Bird Mating Systems

http://www.paulnoll.com/Oregon/Birds/courtship-systems.html

Some Monogamous Birds

In a monogamous Species, the male and female remain together for the purpose of raising a brood of young

1. Bittern, American
2. Blue Warbler, Black-throated
3. Cardinal, Northern
4. Chickadee, Carolina
5. Crow, American
6. Eagle, Bald
7. Falcon, Peregrine
8. Flicker, Northern
9. Golden-Plover, Lesser
10. Grebe, Pied-billed
11. Gull, Herring
12. Hawk, Red-tailed
13. Heron, Great Blue
14. Jay, Blue
15. Junco, Dark-eyed
16. Kestrel, American
17. Killdeer
18. Loon, Common
19. Nuthatch, White,breasted
20. Redstart, American
21. Sparrow, Fox
22. Sparrow, White-throated
23. Swan, Mute
24. Swan, Trumpeter
25. Swift, Chimney
26. Tanager, Scarlet
27. Thrush, Wood
28. Titmouse, Tufted
29. Towhee, Brown
30. Woodpecker, Downy

Some Polygynous Birds

Polygamy occurs when a male mates with several females.

1. Blackbird, Red-winged
2. Bobolink
3. Bunting, Indigo
4. Dickcissel
5. Grackle, Great-tailed
6. Harrier, Northern
7. Meadowlark, Eastern
8. Ptarmigan, Willow
9. Sandpiper, White-rumped
10. Sparrow, Savannah
11. Warbler, Yellow
12. Wren, House
13. Wren, Marsh
14. Wren, Winter
15. Yellowthroat, Common

Some Polyandrous Birds
Polyandry occurs when a female mates with several males.

1. **Phalarope, Red**
2. **Phalarope, Wilson's**
3. **Sanderling**
4. **Sandpiper, Spotted**

Some Promiscuous Birds
This term describes a rather chaotic social structure in which a female may mate with many males or male with many females. All of North American Hummingbirds are promiscuous breeders.

1. **Grouse, Sage**
2. **Hummingbird, Anna's**
3. **Hummingbird, Wilson's**
4. **Prairie-Chicken, Greater**
5. **Sandpisper, Pectoral**
6. **Sandpiper, Spotted**

Monogamy

An estimated 90 percent of all bird species are monogamous. Monogamy is defined as one male mating with one female and forming a "pair bond." That bond may last for a single nesting (House Wrens), an entire breeding season (most bird species, including most passerines), several successive breeding seasons (observed in some pairs of American Robins, Tree Swallows, Mourning Doves, etc.), or life (albatrosses, petrels, swans, geese, eagles, and some owls and parrots).

Presumably monogamy evolved in situations where young have a much better chance of surviving if both parents cooperate in rearing them. Nonetheless, the amount of time and energy invested by monogamous male parents varies greatly. The Willow Ptarmigan male serves only as a sentinel watching for danger. The Eastern Bluebird male provides a site for the rearing of young (by defending a territory containing a nest cavity), but experimental removal of males has shown that they are not essential for successful brood-rearing. In some monogamous species, the male defends a territory in which his mate collects the food required by the offspring, but does not himself feed the nestlings. Levels of male parental investment are even higher in most passerines, where males feed brooding females and/or help to feed the young. In herons, egrets, some woodpeckers, and others, males not only provide food for the young but share in incubation as well. The ante is raised even further in such ground-nesting birds as geese, swans, gulls, terns,

and shorebirds in which males also commonly place themselves in danger by vigorously defending the nest and young from predators.

The traditional view of why more or less permanent monogamous bonds are formed is changing, as interest has become focused on the parentage of offspring reared by "monogamous" pairs. Increasingly, ornithologists and behavioral ecologists have come to view monogamy as part of a "mixed" reproductive strategy in which matings may occur outside the primary pair bond, but both members of the pair still contribute substantially only to the care and feeding of the young from their own nest. Some species are viewed as facultatively monogamous; that is, if released from certain environmental constraints, they would typically exhibit some other form of mating system such as polygyny (one male mating with more than one female) or promiscuity (mating without forming pair bonds). According to this view, for example, North American dabbling ducks are monogamous only because males are unable to monopolize more than one female. These ducks breed synchronously and their populations typically contain more males than females.

