of porphyrin and *N*-alkylimidazoles will bind oxygen reversibly under the same conditions.

Fred Basolo of Northwestern University, Chicago, has demonstrated that complexes of tetraphenylporphyrin and imidazole, piperidine, or pyridine will bind oxygen reversibly at −78°C in dichloromethane and other solvents. And Richard J. Kassner of the University of Illinois at Chicago Circle has shown that a complex of protoheme and *t*-butylamine will bind oxygen reversibly in 1-butanol at −70°C. The observations with *t*-butylamine and piperidine suggest that π-bonding from imidazole or aromatic bases is not necessary for oxygen binding, but that it increases stability of the oxygen complex.

Kinetic studies of each of these systems have been limited because of the difficulties of separating oxygen binding from binding of the nitrogen base. But the data that are available corroborate the observation that increasing polarity of the solvent increases the rate of binding of oxygen and the stability of the oxygen complex. The studies also point out the importance of low temperatures and the exclusion of water in preventing oxidation of the heme iron in the absence of globin. It thus seems apparent that the hydrophobic pocket of the globin moiety of hemoglobin or myoglobin may actually interfere somewhat with the binding of oxygen, but that this interference is counterbalanced by the protection from oxidation.

Because of the importance of excluding water from the model systems and in order to mimic more closely the hydrophobic environment produced by the protein, many of the investigators are studying their systems in the gas phase. Many of Collman's results, for example, are obtained from gas-solid reactions with the crystalline, hindered porphyrins. Traylor and Chang have incorporated their model compound into a polystyrene film to study gas-solid reactions. And Basolo and Robert L. Burwell, Jr., of Northwestern University have developed a new system in which an iron-tetraphenylporphyrin complex coordinates to 3-imidazolylpropyl groups covalently bound to silica gel. Preliminary results in the gas phase show that this material is stable in oxygen at room temperature and that it binds oxygen weakly at 0°C, more strongly at −78°C, and irreversibly at −127°C. Further studies with all of the systems are continuing.

While the mechanisms of hemoglobin and myoglobin are still not yet fully understood, knowledge about them is increasing rapidly, and the day when they will be understood seems in sight. This understanding should be of great value in the study and treatment of the abnormalities of hemoglobins and the blood diseases in which they are involved. Perhaps even more important, the duplication of the function of myoglobin with such simple model compounds suggests that other types of protein catalysis can be duplicated with protein-free small molecules.

—THOMAS H. MAUGH II

Sociobiology (II): The Evolution of Social Systems

Sociobiologists, who emphasize the genetic basis of social behavior, are taking a view of social systems that is becoming increasingly popular among ethologists who do field studies. These investigators believe that social systems evolve to increase the genetic fitness of individuals in specific environments. By combining studies of animal behavior with those of ecology, sociobiologists are beginning to understand why different social systems may have evolved.

The reconstruction of the evolution of social systems of vertebrates gained impetus soon after John Crook (University of Bristol, Bristol, England) and others described the social life of birds. These investigators observed that the social systems of different bird species in the same environment are often similar and that the social systems of closely related species in unlike environments are often different. These observations stimulated students of animal behavior to search for general rules governing the ways that environments affect social systems. Investigators are now trying to ascertain what kind of behavior would allow an animal or its close relatives to rear the largest number of offspring in a given environment and then to see how such fitness strategies change in response to changes in the environment and changes in the animal's interactions with members of its social group.

Spacing patterns among sunbirds in East Africa have been analyzed by Larry Wolf (Syracuse University, Syracuse, New York) and Frank Gill (Academy of Natural Sciences, Philadelphia). They report that male sunbirds, and sometimes females and immature individuals, often subdivide a field of flowers among themselves, each individual occupying its territory and defending it during the nonbreeding season so that only he can feed there.

Although such behavior is commonplace among birds and other animals, Wolf and Gill found two conditions in which male sunbirds will not set up territories: Territories will not be formed when nectar is so sparsely distributed that it would require an inordinate amount of energy for a male to defend a territory with enough food for himself. Nor will territories be formed when nectar is so densely distributed that it is a waste of energy to defend a territory. Wolf and Gill were able to predict whether territories would be formed and how large the territories would be by plotting the distribution of nectar in a field and knowing the metabolic energy required by a sunbird. If territories were formed, each contained slightly more nectar than was necessary to support one bird for 24 hours. Wolf and F. G. Stiles (University of Costa Rica) found, moreover, that their analysis of sunbirds could be applied to hummingbirds of the Americas—a group of species that also eat nectar.

The prediction that territories will not be formed in very sparse or very rich habitats has been tested by investigators who compared the social systems developed by related species living in different environments. For example, David Barash (University of Washington, Seattle) finds that marmots, which are large rodents, set up territories when they live in a moderate environment where the growing season is long but live in colonies in very harsh environments with short growing seasons. When marmots live in environments that are intermediate between moderate and very harsh, they are intermediate in territoriality (animals live in colonies but have ranges for foraging).

