in his often-quoted statement from which all arguments about sex ratio selection are derived. Fisher's argument, that in such a population parents will collectively be expected to invest equally in the two sexes, derives from the fact that in general the genes in any generation come equally from the two sexes, so that, collectively, the two sexes represented in any population are of equal reproductive value. If the population is large, of course, individual parents may occasionally deviate from equality of investment without changing the overall sex ratio sufficiently to penalize them, so we should not be surprised to find even a great deal of variation in the sex ratios of individual broods, and many one-sex broods. As a result, mechanisms of sex determination may be maintained even if they allow or cause such deviations within broods, so long as the overall investment in the two sexes is close to equal and penalties for local variations can be compensated by movements of individuals or gametes. Thus, in a large enough population with sufficiently mobile individuals, sex determination could even be by a coin toss and meet Fisher's criteria, so long as the expense of rearing individuals of the two sexes is approximately the same. [If investment in one sex greatly exceeds that in the other, then a coin toss won't do. Thus, in honeybees, each queen receives an enormous investment of workers, honey, comb, and hive; but the males only a body about the size of that of the queen. As Fisher would have predicted, despite the seeming inefficiency at the group level (maybe it isn't inefficient, for reasons still unknown, but it *seems* to be), hundreds of males are produced for each queen.]

One might say generally that, *with regard to sex ratios, parents are selected to produce broods in which none of their offspring is reproductively penalized because of its sex.* With respect to dividing investment between the sexes in individual broods, parents probably have about the broadest possible latitude in the particular kind of population, described above, that is relevant to Fisher's original theory.

Fisher also stated that differential mortality between the sexes in broods of offspring before the end of parental care would cause increased investment in the sex that died more often. The reason this would follow from his original statement is that whenever an individual died before the end of parental care, the total investment in it would be less than that in an individual that remained alive until the end of parental care. A supporting observation for Fisher's theory is that there is a tendency for mammal parents to start more males, then lose more of them along the way during the period of parental care, thus tending to even out investment in the two sexes.

The last part of Fisher's statement is probably the least intuitive: that parents will not adjust proportions of parental care between the sexes to compensate sex-differential mortality that occurs after the end of parental care (this part was evidently difficult enough that Daly and Wilson chickened out completely and just ignored it!). How do we figure this one out? If a parent increases investment in individuals of the sex that overall is getting less investment for the specific reason that individuals of that sex die more frequently before the end of parental care, the parent thereby tends to increase the number of reared of offspring of that sex, and also to increase the value of its brood because that sex was under-represented in the population, hence more valuable than the other; it also increases the value of its collection of offspring of the other sex, which was low because it was over-represented in the population. So it increases the value of both the more valuable sex and the less valuable sex among its own offspring. This part, then, appears easy to understand.

Offspring of the sex that dies more often after the end of parental care are admittedly more valuable when they reach reproductive age because more of that sex have died. Parents will be favored for *improving* individuals of that sex (as well as the other one), if they can, so that they don't die. But the parent that simply produces more individuals of the sex that dies after the end of parental care, without making them less susceptible to dying, while increasing the total value of that sex in its brood, will lower the value of individuals of that sex because more of them will reach reproductive age; none of this will change the value of individuals of the other sex but it will lower the parent's contribution from the other sex. Thus, if twice as many females as males survive to reproduce, males are on average twice as valuable because on average each will sire twice as many female's offspring -- or half the females won't reproduce. Similarly, if twice as many males as females survive to reproduce, females are worth twice as much because on average one will reproduce for every two males. Increasing the number of males in one's brood in the first case lowers the value of each reproducing male, on average, and also subtracts from the number of females one can produce. As a result, there is no way the parent can obtain a sufficient return on its increased investment. Vice versa in the second case. You have to go painfully through a lot of arithmetic to prove this to yourself (or that's the only way I know to do it), and I have done that, with every kind of situation I could imagine (trust me). I stopped passing out the resulting handout some years ago because it got so complicated no one ever went all the way through it anyway. Because you do not have access to any such calculations, we are not requiring that anyone work out this arithmetic for the question I asked. But we have a special local Nobel Prize for anyone who did, and a one-extra-point congratulation for anyone who realized the problem and proved that in answering the question.