

BREEDING STRATEGIES OF TROPICAL BIRDS

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Contents

1. Introduction
 2. Tropical Birds: Life History and Ecology
 3. Monogamy and Extra-Pair Paternity
 - 3.1. Socially Monogamous Bonds
 - 3.2. Breaking the Bonds: Conflict and Extra-pair Paternity
 4. Polygamous and Promiscuous Mating Systems
 - 4.1. Polyandry
 5. Cooperative Breeding
 - 5.1. Home, sweet home!
 - 5.2. To help or not to help?
 - 5.3. Costs of Cooperative Breeding
 6. Final Considerations
- Acknowledgements
Glossary
Bibliography
Biographical Sketches

Summary

Tropical bird mating systems are extremely diverse and comprise a great variety of social interactions, resulting in a complex relation between what we perceive as the mating system and the actual genetic outcome of such interactions. Monogamy, polygyny, polyandry and polygynandry are classical definitions that take into account the social interactions among individuals but, with the advance of molecular techniques, such terms are being reviewed since the 1990's to also include a genetic perspective. For instance, it is now known that, although 90% of birds are socially monogamous, 86% of all passerine species have been demonstrated to carry out extra-pair copulations as a breeding strategy, with genetic monogamy occurring in only about 14%. This chapter will provide an overview of the current knowledge regarding different aspects that influence the occurrence of a given avian mating system, such as sexual selection, sexual conflict, degree of parental care provided by each sex, ecological features and evolutionary heritage, with tropical species examples provided whenever possible. Special attention is given to the variation in parental care, mate choice and resource access, regarded as major ecological and behavioral factors. Tropical birds are subject to different ecological pressures and thus have particular life history traits such as high

adult survival rates, small clutch size, and high nest predation, which influence the evolution of their mating systems and will be discussed in comparison with temperate zone patterns. Specific topics that concern polygamy (including promiscuous systems) and monogamy are also included. Finally, cooperative breeding systems will be approached, focusing on factors that could have favored the evolution of such breeding systems. Current knowledge about avian breeding systems is temperate-zone biased, and despite the great potential of the tropics to contribute to a broader understanding of this topic, tropical birds remain understudied. This chapter attempts to show the diversity of patterns that is found in the tropics and emphasizes the importance of this source of unexplored knowledge.

1. Introduction

Situated basically between the tropical parallels of Cancer and Capricorn, the tropical ecosystems are characterized by rainforests, savannas and dry deciduous forests, containing the richest diversity of animal life in the planet, including more than two thirds of bird species. Unlike temperate climates, the most prominent feature of the tropics are the generally high temperatures yearlong, with constant high precipitation indexes in the equatorial part, while the outer margins of the tropical zone have a climate of their own, with marked rainfall seasonality. Such ecological differences have profound influences on bird life-histories and, consequently, on their mating systems.

Birds exhibit a diversity of mating systems, which range from stable formation of social pair bonds to cases in which the only social contact between males and females is for fertilization. Interestingly, although polygamy is the rule among animals, only 10% of bird species have non-monogamous mating systems, which are known especially in tropical groups such as many hummingbirds, manakins, cotingas, bowerbirds and birds of paradise. Mating systems are traditionally classified according to the number of mates each adult has per breeding attempt: polygyny (when males pair and reproduce with two or more females); polyandry (when females mate and reproduce with two or more males); promiscuity (when males and females form no pair bonds, associating solely for copulation), and monogamy (when both sexes form exclusive pair bonds persisting through at least one reproductive attempt). Polygyny and polyandry may also co-exist within the same species, resulting in the so-called polygynandrous systems. This happens for instance when males incubate the eggs, but attract several females to lay in their nests, while females also visit multiple males, such as in the mating systems of the American Rhea (*Rhea americana*) and the Great Tinamou (*Tinamus major*). However, rigid classifications must be dealt with carefully, for they can overlook the underlying complexity of mating systems, especially when considering genetic issues. Distinction between the genetic (who are the biological parents of each nestling) and social (what are the bonds and interactions between individuals) aspects of a species' mating system has been made possible due to advances in molecular techniques achieved since the 1980's. For instance, socially monogamous birds may have a similar variance in individual fertilization success compared with a socially polygynous species, due to extra-pair fertilizations.

The question of how a certain mating system evolves to the detriment of others is a major issue in behavioral ecology. Some of the factors that play an important role are:

natural selection (mating behaviors resulting in higher fitness will generally be preserved); sexual conflicts (how the optimum fitness strategies of each gender coexist); sexual selection (how mate choice and intrasexual competition result in differential variation in male and female reproductive success); sex ratio (resulting in competition for and limited availability of mates); parental care (how each parent benefits from taking care of the young as opposed to investing in their own survival or further reproductive effort); ecological features (such as the availability and spatial distribution of food and possible mates); and evolutionary heritage (how a taxon is phylogenetically predisposed to develop a given mating system).