Two lines of evidence have contributed to the shift in viewpoint about the nature of monogamy. First, ecologist Yoram Yom-Tov showed intraspecific nest parasitism ("egg dumping" by females in nests other than their own) to be much more frequent than previously assumed. Consequently, females of birds as different as Common Goldeneyes, Cliff Swallows, and Savannah Sparrows may often incubate clutches containing one or more eggs laid by another female that may or may not have been sired by her mate. The parasitic female may be monogamous, but she is "stealing" parental investment from another pair. Therefore, the situation is not one in which mated pairs rear only their own offspring, as traditional use of the term monogamy has implied.

Second, a few recent studies employing new techniques of genetic analysis have allowed investigators to determine whether one or both members of a pair are the parents of all of the nestlings or fledglings they are rearing. Investigations of cooperatively breeding Acorn Woodpeckers and "monogamous" Eastern Bluebirds demonstrate conclusively that clutches with mixed parentage (containing offspring of more than one female, more than one male, or both) are not infrequent, indicating some infidelity by either or both sexes and/or egg dumping by females. Because so few species have been investigated using this technique, the results of future analyses may lead to a further reevaluation of the evolutionary significance of monogamy. At the moment it is perhaps best simply to consider monogamy as a social pattern in which one male and one female associate during the breeding season, and not to make too many assumptions about fidelity or parentage.

Polygyny

Polygyny, where one male mates with more than one female while each female mates with only one male, is thought to be the fundamental mating system of animals. The reason is straightforward. By definition, the sex that produces the larger reproductive cells (eggs) is the female, and the one that produces the smaller (sperm) is the male. Males therefore make a smaller investment in the embryos that result from the fusion of egg and sperm cells. The difference is especially pronounced in birds, since the sperm is microscopic and the egg (relatively) gigantic. The male thus puts proportionately little effort into any single embryo, while the female has a great stake in each one, since she can produce relatively few eggs in her lifetime. Females must therefore exercise care in choosing the fathers of their limited number of young. It would seem, in contrast, that male birds should be much less choosy and attempt to have as many mates as possible, since evolution favors behavior that leads to leaving a maximum number of offspring. A male that mates with a weak or otherwise unfit female loses a small part of his reproductive potential; a female making a similar mistake may sacrifice all or almost all of hers.

Most birds, however, are monogamous. Apparently, both parents must help to rear the young if the adults are to have much chance of leaving any genes to posterity. Under what circumstances, then, can polygyny occur? One idea is that polygyny is likely when males hold territories that vary greatly in the quality of resources. Females will tend to choose superior males -- by inference those that have high-quality territories. When those males already have mates, females have a choice. They can either select a male that holds an inferior territory, or they can become the second mate of one of the superior males. If the difference between high- and low-quality territories is great enough, the latter strategy will be better -- little or no aid from a male holding a resource-rich territory will yield a better chance of producing surviving offspring than the full cooperation of a male with an inferior territory. The male with a superior territory will benefit by increased reproduction, as will the second female.

Often that is precisely what is found. For example, female Marsh Wrens near Seattle, Washington, sometimes mate with already-mated males, even when bachelor males are available. The number of females mated to each male is related to the amount of emergent vegetation in the males' territories, which, in turn, is presumably an indicator of the availability of insect food. Studies of Red-winged and Yellow-headed Blackbirds, Dickcissels, Indigo Buntings, and Lark Buntings also show clear relationships between various aspects of territory quality and the likelihood that a male holding a given territory will have more than one mate.

Polygyny is not always associated with territoriality. Certain seed-eating savanna species of African weavers (relatives of House Sparrows) have superabundant resources, and the males are not territorial, presumably because defending an area does not increase their access to food. The females apparently do not need help from males to raise the young, and the weavers nest in colonies, minimizing the need for a partner in nest defense. The female is thus free to choose any male to father her offspring, regardless of his other attachments. Here, as in situations where males are territorial, polygyny is related to the availability of resources -- in this case their superabundance rather than their uneven distribution.

Polyandry

The mating of one female with more than one male while each male mates with only one female is known as polyandry (literally, "many males"). It is a rare mating system, occurring in less than one percent of all bird species, and is found mostly in shorebirds. Polyandry is often accompanied by a reversal of sexual roles in which males perform all or most parental duties and females compete for mates. The common pattern of sexual dimorphism is often reversed in polyandrous birds: the female is often larger and more colorful than the male. This reversal confused early biologists and led Audubon to mislabel males and females in all of his phalarope plates.

Two types of polyandry have been documented: simultaneous polyandry and sequential polyandry. In simultaneous polyandry, each female holds a large territory containing the smaller nesting territories of two or more males who care for the eggs and tend the young. In our region, only Northern jacanas characteristically practice this form of polyandry. Females may mate with all of their consorts in one day and provide each male with help in defending his territory. A female will not copulate with a mate while their eggs are being incubated or during the first six weeks of the fife of the chicks. If a clutch is lost, she will quickly copulate with the broodless male and lay a new batch of eggs within a few days.

