specialists, with the predictable outcome: a glut of daughters. Once again the pendulum will swing back toward son producers. And on it goes, with the pendulum swinging first to daughters, then to sons. The outcome? A population with more or less equal numbers of sons and daughters.

Fisher's model helps to explain why one-to-one sex ratios should be so common among many animals. But alter the critical underlying variables—for example, step up inbreeding—and the rules of the game change. This is just what seems to have happened to some little lemmings of the north.

The wood lemming of northern Europe and the varying lemming, which ranges from Canada to Siberia, have evolved a wasplike capacity to dramatically bias the sex ratio of their offspring. In the lemmings' case, the skew is always toward daughters. Three to four times as many females as males are born in the population, with some individual mothers producing no sons at all. The lemmings' trick is accomplished by curious changes on the X chromosome. In the case of the wood lemming, a peculiarly "imperialistic" version of the X chromosome has evolved with the power to overwhelm the male-producing Y chromosome. Paired with one of these "super-X" chromosomes, a Y chromosome fails to express itself and the X-Y individual develops into a female.

Just why such chromosomal oddities have evolved in these lemmings and, so far as we know, in no other mammals remains a matter for debate. But as they tunnel through moss in the dark recesses of fir forests, feeding on red wortleberries and the bark of juniper trees, these lemmings are subject to the vagaries of good and bad years, and a consensus is emerging that the boom-or-bust population cycles characteristic of these small arctic mammals play a role. According to this interpretation, lemmings in a "bust" year would find themselves scarce, isolated in pockets where brothers would have little choice but to mate with their sisters. The same local mate competition that led mother fig wasps to produce ten daughters for every son may at some point in the past have also favored the one-in-a-million wood lemming carrying the aberrant super-X chromosome.

Most other mammals, however, have never been subject to such inbred conditions, and current wisdom still rates mammals and birds as resolutely committed to more-or-less equal production of sons and daughters. Yet recently, biologists have been turning up instance after instance in which the sex ratio at birth (or shortly after) *is* significantly different from the expected 1/1. At issue are not the striking biases found in fig wasps, but more subtle biases on

Manipulating Mothers

The jewel wasp is a consummate artist at controlling the sex of its offspring. Found throughout the world, this small parasitic wasp (at 3 millimeters, it is smaller than a fruit fly) delivers a lethal sting and then lays its eggs in the pupae of various species of blowfly. Typically, from twenty to forty young wasps develop on each host. The wasps mate immediately upon emerging from the host pupa, and mated females then disperse in search of new fly pupae in which to deposit their own eggs. The pupae relished by the wasps are usually found under carcasses or in bird nests. Despite the—to the delicate human sensibility—rather repulsive circumstances under which it lays its eggs, I have found the reproductive affairs of this little wasp to be intriguing.

Male jewel wasps have short wings and cannot fly. Since the wasps mate right after emergence, brothers and sisters sometimes have only each other to mate with. Such inbreeding occurs, for example, when all the wasps emerging from one bird nest or carcass are produced by a lone female. At other times, many females will parasitize the same nest or the many blowfly pupae patchily distributed under a carcass, and then mating is spread among many families.

Impressively, the jewel wasp can alter the sex ratio of her progeny depending on how many other females have discovered the same patch of potential hosts. When by herself, a female will produce about 85 percent daughters, with just enough sons to inseminate all her daughters and thus with a minimum of energy wasted on sons competing with one another. When she finds herself in the company of other egg-laying females, however, she changes her tactics dramatically. Now, she needs more sons to compete with males of other families, so she shifts the sex ratio of her offspring closer to 50/50.

Sometimes two females lay their eggs in the very same blowfly pupa. If that pupa is some distance away from any others, then mating competition will be restricted to the offspring of those two females. In that case, the first wasp to find such a host lays about 85 percent daughters, as expected. However, if the second female encounters the pupa within a day or two, she can detect that it has already been attacked. She accomplishes this by "tasting" chemical changes in the host with her stinger, which is also a complicated sensory organ. If she "decides" to insert a single egg into the host, it will be a son. Because of the many daughters laid by the first female, the second female's son will undoubtedly have many mating opportunities. (Eggs laid within two days of each other routinely emerge as adults at the same time.) If, however, she "decides" to lay many eggs, she will produce both sons and daughters. The more eggs she lays, the more she will bias her own production toward daughters.

Understanding the intricacies of the jewel wasp's ability to manipulate the sex ratio of its offspring is challenge enough. Complicating the picture is a recently discovered assemblage of "parasitic" genetic factors within the species that can usurp and undermine this ability. These parasitic genes (both inherited microorganisms and "renegade" chromosomes have been found) promote their own transmission by distorting the wasp's sex ratio. One of these genes—known as the paternal sex ratio element—is carried by about 10 percent of jewel wasps and causes the female to produce all males, whether or not she has fertilized some of her eggs. (In wasps and other haplodiploid organisms, only fertilized eggs develop into females.) Males carrying the paternal sex ratio element transmit it through their sperm to eggs during fertilization. Normally these eggs would develop into females, but instead the paternal sex ratio element somehow destroys the paternal chromosomes in the egg, thus converting a diploid female into a haploid male. This amazing accomplishment is evolutionarily advantageous for the paternal sex ratio element since—unlike all other known parasitic genes—it is transmitted through males but not through females. In contrast, it is decidely detrimental to the rest of the father's genome. Such a gene can also cause problems for the whole population since an all male population will obviously go extinct. This system of birds parasitized by flies parasitized by wasps parasitized by genetic elements makes poignant Jonathan Swift's famous quote:

So, Nat'ralists observe, a Flea
Hath smaller Fleas that on him prey;
And these have smaller fleas to bite 'em
And so proceed *ad infinitum*

John H. Werren

Female jewel wasp on fly pupa

Raymond A. Mendez