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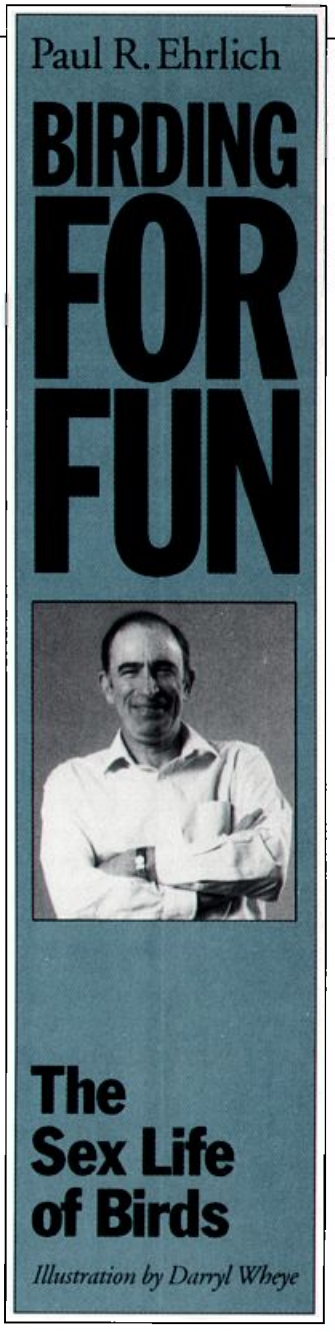

ONE OF THE GREAT attractions of watching birds is that you don't need a TV to enjoy sex and violence at home. All you need is a pair of binoculars and some patience. Avian violence has already found its way into this column in the form of predatory Scrub Jays; now it's time to turn to sex.

Biologists consider the basic mating system in mammals to be polygynous — one in which a single male mates with several females. The male makes relatively little "investment" in each mating: a few minutes or hours of courtship and a small amount of fluid containing the sperm. In contrast, the female is stuck first with bearing and then with nursing the offspring. Small wonder that most female mammals seem to be more choosy than males in selecting their mates. An evolutionary "mistake"— choosing an inferior partner—would result in the loss of a much greater portion of a female's lifetime production of high-quality offspring than would a similar error on the part of a male. Since evolution favors having as many descendents as possible, and males can father numerous offspring with little effort, male mammals tend to be more promiscuous than females.

The same reasoning ought to apply to birds, since the male makes a tiny physical contribution to the relatively gigantic egg produced by the female. Nonetheless, something like 90 percent of bird species are monogamous; that is, a male and a female stay together for at least an entire breeding season, and in some cases for life. Why? The basic answer appears to be that, for most birds, the care of two parents gives the chicks a better chance of growing up. Males that don't help take care of the kids may not leave any descendents at all. Help in feeding may be critical; female birds cannot nurse their young.

While the vast majority of bird species are monogamous, some are polygynous, and a few are promiscuous, forming no pair-bonds at all. A few others are polyandrous, with one female bonding with more than one male. Among the latter, typified by phalaropes, the usual color schemes are reversed, and it is the females that have the bright nuptial plumage. All of these mating systems are interesting and deserving of exploration, but in this column I want to focus on monogamy, for it has recently been shown that avian monogamy is not quite what it was once thought.

The degree to which monogamous males participate in raising their young varies enormously among bird species. In many ground-nesting birds such as shorebirds, gulls, and geese, males are full partners and even put their lives in jeopardy when predators threaten their offspring. Most songbird males bring food to

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their young or to the nesting female. In a few monogamous species, however, the father's contribution is minimal. Male Willow Ptarmigans help the female only by serving as lookouts against danger. And male Eastern Bluebirds only supply a place to raise the young by defending a territory containing a suitable hole in which to nest. When male bluebirds were experimentally removed after the nest had been established, it made no difference to the survival of their offspring.

