Brotherly Alliances Help Avoid Inbreeding

Patterns of inbreeding avoidance behavior in vervet monkeys has a profound influence on the social organization of neighboring groups

The behavior of nonhuman primates can at first sight appear to be a mélange of capricious and chaotic interactions between individuals within and between groups. But, as the considerable progress in primatology has taught during the past couple of decades, there are subtle social patterns to be discerned in this apparently formless muddle, patterns that are frequently woven upon a framework of kinship. Dorothy Cheney and Robert Seyfarth, of the University of California, Los Angeles, have been studying three vervet monkey troops in Kenya since 1977 and they now report unsuspected features of social organization and life history strategies in this small, ground-living cercopithecoid.

In common with most higher primates, male vervets on reaching sexual maturity leave their natal troop and seek to establish themselves elsewhere, a behavior pattern that traditionally is associated with the avoidance of inbreeding. Cheney and Seyfarth are interested not so much in the ultimate cause of male transfer as in the manner in which it occurs. "Given that an individual migrates from its natal group, which group should it join? What are the genetic and social consequences of different distributions of transfer among particular groups?" What, in other words, are the costs and benefits of transferring randomly as against nonrandomly to another group; of transferring alone or in company with a brother or an age-mate; and so on? "In certain cases there may be social advantages to a given pattern of dispersal even though this pattern appears on first examination to carry some genetic costs."

The answers to these questions, it transpires, affect not only the future success of the individual migrant but also the more complex group interactions between neighboring social units. "The social organization of vervets is best regarded as a 'community' of groups," say Cheney and Seyfarth. "This is a higher level of social organization than we are used to thinking monkeys have."

The pattern of male transfer at maturity that is so prevalent among primates is imposed principally by the nature of the food resource requirements of the females, argues Richard Wrangham, of the University of Michigan. "When a species' food resources are of a type that can be defended effectively by a coalition of females, then the females will form the resident sex and the males will transfer." If, however, food is patchily distributed, though locally abundant and therefore cannot be collectively defended, related females avoid coming into competition with each other by transferring to another group at sexual maturity; in this case the males are the resident sex.

As this latter pattern—female transfer—is repeated only four times among Old World monkeys and apes (in the gorilla, chimpanzee, red colobus, and hamadryas baboon), the "typical" large primate social structure is centered on a core of related females and their offspring. There is little or no obvious paternal behavior among adult males who transfer into the group and sire the young.

The specter of reduced genetic fitness through inbreeding looms large in the calculations of population geneticists, though supporting data are frustratingly sparse. Because of the nature of the problem there will be few "natural experiments" that might be observed in free-living populations. Nevertheless, there is a strong conviction among ethologists that when they see the transfer between groups of one sex at sexual maturity they are witnessing the proximate response to the ultimate danger of inbreeding.

"[There is] a community of groups, within which individuals recognize each other and share a high degree of genetic relatedness despite the maintenance of otherwise discrete social units."

An alternative view, says Wrangham, is that the transferring individuals are seeking more promising reproductive opportunities away from their natal group. Indeed, maturing male baboons have been observed to experience difficulty in establishing themselves in the dominance hierarchy of their natal troop and are frequently rebuffed when attempting sexual alliances. Their dominance status and reproductive success are usually greatly enhanced on entering a novel troop. Proximate and ultimate causes are, however, almost hopelessly entangled here, and inbreeding avoidance remains a very reasonable working model.

If inbreeding avoidance were the only factor in the balance of a young male's future, one might reasonably expect him to embark on faraway migrations that would maximize the genetic distance with potential mates. This, however, is rarely the case. Many birds, rodents, and other animals cling close to their natal territories when they move to another social group, presumably for good reason.

Patrick Bateson, of Cambridge University, England, has been developing the concept of optimal outbreeding, in which there are selective benefits to choosing a mate who is not so closely related as to risk inimical genetic consequences, but not so distant that any specific genetic adaptations to local circumstances might be diluted and lost. The optimal genetic distance, Bateson finds in free-choice experiments with quail, is around the first cousin level. Not straying too far while transferring from the natal group might therefore have its advantages.

A second, highly practical, reason why transfers might be local rather than distant is that for many species, including vervets, there is a very real and significant risk of predation and starvation in traveling alone across even modest distances.

For vervets, a third reason why migration to a nearby group might be prudent relates directly to the migrant's future reproductive success.

Vervets typically occupy small home ranges (0.4 square kilometer in the groups monitored by Cheney and Seyfarth at Amboseli) and individuals from one group can therefore readily observe those in another. "The animals spend a lot of their time watching neighboring groups," says Seyfarth. That this time is productively spent in assessing the social dynamics of the neighbors, rather than being mere idle curiosity, is indicated by the fact that of 13 males over the age of 5 years who transferred between the study groups, ten assumed higher dominance ranking in their new groups. "[The] males may have been able to time their transfer to maximum beneficial effect," comment Cheney and Seyfarth.

