ments of Iran. The McHarg firm did an ecological study of the whole country, dividing it into 21 "biophysical-cultural" regions. The park will contain a museum of natural history, an academy of natural sciences, a planetarium, an aquarium, a botanical garden, and a zoological garden. Speicfic environments will be replicated, and the history of man, the history of Iran, and the history of biological and human adaptations to environments will be explained through multitudinous means. Pardisan, as the project is called, will also be a research center. In the words of Firouz "it must transform Iranian attitudes towards the environment" and "it must help modern Persians to solve modern problems."

According to the richly illustrated book describing the plan, Pardisan is conceived in the image of a Persian Garden, a "powerful metaphysical symbol" that represents, through irrigation and airflow regulation, the creation of paradise in a wasteland. 'Nichols finds it "very curious for the guru of natural systems to be involved in the creation of an artificial system." Yet the garden metaphysic—or the garden as metaphor—is one that has long attracted McHarg. He is fond of citing Renaissance gardens as an example of good art but unhealthy metaphysic, in that unnatural discipline and symmetry symbolized man's drive to quell nature. On the other hand, he sees the landscaping that went beyond the garden walls to transform the face of 18th-century England as a healthy metaphysic—one in which human activities and nature's beauties were harmoniously combined. At another extreme is the metaphysic of Oriental gardens which represent naturalism rather than anthropocentrism—the subordination of the individual. The Persian Garden is yet another metaphysic: making the desert bloom.

Although McHarg does not see a whole lot being done right in this country, he is hopeful that attitudes are changing and cites with approval the spate of new books on ecology that have come out in recent years. Still, he believes we lack a guiding metaphysic for our relationship with nature.

In *Design With Nature*, he writes: "Our failure is that of the Western World and lies in prevailing values. Show me a man-oriented society in which it is believed that . . . man is exclusively divine and given dominion over all things . . . and I will predict the nature of its cities and their landscapes . . . the hot-dog stands, the neon shill, the ticky-tacky houses, dysgenic city and mined landscapes. This is the image of the anthropomorphic, anthropocentric man; he seeks not unity with nature but conquest. Yet unity he finally finds, but only when his arrogance and ignorance are stilled and he lies dead under the greensward."

—CONSTANCE HOLDEN

RESEARCH NEWS

Sexual Dimorphism and Mating Systems: How Did They Evolve?

Sociobiologists tend to look for the simplest explanations of evolved forms and behaviors. And for many years, the question of why members of one sex often evolved to be different in size from those of the other (sexual dimorphism with respect to size) seemed to have a simple explanation. This theory has been used to explain the origin of human sexual dimorphism with respect to size and has been used to infer information on how members of prehistoric human groups behaved. But in recent years investigators have taken a new look at the question of how this kind of sexual dimorphism evolved and have begun to conclude that no single theory suffices to explain this phenomenon.

For more than a century, a theory advanced by Charles Darwin has dominated research on sexual dimorphism. Darwin proposed that sexual dimorphism occurs in response to competition among members of one sex for access to members of the other sex. Males of a species may be larger than the females, more brilliantly plumaged, or may behave differently when they must compete with each other for mates. In cases of sexual dimorphism on the basis of size, males would evolve to be large whenever large size confers an advantage in intrasexual competition.

Darwin left unanswered the question of the conditions under which intrasexual competition will occur. Others have subsequently suggested that the answer might hinge on parental care. A few years ago Robert Trivers of Harvard University formalized these ideas and proposed that whichever sex invests the most in the offspring will tend to be in short supply and will be competed for. Since female birds and mammals usually contribute more than males to parental care, females will tend to be the prizes in a competition among males of these species. Trivers suggested that ecological factors, such as the abundance and distribution of food, affect the evolution of intrasexual competition by affecting parental investment.

Trivers' extension of Darwin's theory won widespread acceptance and has been widely applied to vertebrates. This theory also leads to predictions of what sorts of mating systems will occur. When members of one sex compete with each other for mates, some individuals will be inordinately successful and will have many mates. The extent of intrasexual competition has been linked to the development of monogamous, polygynous (individual males tend to mate with more than one female), and polyandrous (individual females tend to mate with more than one male) mating systems.

Richard Alexander and his associates at the University of Michigan recently reviewed the literature and reconfirmed that there is a positive correlation between the extent of sexual dimorphism (and so, presumably, intrasexual competition) and the mating systems of primates, artiodactyls (deer, antelopes, and their relatives), and pinnipeds (seals, walruses, and their relatives). These investigators explain their findings in terms of the theories of Darwin and Trivers. Moreover, they believe that the fact that human males tend to be larger than females is evidence of past mating systems in which males competed for females and the most successful males fathered offspring of more than one female. Alexander notes that social constraints have forced many people into monogamy. But the prevalence of divorce and promiscuity makes our society effectively a polygynous one.

Although Alexander and others still stress the theory linking parental investment to mating systems and sexual dimorphism with respect to size, some investigators are now beginning to question it. They ask whether intrasexual competition is the dominant factor in the evolution of this kind of sexual dimorphism and whether parental investment is the clue to understanding intrasexual competition and the evolution of mating systems. Several researchers are concluding that physiological factors and competition for ecological resources may often be more important than competition for mates in determining the evolution of this kind of sexual dimorphism. Moreover, physiological and ecological factors may be at least as important as parental investment for the evolution of mating systems.