It turns out, though, that the formation of a monogamous pair bond in birds does not necessarily mean that all sexual activity takes place within the social pair. New techniques of genetic analysis have shown, for example, that clutches of supposedly monogamous species such as Mallards, Indigo Buntings, and White-crowned Sparrows contain offspring of more than one male, more than one female, or both. This may be the result of females laying their eggs in the nests of others — in essence "stealing" parental investment from the unknowing foster parents. Or it may be the result of infidelity. Indeed, extra-pair copulations commonly occur in many monogamous bird species.

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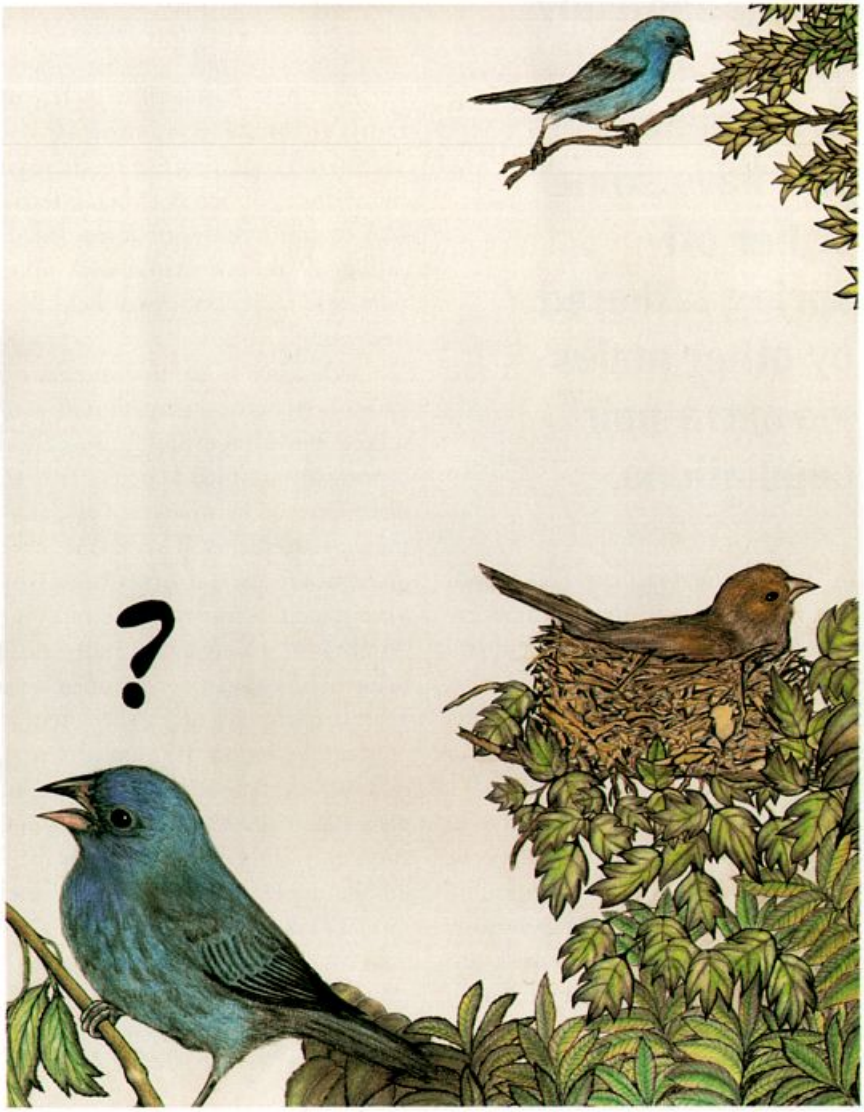

One of the fascinating questions of avian behavior is why infidelity has evolved. A recent article by David Westneat, Paul Sherman, and Martin Morton provides a review of what is now know about avian cheating (*Current Ornithology* 8:331-369). The immediate reasons for cheating may differ for males and females, but the basic answer is presumably the same for both. It evolved when unfaithful individuals had, on average, more offspring reproducing in the next generation than faithful mates. For example, in situations where a female can successfully raise the young with little or no help from her mate, the male has everything to gain from sneaking around trying to copulate with others. If he is successful in fertilizing the eggs of other females, his contributions to the next generation will increase. If he is not successful, he will, in most cases, have lost little.

