Letter from the Desk of David Challinor September 1992

Breeding strategies among animals probably evolved to ensure the maximum surviving population of offspring and the perpetuation of the species. Most species follow one strategy to secure their survival. Humans are unusual because they follow three different ones: legal polygamy (one husband, more than one wife), monogamy (one husband, one wife at one time), and polyandry (one wife, more than one husband). Each strategy has its costs and benefits about which you can speculate. This letter, however, is about the breeding strategies of birds, which parallel those of humans, but which $I$ can discuss without moralistic constraints.

Polygamy is common in other mammals such as horses, seals, gorillas, etc. as it is in humans. This strategy is not often associated with birds, although you may recall my description of the cost to polygamous males among the ratites (ostriches, rheas, etc.) in my letter of November 1991. Ratite males brood and care for the precocial chicks, whereas ratite females appear to be relegated primarily to egg-laying.

In the New World tropics, male Montezuma oropendulas (a crowsized relative of the oriole) have the best of all worlds. Oropendula females are colonial nesters. Sometimes more than 100 of them will weave their four-foot-long nests from the branches of a single large tree. The male supervises his harem from the top of the tree, which is festooned with the nests of his wives. Like sea lions and some other mammalian harem masters, he is much larger than the females. He ensures his access to the harem by driving away invading males. Fortunately for him, as reported by Michael Webster of the University of Chicago, ovulation in the harem females is synchronized for some unknown reason within groups nesting on the same branch. This allows the male to concentrate his energy on a compact group in short periods of time, and thus he does not have to dash about the entire tree trying to disperse invading males. The female oropendulas have competed with each other for nesting sites and thus increase their odds that their progeny will be sired by a big, strong male. An offsetting disadvantage, however, is that the genetic variation in the young of the colony will be limited on the male side.

In contrast to the oropendula breeding strategy is the polyandrous approach of the female jacana, a quail-sized bird with long legs and very long toes, which allow it to walk on lily pads. Both jacanas and oropendulas are common around Barro Colorado Island in Panama. The hen jacana weighs $60 \%$ more than the cock and maintains a harem of three to five males. Stephen Emlen of Cornell reported that only the male develops a brood patch (a featherless portion of the lower breast which allows the brooder's bare skin to be in direct contact with the eggs) and that the female never tends to the nest. Instead the female is very aggressive, and when moving into a new territory, often kills the young of other females so that she will not have to wait for the local males to finish raising another female's young. Emlen theorizes that this strategy is advantageous to the female because she lays only four eggs, and since most jacana colonies are located in lily pad-covered, shallow lake shores, on average half of all egg clutches are lost to predators. Her incentive, therefore, is to devote her energy to egg production rather than to brooding and caring for the young. Genetic diversity is achieved by having more than one mate.

Recent studies of purportedly monogamous birds have uncovered some unexpected behaviors. "Monogamous" birds include geese, cranes, most raptors (eagles, hawks, owls), and robins. As recently as 1968 a survey of birds claimed that over $90 \%$ of bird species were monogamous. New evidence has drastically altered that impression.

In the 4 July 1992 New Scientist, Birkhead and Moller concluded that "adulterous" females in socially monogamous bird species gave a better gene mix to their progeny than those females that bred only with the bonded male of the pair. Their research capitalized on the discovery in the mid-1980's that each human has her/his own set of DNA particles which can be used as "fingerprints" to identify individuals. By applying this technique to birds, researchers could determine the parentage of individual young in a single clutch. Birds are relatively easy to identify in this way because their red blood cells have nuclei, which mammal red blood cells lack; thus only very small drops of blood are needed to determine parentage. By this technique bird researchers looked at the Australian fairy wren, which breeds in communal groups comprised of male/female pairs and several male helpers who cooperate in raising the pair's young. A DNA fingerprint study showed that $65 \%$ of the young in a given clutch were progeny of males outside the communal group. polyandry turns out to be common in such breeding pairs as indigo buntings, where almost half of all broods tested had DNA from roving males.

As more and more bird species are studied, however, some puzzling discrepancies arise. For example, in some species, such as the colonial nesting fulmars (a northern seabird), although copulations outside the pair bond occur, they produce no fertile eggs for reasons which we do not yet understand.

We can only speculate on the reasons for the evolution of some breeding strategies. One underlying important assumption is that the females do not pick their mates at random, but rather make a positive choice. Evidence is accumulating that females are always looking for the "best" male, but as humans we cannot judge what is "best" for females of different bird species. The other strategy is that males compete for female birds and there is no female choice in most cases.

When studying the behavior of purple martins, for example, my colleague Gene Morton at the Zoo found that a mature male will normally monopolize access to a martin house and pair with one female. Once this female is bred and brooding, the senior male then encourages other males to occupy vacant boxes in the martin house. The newly arrived males in turn attract females with which to pair. Surprisingly, the new females also copulate with the senior male which, tests show, sires about $70 \%$ of the colony's offspring without having to bother with the chores of helping raise his many offspring. In this case, it seems that the females are actively choosing a "superior" male to father some of their offspring.

The process of mate selection and breeding strategies is complicated, not only in birds but in all sexually reproducing animals. However, with new discoveries such as DNA analysis to determine parentage and close observation of behavior, we can improve our knowledge. It is unlikely that we will ever find all the answers, because each answer found will trigger innumerable new questions. I may have used the following quotation before, but I believe it is appropos here. It was written by my great friend D.R. Stoddart in his fine collection of essays titled on Geography: "Knowledge is an island in a sea of ignorance, for the more the island expands, the longer its shoreline will be with the unknown."