By restricting migrations to immediately neighboring groups, any particular vervet group is in danger of limiting the size and therefore the genetic diversity of the effective breeding population. The benefits that might accrue from optimal outbreeding, physical safety in short migrations, and enhanced dominance status on transfer are therefore potentially imperiled by the accumulation of inbreeding coefficients. However, population genetics calculations show that even a modest rate of migration into a cluster of neighbors from more distant groups significantly lessens, if not obviates, this danger.

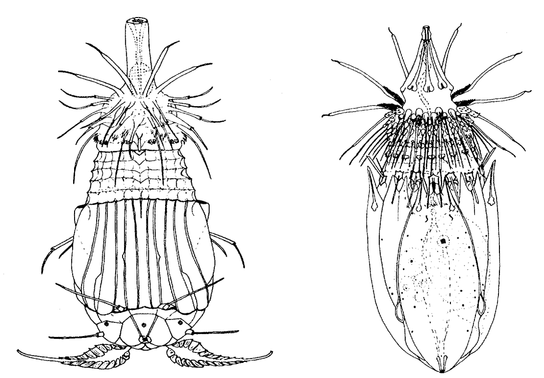
Whenever a male moves from one group to another he risks mating with his father's daughters and his brothers'

New Phylum Discovered, Named

For only the third time this century a new phylum in the animal kingdom has been discovered and described, bringing to 35 the total of these high-level (just below the subkingdom) classification groups. Robert Higgins, a researcher at the National Museum of Natural History, Washington, D.C., predicted the existence of the newly described animal in 1961 while still a graduate student. Higgins even found one in 1974, but failed at the time to recognize it as a novel organism. The honor of discovering and describing the new animal and naming the new phylum fell to Reinhardt Kristensen, of the University of Copenhagen, Denmark, who collaborated with Higgins on some of the work during 1982.

The organism, which is called *Nanaloricus mysticus* and occupies the newly erected phylum Loricifera, is one of many minute animals that live among marine sand and gravel at depths of tens to hundreds of meters below the sea surface. Known collectively as meiofauna for their diminutive size, these organisms represent relatively unexplored biological territory of great diversity (at least five separate phyla are represented, including the new one). The new organism has characteristics that, separately, are reminiscent of several other phyla but are unique in their combination. In addition, the mouth structure is a flexible tube that can be retracted into the animal, making the organism's body plan distinct from all others.

Kristensen first came across Loricifera in 1975, but mischance during tissue preparation for microscopy destroyed the single specimen he had. A year later he found larval forms in shell gravel off Western Greenland and in



Nanaloricus mysticus

The larval form (left) measures less than 195 micrometers; its rotor-like appendages allow it to swim very effectively. The mature form, right, measures about 230 micrometers and is sedentary. The combination of a free-swimming larva with a sedentary adult is unusual in the meiofauna.

a sample of coarse crystalline sand from the Chesterfield Reefs in the Coral Sea. Mature forms remained elusive, however, until April 1982 when Kristensen was on a field project at the Marine Biological Station in Roscoff, France. "I obtained a huge sample (more than 100 kilograms) of nearly clean shelly gravel from a depth of 25 to 30 meters," he recalls. "Unfortunately, it was my last day and time would not permit my using the standard $M_gCl_2^-$ extraction method; instead, I osmotically shocked the entire sample with fresh water." This expediency proved especially effective at loosening the tenacious grip that the Loricifera organisms hold on sand particles: "I found a complete series of life history stages of the new animals." Using the same technique, Kristensen found mature specimens of the new animal, although a different species, in Western Greenland a month later.

When Kristensen went to work with Higgins in August 1982, the two were able to confirm that Higgins's 1974 specimen was indeed a member of the new phylum, though a larval form. This specimen is of a different species, genus, and perhaps family, says Higgins. Early in 1983 Kristensen and Higgins found mature animals near the Smithsonian's marine biological station at Fort Pierce, Florida.

Kristensen's new phylum has been formally presented and well received at two international conferences in the past 2 months, and will be officially described in the next issue of *Zeitschrift für Zoologische Systematik und Evolutionsforschung*. For Higgins, there is the consolation prize of having the larval form named after him: Higgins-larva. "I'm very pleased of course, even though it is such an ugly creature."—**ROGER LEWIN**

"In certain cases there may be social advantages to a given pattern of dispersal even though this pattern appears on first examination to carry some genetic costs."

daughters, which, presumably, should be avoided. Statistically speaking, this risk would seem to be minimized if transfers are randomly distributed among potential recipient groups. In fact, as has been observed to some extent in other species, transfer among vervet groups in the Cheney-Seyfarth study is anything but random. Repeated transfer between groups is much more likely than not. Moreover, brothers often transfer together to the same group, as do age-mates, who, given the breeding pattern among vervets, are likely to be paternal half-brothers.