Thus extra-pair copulations should be more common in species where the male's contribution to the rearing of offspring is minor than where his help is essential. For example, where there is more joint defense of the young (as in the Killdeer and raptors), one would expect there would be more faithfulness.

That this explanation is correct is suggested by the patterns of parental care in most of our passerines: males do relatively little nest-building or incubating; when they do lend the female a hand, it tends to be later, caring for nestlings or fledglings. A male's investment in early care would require time and exposure to predators, add little to the chances of his offspring surviving, and carry a high risk of being wasted because of the prevalence of nest predation.

At the same time, frequent destruction of nests means that large numbers of fertilizable females are available for extra-pair copulations. During the early stages of nesting, a male can do better by trying to copulate with other females than he can by helping his mate. Later, however, the benefits of cheating may be overbalanced by the costs of not putting enough care into the maturing offspring, which with each passing day have a higher probability of representing the male in the next generation.

According to this explanation, one would expect the frequency of cheating to taper off more swiftly in colonial birds with synchronous breeding (every nest's eggs hatching at about the same time) than in noncolonial species. In both synchronous and asynchronous breeders, the pay-off to the male in caring for his young would generally increase until the young are virtually able to fend for themselves. But among the synchronous breeders, the availability of females for extra-pair copulations would decline more rapidly.

Males often face a complex calculus on whether or not to cheat. Time a male spends sneaking around is time not spent guarding his own mate or territory, or caring for his mate's young. One factor determining male strategies is doubtless the degree of environmental heterogeneity — that is, how much difference there is between territories. If there is much heterogeneity, a male with a top-notch territory might do best to concentrate on attracting additional mates to nest within it — that is, to form additional polygynous pair bonds. One with a less desirable territory might father more offspring by sneaking as many extra-pair copulations as possible. A male stuck with a poor territory could perhaps do best by helping his mate raise the young.

If there is little environmental heterogeneity, however, then the strategy of attempting to attract more mates is less likely to be successful, and the frequency of extra-pair copulations might go up. Unfortunately, there are few data with which to test these notions. About all that *is* known is that there can be great differences in male mating behavior and contributions to parental care from population to population of the same species. Male Red-winged Blackbirds in some colonies tend to have many mates and not help with the young; in others, they are less polygynous and more helpful. These differences may be tied to how much the qualities of territories vary in each site, but unfortunately, information on that and the frequency of extra-pair copulations is not yet available.

If a familiar territory is held by a genetically inferior male, the female can still have some of her offspring fathered by other males *via* extra-pair copulations.

Choices among male strategies would probably be influenced by the need the male perceives for guarding his own mate from intruders seeking extra-pair copulations. Male Dunnocks, small sparrow-like European relatives of pipits, go to unusual lengths to prevent the consequences of extra-pair copulations. Monogamous male Dunnocks follow their mates closely to ward off other males. They also go through an elaborate display before copulation that includes pecking at the cloaca of the female. The female, which voluntarily exposes the cloaca, ejects sperm from a previous mating before the male copulates with her. The cloaca-pecking display is most intense in situations where extra-pair copulations are most probable.

Why would females seek or accept extra-pair copulations? There are several possible reasons, but one of the most likely is that it allows choice of territory and choice of mate to be at least partially independent. The female can nest in a familiar territory where she has previously successfully reared young. If that territory is held by a genetically inferior male, she can still have some of her offspring fathered by other males *via* extra-pair copulations. A female Dunnock may cooperate in the sperm removal process to increase the chances of her eggs being fertilized by more than one male. In addition, if she has mated with more than one male, both may help feed her young.

Further investigation is needed to show how widespread clutches of mixed parentage are in so-called monogamous bird species, and to discover exactly what factors determine avian fidelity. This is one more place where careful observations by birders could contribute important insights — as long as the individuals being observed can be identified with certainty by banding or natural plumage variation. It is already clear, however, that the romantic picture of pairs of birds always faithful to one another, raising only their own little broods, is as far from the mark as a similar view of human families. ■

–Paul Ehrlich is Bing Professor of Population Studies at Stanford University, co-author of The Population Explosion *and co-author of* The Birder's Handbook