A very rare variation on the preceding theme is "cooperative simultaneous polyandry," in which more than one male mates with a single female and the single clutch of mixed parentage is reared cooperatively by the female and her several mates. This arrangement occurs in some populations of Harris' Hawks and occasionally in Acorn Woodpecker groups.

In sequential polyandry (the most typical form of this mating system), a female mates with a male, lays eggs, and then terminates the relationship with that male, leaving him to incubate the eggs while she goes off to repeat this sequence with another male. Spotted Sandpipers, Red-necked and Red Phalaropes are examples of sequentially polyandrous species that breed in North America. A possible evolutionary precursor of sequential polyandry is found in Temminck's Stint, Little Stint, Mountain Plover, and Sanderling. In these species, each female lays a clutch of eggs that is incubated by the male, followed by a second clutch that she incubates herself. These two-clutch systems can be envisioned as a step toward the sort of sequential polyandry seen in the Spotted Sandpiper, but females of that species never incubate a clutch alone unless their mate is killed -- even when resources are abundant.

There is an interesting sidelight to the story of polyandry in birds. In polygynous mammals (one male mating with several females) such as lions and gorillas, infanticide can occur when a new male takes over a harem. By killing the young of the previous harem ruler, the new male presumably brings females back into heat. This gives him a chance to increase his own reproductive contributions and, perhaps, to reduce use of resources by unrelated offspring. In Northern jacanas it has been reported that females taking over the territories of other females occasionally practice infanticide, destroying the offspring of previous females. The males attempt to defend their broods (which represent their genes, but not those of the new female), just as lionesses attempt to defend their cubs from infanticidal male lions taking over a pride. However, the actual killing of young has not been observed -- only empty nests. If substantiated, this behavior in

jacanas is the first known example of infanticide being used as a reproductive strategy by females.

Promiscuity

Some species of birds do not form pair bonds; but instead consort only briefly -- for minutes or hours. The male's investment in offspring is limited to sperm, and the female raises the young alone. Male hummingbirds, for instance, court females for a short time, mate, and then resume their quest for other females. Males of many grouse species and some shorebirds display on leks (mating grounds used each year) to attract females that depart immediately after mating. The males may subsequently mate with additional females. Such mating systems, in which no pair bond is formed, are termed promiscuous. Presumably promiscuous mating systems can evolve only where the advantage of the male remaining with the female to help in raising the young is negligible.

Brood Parasitism

Some species of birds thrive not by carefully rearing their own young, but by pawning that task off on adults of other species. The European Cuckoo, whose distinctive call is immortalized in the sound of the "cuckoo clock," is the bird in which this habit has been most thoroughly studied. Female European Cuckoos lay their eggs only in the nests of other species of birds. A cuckoo egg usually closely mimics the eggs of the host (one of whose eggs is often removed by the cuckoo). The host may recognize the intruding egg and abandon the nest, or it may incubate and hatch the cuckoo egg. Shortly after hatching, the young European Cuckoo, using a scoop-like depression on its back, instinctively shoves over the edge of the nest any solid object that it contacts. With the disappearance of their eggs and rightful young, the foster parents are free to devote all of their care to the young cuckoo. Frequently this is an awesome task, since the cuckoo chick often grows much larger than the host adults long before it can care for itself. One of the tragicomic scenes in nature is a pair of small foster parents working like Sisyphus to keep up with the voracious appetite of an outsized young cuckoo.
Interestingly, different females within a population of European Cuckoos often parasitize different host species. Some cuckoos may specialize in parasitizing the nests of Garden Warblers; others of the same population may lay in the nests of Reed Warblers, and yet others may lay in nests of White Wagtails. The eggs of each female very closely mimic those of the host selected (even though one host may have large, densely spotted eggs, and another may have smaller, unmarked pale blue eggs), and the mimetic patterns are genetically determined. The different genetic kinds of females (called "gentes") apparently mate at random with males. How these gentes are maintained within the cuckoo populations is not fully understood.
The North American Yellow-billed and Black-billed Cuckoos only rarely lay their eggs in the nests of other species, but occasionally lay some of their eggs in the nests of other members of their species. Our cuckoos usually build nests of their own and rear their own young. Only about 40 percent of cuckoo species worldwide are brood parasites, the rest care for their own eggs and young.