Because social standing and reproductive success for male vervets, as for many large primates, is a matter of effective fighting skill and a keen talent for forming alliances, there are obvious advantages in transferring to a group in company with a brother or to a group to which an older brother has already moved. A lone male, particularly one who has just reached sexual maturity but has not yet attained full adult body size, is often the object of aggression from males and females alike as he tries to enter a foreign group. An alliance of two individuals has often been observed to be more successful than single animals in many different circumstances.

The social advantages of nonrandom transfer and transfer with a brother or an age-mate therefore weigh effectively against the potential risk of reduced genetic diversity and inbreeding depression. This risk, as Cheney and Seyfarth discovered, may actually be rather less than has been supposed, and in some circumstances unexpectedly nonexistent. The UCLA workers calculated the probability of mating with close kin among males who transfer twice during their lifetime, following either random transfer, or nonrandom transfer.

Although randomly transferring males maximize the effective population size and therefore minimize inbreeding depression, there of course remains a finite risk of mating with close kin. By contrast, nonrandom transfer minimizes the size of the breeding population and maximizes the danger of inbreeding depression. But, counterintuitively, brothers who transfer together can effectively avoid mating with close kin, especially if they retransfer when brothers' daughters reach sexual maturity. "Brothers not only can form alliances in their new group, but they also have a means of keeping track of close kin that should be avoided as mating partners."

Mature males who have been in a new group for 5 years or so may once again move on. By moving they would avoid the danger of mating with their own or their brother's offspring and they would likely bolster a sagging dominance ranking. As full-size adult males they would be less vulnerable to the dangers of predation, to the physical assault of a hostile reception at a new group, and in any case would be more socially adept at gaining acceptance by strangers. In other words, in their second transfer males need not be so constrained by distance or by the need for alliances, either during transfer to, or assimilation into, a new group. The retransferring male can therefore adopt a random mode of group transfer and still maintain a low risk of mating with close kin. These older males, by transferring randomly and further afield, provide a steady supply of migrants, and therefore new genes, across the clusters of neighboring groups.

The age profile of transfer strategies is, note Cheney and Seyfarth, both striking and significant. The exchange of young males in company with brothers or age-mates between groups brings great social advantages to the migrants while the potential dangers of inbreeding depression are minimized. The more random transfer of single, older males means that "a population in which groups exchange males at high rates always receive at least some migrants from different groups."

One consequence of these observations, says Seyfarth, is that "population geneticists should be aware of the kinds of behavioral costs and benefits that apply in long lived mammalian populations." These costs and benefits might either counteract or reinforce the genetic costs that have been identified in population studies. "When we look at population genetics models we have to take into account factors other than those that are traditionally expressed in the equations."

Ethologists typically study single social groups rather than a set of neighboring groups, usually for sound practical reasons. No one doubts the existence and importance of interactions between contiguous groups, but few opportunities as manageable as the Amboseli study are available in which to observe them in some detail. Cheney and Seyfarth were not only able to demonstrate that individual animals have a keen and broad appreciation of kinship structures within a group, but also revealed an ability of individuals in one group to recognize individuals in another group, even though the animals might have interacted only at a distance. "[This] provides us with a glimpse of social structure from the monkey's point of view."

Because they occupy contiguous and to some degree overlapping ranges, neighboring groups often interact with each other at their boundaries, usually with determined displays of aggression. It transpires, however, that groups that frequently exchange males experience less aggression and more friendly encounters than do groups between which there is little or no exchange. The consequences of repeated, nonrandom transfer between groups clearly extend beyond the immediate social benefits enjoyed by the individuals directly involved, and one is reminded of Claude Levi-Strauss' suggestion of decreased aggression and increased alliances between human groups through the regular exchange of individuals, usually through marriage.

The vervet work at Amboseli begins to reveal, notes Cheney, "a more complex picture of social organization than is usually seen by observing just one study group." There is, as the UCLA workers point out, "a community of groups, within which individuals recognize each other and share a high degree of genetic relatedness despite the maintenance of otherwise discrete social units."