When food is randomly distributed in patches, each of which contains enough food for many members of a species, animals often form colonies instead of setting up territories or living independently of each other. The potential advantage of this form of social organization was mathematically modeled by Henry Horn (Princeton

University, Princeton, New Jersey). Horn suggested that when food is located in unpredictable patches, a group that forages in an area would be more likely to find food, which the group members could share, than would an animal that forages alone. From the model, it is expected that maximum group size would be a function of the average amount of food in a patch.

Stephen Emlen (Cornell University) believes that patchy food distributions are the reason that swallows and other birds that eat insects while flying live in large colonies. Since the distribution of insects is subject to wind currents, the food distribution for the birds is patchy. According to Philip Ashmole (Edinburgh University, Edinburgh, Scotland), the same idea can be applied to explain why marine birds that eat schools of fish travel in large groups. Stuart Altmann (University of Chicago) suggests that patchy distribution of food and water is a cause of group foraging by yellow baboons on savannahs in Kenya; in contrast he points out that Hamadryas baboons living in Ethiopia, where food is distributed in very small patches, do not forage in large groups.

Distribution of food supplies is thought to be related to the evolution of some mating systems as well as to group size and territoriality. Jack Bradbury (Rockefeller University, New York), notes that females usually compete for access to an ecological resource (such as food or nesting sites) whereas males usually compete for access to females. A male, then, could obtain access to females by controlling a resource the females need and then excluding other males from that resource.

Bradbury showed that male bats in Central America often control territories in which insects live. Such territories include enough insects to support several females, so that male bats form harems. Another species of bat in the same area eats certain fruits that are sparsely distributed. These bats do not hold feeding territories, but the males of this species control hollow trees that females use for roosting.

Males that cannot defend a resource in order to gain access to females, Bradbury points out, may employ one of two other strategies to mate. If females form groups (to forage for food or to protect themselves against predators), a male may associate himself with one group of females and exclude all other males. Such behavior has been observed in many species. If

Male hammerhead bat. The enlarged flared lips and the large larynx (about two-thirds of the body cavity) are specializations for display typical of males in species that use leks. [Alain Devez, Laboratoire de Primatologie et d'Ecologie Equatoriale, Makokou, Gabon]

females do not form groups, males and females may meet at a special mating ground called a lek.

Most animals do not use leks for mating, and those that do exhibit bizarre behavior at these mating grounds. This extreme form of social organization has received a great deal of attention from animal behaviorists. Females go to leks for the sole purpose of meeting males. Males spend a great deal of time at these areas, defending tiny territories that usually are much too small to be used for feeding or nesting. While on the lek, males display: that is, they emit special calls or behave in other ways designed to attract females. Bradbury mentions that males in societies that have leks look different from females in those societies. For example, males may be brilliantly colored or have exaggerated features in comparison to females. Leks have been found among a small percentage of bird species and, recently, among a few mammalian species such as the Uganda Kob antelope and the hammerheaded bat.

According to Peter Marler (Rockefeller University), only a few males on a lek do most of the mating in any one breeding season. Marler stresses that little is known of the rules that govern whether a male succeeds or fails in getting a mate when he displays on a lek. Often there are favored sites on a lek, and Haven Wiley (University of North Carolina) found that it may take a male sage grouse several years to establish a territory at such a mating center. Thus a male's capacity to survive to a mature age becomes one correlate of mating success. This factor, sociobiologists believe, assures the propagation of genes from hardy, and not weak, males.

Parental care is another form of social behavior that varies in response to environments. Behavioral interactions may serve to enable parents to force the dispersal of their offspring when the offspring are likely to survive on their own. One of the best-documented examples of this phenomenon is the "greeting" system of marmots. This system provides an illustration of how changes in the usage of a communicative action may have far-reaching consequences.

Barash observed that marmots may greet each other by touching mouth to mouth or mouth to head and showed that these greetings are correlated with the maintenance of social cohesiveness in a group. In extremely harsh environments with short growing seasons where the animals live in colonies, each animal greets its offspring and its neighbors daily in the morning and at other times during the day as well. When a young marmot in such a colony is 2 years old, it becomes mature and needs to wander farther and farther afield to get food. It eventually spends a night away from its colony and misses the morning greeting behavior. At that time its estrangement from the group begins. In contrast, marmots that live in environments with long growing seasons where these animals hold territories and are solitary, have no greeting systems and the young disperse before they are a year old. In environments with growing seasons intermediate between the two extremes, the marmots have far fewer greetings among family members and neighbors, and the young usually disperse when they are 1 year old.

Analyses of the ways that environments and evolution affect social systems have only recently become possible with the advent of long-term field studies of individual animals whose social histories and kinship relations are recorded. Because these studies require extensive field research, investigators who work in the traditional university framework often find it difficult to obtain sufficient time and funds for such studies. Nonetheless, most sociobiologists believe that this approach will characterize future research on social systems. Moreover, since reconstructions of the evolution of social systems from field studies and analyses of parental care and other forms of interactions based on genetic theory appear to be founded on the same basic premise, many investigators predict that the two lines of research will converge to provide a unified theory of sociobiology.—GINA BARI KOLATA