Brood parasitism is much less common in other groups of birds. It is found in about 1 percent of bird species, including members of such diverse groups as ducks, weavers, and cowbirds. In North America the only obligate brood parasites (those which must parasitize and cannot build nests of their own) are the Bronzed and Brown-headed Cowbirds, which may be important enemies of other birds. The Brown-headed Cowbird has been recorded as a parasite of more than 200 other species. Cowbird eggs do not closely mimic host eggs, nor do the young oust host eggs and young from the nest. But cowbirds do tend to hatch earlier than their hosts, to grow faster, and to crowd out or at least to reduce the food intake of the host's young.

Cowbirds thus can place powerful selection pressure on a host bird species to learn to recognize and reject cowbird eggs. Behaviorist Stephen Rothstein of the University of California at Santa Barbara has shown experimentally that some North American species have, indeed, learned to do this. He placed artificial and real Brown-headed Cowbird eggs in the nests of 43 other species and found that those species divided rather neatly into acceptor species and "rejector species." Acceptors include many warblers, vireos, phoebes, and Song Sparrows, while robins, catbirds, Blue Jays, and Brown Thrashers are rejectors. The Song Sparrow just happens to have eggs very similar in size and spotting pattern to those of the cowbird, and almost invariably raises the cowbird young. In contrast, catbirds and robins, which lay unmarked blue eggs, almost invariably eject cowbird eggs from their nests. Phoebes, strangely, usually have unmarked eggs but are acceptors -- perhaps their habit of nesting in dark recesses has reduced their awareness of egg pattern.

Rothstein found very little sign of transitional species -- that is, ones with some individuals that accepted and others that rejected. The reason, he hypothesized, was that once the genetic ability to reject appeared in a species, it would spread very rapidly and very soon all individuals would be rejectors. That notion is certainly supported by rates of parasitism observed in acceptor species. In various studies, for example, 40 to 70 percent of the nests of Red-eyed Vireos were parasitized, about 20 percent of Eastern Phoebe nests were parasitized, and about 40 percent of Song Sparrow nests were parasitized. Reduction in the fledging rate of parasitized nests was well over 50 percent in the vireos and phoebes, and about 40 percent in the Song Sparrows.

A central mystery remains, however. Acceptors and rejectors do not represent different taxonomic groups, they do not have different lengths of association with cowbirds, most have eggs that can be easily distinguished from cowbird eggs, and they are capable of ejecting cowbird eggs from their nests. Why then have some species evolved the ability to reject, and others not. Rothstein suggests that nest concealment, large bill (to make ejection easier), and chance may play key roles. More careful observation and experiment will be needed before we will know if he is right.

Brood parasitism is not restricted to females of one species laying eggs in the nests of other species. In addition to some of our North American cuckoos, females of a wide variety of species sometimes lay eggs in the nests of other females of the same species. This behavior is examined in other essays.

Cooperative Breeding

"Cooperative" or "communal" breeding occurs when more than two birds of the same species provide care in rearing the young from one nest. About 3 percent (approximately 300 species) of bird species worldwide are cooperative breeders. There are two types of cooperative arrangements: those in which mature nonbreeders ("helpers-at-the-nest" or "auxiliaries") help protect and rear the young, but are not parents of any of them, and those where there is some degree of shared parentage of offspring. Cooperative breeders may exhibit shared maternity, shared paternity, or both.

The best-studied North American cooperative breeders, the Scrub-Jay, Gray-breasted (Mexican) Jay, Groove-billed Ani, and Acorn Woodpecker, differ from each other in the details of their breeding biology. Scrub jays in Florida represent a group of populations that probably were once in contact with the widespread western populations but are now totally isolated. Only in Florida are Scrub Jays cooperative breeders, and there they reside in permanent, group-defended territories. Ornithologists Glen Woolfenden and John Fitzpatrick have found that groups consist of a permanently bonded monogamous pair and one to six helpers, generally the pair's offspring of previous seasons. About half the territories are occupied by pairs without helpers, and most other pairs have only one or two helpers. Although pairing and breeding can occur after one year spent as a helper, birds often spend several years as nonbreeding auxiliaries. Males may remain in this subsidiary role for up to six years; females generally disperse and pair after one or two years of helping. Helpers participate in all nonsexual activities except nest construction, egg laying, and incubation. Pairs with helpers are more successful -- they fledge one and a half times more young than pairs without helpers.

Florida Scrub-Jays are largely restricted to the scattered and now much reduced oak scrub habitat; reproductive success outside of oak scrub is very poor. All available habitat is occupied, and populations appear to be stable from year to year, which means young birds are unlikely to find vacant space to set up territories of their own. In contrast, Western Scrub-Jays generally are not space-limited, and the probability of a young bird leaving home and finding a territory in which to breed is high.