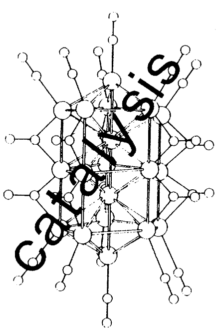
Social dynamics within and between groups are exceedingly complex, involving subtly shifting alliances and dominance hierarchies around kinship lines. The intellectual exigencies of coping with so complex a puzzle might explain why many nonhuman primates are able to play the demanding classification games that behavioral scientists love to challenge them with, suggest Cheney and Seyfarth. "It may well be that this ability derives from the selection pressure acting upon individuals to make complex hierarchical classifications of what is perhaps the most important feature of their environment—each other."—ROGER LEWIN

Additional Readings

1. *Am. Zool.* **22**, 519 (1982).
2. *Am. Nat.* **122**, 392 (1983).

Fuels from Solar Energy: How Soon?

Texas Instruments has the jump on a commercial photoelectrochemical system, but other systems under study could eventually be cheaper



"Now that good photoanodes and good photocathodes have been developed,"* says Mark S. Wrighton of the Massachusetts Institute of Technology, "the big problem is this: Are there in existence systems that would be durable and efficient and that can also be constructed on a large scale, in terms of area, and on a cost-competitive basis?" For now, the answer to that question is still no, he adds, but "people are making steps in that direction." In most cases, they are doing this with a unified system that contains both a photoanode and a photocathode. They are also attempting to carry out the photoconversions with materials that are much less expensive than those that have been used for research.

The impetus for this approach lies in the simple fact that most applications of photoelectrochemical cells will require voltages of at least 2 electron volts (eV). The optimum band gap for a semiconductor powered by sunlight, in contrast, is 1.3 eV. Says Wrighton: "Why not use two photoelectrodes whose combined potentials are great enough to carry out the desired reaction?" This is exactly what plants do; they have two photosystems of slightly different energies to develop sufficient potentials to split water. The process is inefficient, however, since plants use only about 1 percent of incident light. This low efficiency can be tolerated because the system is self-replicating.

*For a discussion of photoanodes and photocathodes, see *Science*, 30 September, p. 1358. Other articles in this series have appeared in the issues of 4 February, p. 474; 25 February, p. 944; 25 March, p. 1413; 6 May, p. 592; 3 June, p. 1032; 17 June, p. 1261; and 22 July, p. 351.

There is some debate, however, about whether a solar cell should be used to split water. Investigators such as John O'M. Bockris of Texas A&M University argue that oxygen is an important chemical to produce because its cost determines the cost of many environmental controls. He also argues that a new generation of aircraft could use liquid hydrogen and oxygen as fuels.

In contrast, Adam Heller of Bell Laboratories argues that "Oxygen is cheap and abundant, and making it together with hydrogen wastes effort and money." A much better course, he argues, is to split a halogen acid. The half-reaction that converts halide ions into halogens at a photoanode requires less voltage than the oxidation of water to oxygen; it is also easier to accomplish because it is a one-electron process, whereas oxidation of water requires two electrons. Furthermore, the recombination of hydrogen and oxygen in a fuel cell to produce electricity is inefficient because of inherent problems at the oxygen electrode, whereas recombination of hydrogen and a halogen proceeds efficiently.

> "Why not use two electrodes whose combined potentials are great enough to carry out the desired reaction?"

The most straightforward way to employ two electrodes is to put individual photoanodes and photocathodes into each cell. This is how the Texas Instruments Solar Energy System (TISES) is constructed. TISES, conceived by Jack S. Kilby, who is now a consultant to TI, has more or less conventional photoelectrodes that have been reconfigured so that manufacture can be almost completely automated. "There are parallels for our semiconductor technology in research labs," says project leader E. L. "Pete" Johnson, but the way TI puts the cells together is "pretty damn unique." The company has been working on TISES since 1976 and, with the U.S. Department of Energy, has invested more than $20 million in its development. It is the only reported commercial program.

The system uses spherical silicon particles that average 10 to 16 mils (0.25 to 0.4 millimeters) in diameter. During most of the studies, the spheres were formed by dripping molten silicon from a capillary tube, allowing the silicon to cool while dropping through an inert gas atmosphere; this is the same process that is used to make lead shot in a shot tower. The process was not fast enough for full production, however, and TI now drops molten silicon onto a rapidly rotating disk which throws off small droplets that, again, cool in free fall.

These spheres are polycrystalline but are converted into mostly single crystals by annealing. In this process, the spheres are heated just to their melting point, then allowed to cool slowly. Surface tension draws the beads into spheres and the slow cooling allows single crystals to form. The spheres are then doped with boron to form *n*-type semiconductors or with phosphorus to form *p*-type. The surfaces of the spheres are then heavily doped with the opposite element to form n^+-p anodes and p^+-n cathodes. Each type of electrode is then embedded in a thin sheet of glass that acts as a support.

One side of the glass and the semiconductor junction is etched away and replaced with a reflective coating and insulator; it is then coated with a thin layer of metal that acts as an electrical contact.