Katherine Ralls of the National Zoological Park of the Smithsonian Institution recently compiled data on mammals in which females are larger than males in order to see whether these females behave as would be predicted by the theories of Trivers and Darwin. It is expected, according to these theories, that females of these species should compete for access to males and that males should help care for their offspring. Donald Jenni of the University of Montana points out that this prediction is fulfilled for several bird species in which females are larger than males, such as the American jacana of Costa Rica, which he has studied extensively. Not all birds of species in which females are larger than males exhibit this behavior, however; and, according to Ralls, many mammals also do not behave as expected. For example, females are larger than males among the golden hamsters and in most species of bats and seals. But, after copulation, males of these species make little or no contribution to their offspring. In general, Ralls says, female mammals almost never compete for males.

Why Females Are Large

Ralls and others suggest that selective pressures caused by the demands of pregnancy and lactation can be major influences in determining the size of females. Ralls points out that females of many of the mammalian species in which females are larger than males have large babies. She cites evidence that large mothers are likely to produce large babies with better chances of survival than small babies. Large mothers may also enable their babies to grow more quickly by providing more or richer milk, and they are often better at carrying and defending their babies.

Philip Meyers of the University of Michigan believes that the demands of motherhood cause female bats to be larger than males. Bats have large babies that mature quickly so as to be ready to hibernate in cold weather. Bat fetuses are so large that they can add as much as 20 to 30 percent to the weight of females. Female bats must fly while pregnant and often carry their young to new roosting sites if they are disturbed. Meyers believes that female bats evolved to have large body sizes so as to reduce the proportionate load of flying with their fetuses or newborn and to reduce the relative cost of lactation. He finds that female bats have wings that are larger in relation to the size of their bodies than the wings of males. This would be expected if the bodily proportions of females evolved in response to the stress of bearing and rearing young.

To test his hypothesis, Meyers compared the sizes of different female brown bats. Brown bats on the East Coast of the United States bear two young, whereas those on the West Coast bear one; and Meyers found that the females on the East Coast are correspondingly larger than those on the West Coast. However, on both coasts, the males are the same size and the social organization is the same. This effect is also seen, he reports, in other bat species in which some groups bear more offspring than others.

Demands of reproduction may also affect sexual dimorphism in birds, according to Jerry Downhower of Ohio State University. Downhower proposed that if bodily resources for laying eggs are accumulated shortly before breeding occurs small females, which can accumulate these resources more rapidly, should have shorter breeding seasons than larger females. He predicted that female birds from such species will be smaller when they live in fluctuating environments, in which it is advantageous to breed quickly. After testing this hypothesis with Darwin's finches on the Galápagos Islands, he concluded that it would explain the varying degrees of size-related sexual dimorphism among these birds.

Downhower points out that if bodily reserves for breeding are acquired and stored before breeding begins, large females will have more reserves for egg production and will be at an advantage. He believes that this can account for the large size of the females of many bird species.

Proponents of these alternate explanations of sexual dimorphism with respect to size point out that the degree of sexual dimorphism is related to the mating systems of many animals. This is most pronounced in the extreme cases. For example, Ralls reports that most monogamous species of mammals display little size-related sexual dimorphism and that most species that are extremely polygynous display extreme dimorphism. But, she says, this relation has never been evaluated for the insectivores, bats, and rodents, which make up 70 percent of recently evolved mammals.

Nearly everyone agrees that intrasexual competition can play a role in the evolution of sexual dimorphism and of mating systems. But whether parental investment is the key to understanding mating systems remains controversial. For example, Ian Stirling of the Canadian Wildlife Service in Edmonton emphasizes the effects of ecological factors on the mating behavior of seals and Ralls believes ecological factors are often at least as important as parental investment in determining mammalian mating patterns. Stephen Emlen of Cornell University and Lewis Oring of the University of North Dakota state that ecological factors are more important than parental investment in determining the mating systems of birds and possibly those of many mammalian groups, certain insects, and lower vertebrates.

Emlen and Oring suggest that intrasexual competition occurs whenever some individuals are able to control the access of others to potential mates. This control is often exerted indirectly; for example, some individuals will control resources that are critical for either the attraction of mates or successful reproduction. The greater the control or monopolization of these resources, the greater the variance in reproductive success among individuals and the greater the intrasexual competition.

Emlen and Oring find that the distribution of key resources and the ease with which they can be defended are crucial factors in determining whether an individual can monopolize more than its fair share of them. Thus, this ecological distribution determines the degree of intrasexual competition in a population. They point out that an individual's ability to monopolize key resources depends on its relative freedom from parental care. But this freedom is not in itself sufficient to ensure that polygyny (or polyandry, if females do not care for their young) will develop. Emlen and Oring report that they can predict the types of avian mating systems that will occur on the basis of ecological factors.

Thus, as researchers look more closely at the relations between intrasexual competition, sexual dimorphism with respect to size, and mating systems, they are recognizing that no one theory seems sufficient to account for all of their findings. The theories of Darwin and Trivers are still useful, but they apparently must be fleshed out to take into account the important effects caused by physiological and ecological factors.

—GINA BARI KOLATA