Like the Florida Scrub-Jay, the closely related Gray-breasted Jay of the southwestern U.S. lives in permanent group-defended territories, and breeding adults are monogamous. Studies by ethologist Jerram Brown and his colleagues have shown that the cooperative system of this species is more complex than that of its southeastern relatives in several ways. Gray-breasted Jay groups are much larger, ranging from 8 to 18 individuals; thus, they usually include offspring from more than just the preceding year. Within each group, two and sometimes three breeding pairs nest separately but simultaneously each season, and some interference among them often occurs. Interference usually involves the theft of nest-lining materials, but can include the tossing of eggs from nests by females of rival nests. Although the laying female does all the incubating, she is fed on the nest both by her mate and by auxiliaries. Nestlings receive more than half of their feedings from auxiliaries.

Although the Groove-billed Ani breeds in southern Texas, our knowledge of its breeding biology comes from the work of sociobiologist Sandra Vehrencamp and her colleagues who studied the species in Costa Rica. The groups defending permanent territories consist of one to four monogamous breeding pairs that occasionally include an unpaired helper. All members of the group participate in building a single nest into which all

females lay their eggs. Incubation and care of the young are shared by all members of the group. Beyond a certain clutch size, some eggs tend to be buried and fail to receive proper incubation, leading to a decreased probability of any given egg hatching.

Unlike the "cooperative" breeders that they appear to be, female anis engage in behaviors that increase the probability of their own eggs being the successful ones in the communal clutch. The most effective of these behaviors is the tossing of other females' eggs from the nest. In spite of the increased competition and conflict, multipair groups manage to fledge more young per individual than do single pairs in similar habitats.

Long-term studies of Acorn Woodpeckers have been conducted by a succession of ornithologists, including M. H. and B. R. MacRoberts, Walter Koenig, Ron Mumme, and Frank Pitelka at the University of California's Hastings Natural History Reservation in central coastal California. There Acorn Woodpecker groups are composed of up to 15 members whose territories are based on the defense and maintenance of granaries in which they store acorns. Groups consist largely of siblings, their cousins, and their parents. Some of the sexually mature birds are nonbreeding helpers. Within each group, up to four males may mate with one (or occasionally two) females, and all eggs are laid in a single nest. Thus, paternity and sometimes maternity of the communal clutch is shared.

Per capita reproductive success generally increases with group size up to 7 or 8 members, and then declines. Clutches produced by two females are somewhat less successful than those of single females due to behavioral interference between the two females and some egg tossing. Although there is some geographic variation in the size of groups and other aspects of the Acorn Woodpecker system, it breeds cooperatively throughout its range.

Why has evolution produced cooperative breeding systems? Initial hypotheses were based on kin selection (seemingly "selfless" behavior like helping at the nest being favored because it increases the reproductive success of relatives genetically similar to the helper) or on maximizing of reproductive output. As more cooperatively breeding species have been examined worldwide, these explanations generally have not been supported. Instead, cooperative systems appear to arise when environmental constraints force birds into breeding groups because the opportunities for younger birds to breed independently are severely limited. Limitations may include a shortage of territory openings because higher quality habitats are saturated with established breeders; a shortage of sexual partners (generally females), indicated by the skewed sex ratios that are common in groups; and unpredictable availability of resources, which could make it too risky for individual pairs to commit themselves to reproduce in any given year. That cooperative breeding is a common strategy in arid and semiarid portions of Africa and Australia lends strong support to this line of reasoning. Cooperative breeding may be viewed primarily as a means by which young adults put off the start of their own breeding in order to maximize their lifetime reproductive output, and in the process occasionally promote genes identical with their own via kin selection.

Potential or Actual Costs and Benefits of Co-operative Breeding

Costs

To Breeder:

1. **More birds in territory eat more food.**
2. **Activity of helpers draws predators' attention.**
3. **Helpers' incompetence may be detrimental.**
4. **Helpers may compete with breeders for the right to breed.**

To Helper:

1. **Rearing parents' offspring demands time, energy and exposure to predators.**

Benefits

To Breeder:

1. **Assistance in rearing young.**
2. **If one parent dies, helpers ensure that some young survive.**
3. **Inter-group competition for territories favors large group size for territorial defense.**
4. **Other advantages of group living, e.g., increased foraging efficiency and detection of predators.**

To Helper:

1. **Experience in rearing young.**
2. **Access to resources (e.g., food) in the group territory.**
3. **Other advantages of group living, e.g., increased foraging efficiency and detection of predators.**