Since females are the egg generators, they start-off with a larger energetic expenditure than males (a fact known as the 'cruel bind'). What happens after the egg is laid – *e.g.* if one parent takes on most or all parental duties, or if a pair maintains its bond throughout the whole reproductive season mutually caring for the young – will determine which kind of mating system occurs in a particular species. Mating systems should be viewed as a continuum of breeding strategies that ultimately differ according to the amount of parental investment of each male and female, in addition to the number of mates each individual has. This ranges from lekking species, in which males associate with different females exclusively for copulation, providing no parental care whatsoever, to cooperative breeding species, in which the main pair rear their offspring with the help of other individuals.

All bird species provide some form of post-hatch care for their chicks, with the exception of interspecific brood parasites such as the Shiny Cowbird (*Molothrus bonariensis*). Brood parasitism is a strategy used by females of some species, which consists of laying their eggs on nests of either conspecifics (intraspecific brood parasitism) or nonspecifics (interspecific brood parasitism), so that other individuals will rear the offspring as their own. The genetic parents, thus, are able to spend more time foraging and producing additional offspring, free from the costs of parental care. Intraspecific nest parasitism has emerged in about 2.5% of birds, occurring in 16 orders, while interspecific brood parasitism is rarer, appearing in 1.0% of species. It has been proposed that such behaviors have evolved through intermediary steps, such as facultative brood parasitism, which in turn might emerge through nest takeover or use of abandoned nests built by other conspecifics or even nonspecifics. Nevertheless, it has been shown (in a study which analyzed 565 genera) that, among altricial birds, obligate interspecific brood parasitism has evolved directly from normal breeding mode, instead of, for instance, intraspecific nest parasitism.

Males are traditionally the bearers of small and numerous gametes, so they usually try to fertilize as many eggs as possible, copulating with several females. Although birds' external development enables males to perform parental duties equally well as females, most offspring care is provided by females. Considering that parental care imposes trade-offs with copulation effort and future parent survival, each individual generally reduces parental care to a minimum. Males are usually able to achieve that before females due to different reasons, one of them being the uncertainty of paternity that males face because fertilization is internal and females may copulate with more than one male. From the female perspective, on the other hand, there is a high degree of parental certainty, generating higher benefits in caring for the offspring, which most

certainly is theirs. Also, females produce larger and more costly gametes, which are limited in number and thus are the object of male competition. This allows females to be the choosy sex, selecting males according to their preferences. Choosy females generally evolve to maintain their preferences, to avoid being misled and/or having their choices subverted by the opposite sex. Males, on the other hand, may evolve to bypass the choices made by females. In evolutionary terms, each individual will try to maximize its genetic contribution to subsequent generations, exploiting the contributions of individuals of the other gender whenever possible, which may result in sexual conflicts when the costs and benefits for females and males are asymmetric.

Some species, such as the temperate-zone Dunnock (*Prunella modularis*), may show more than one mating system, in which social monogamy, social polygyny, social polygynandry and social polyandry may even occur in the same population. Each of these is more advantageous to either male or female in terms of reproductive success, which means that conflicting preferences are at play. In a classical study it was shown that the ability of Dunnock males to monopolize females varied according to the size of a female's range, which in turn was dependent upon the degree of food distribution. When patches of food were clumped, female ranges were small, making it possible for males to easily monopolize several of them, which gives rise to polygyny and polygynandry (higher male mating success variability). On the other hand, when food was widely distributed, female territories were large, thus making it difficult for one male to monopolize them, giving rise to polyandry or monogamy (with lower variation in male mating success). When territories were enhanced with extra food, the size of female ranges became smaller and the mating system shifted to one in which males are able to monopolize one (or more) females (*e.g.* from polyandry to monogamy).

One of the most important mechanisms in the evolution of avian mating systems is sexual selection. It generally arises when genetically dissimilar individuals differ in regard to their reproductive success, as a result of either intrasexual selection (competition within one sex for the access to the opposite sex) or intersexual selection (differential attractiveness to members of the other sex, which is usually reflected by female choice). Both types of sexual selection are held equally important in birds. In intrasexual selection, some males end up achieving privileged status among others, thus gaining greater sexual access to females. As a result of this, male-male fighting traits may evolve, consisting of exaggerated features that perhaps would not arise by natural selection alone.

The mechanisms underlying female choice may be guided either directly or indirectly by natural selection, increasing female fitness. Some of the benefits of female choice may be 1) females and offspring get direct benefits from the chosen males, such as nuptial gifts, resources monopolized in male territories or male parental care, including protection from predation; 2) searching for conspicuous males may save time and energy instead of looking for dull-colored ones, which could require more search time; 3) males may be chosen for their parasite resistance, thus making them less likely to transmit parasites or diseases to females; 4) females may choose male traits that are genetically associated with other phenotypic traits, which end up improving offspring viability.

Female choosiness may be maintained if the benefits of choice, such as increased offspring viability, outweigh those of mating at random. The “good genes” hypothesis argues that some of the benefits resulting from female choice may be that, by choosing males with more elaborate ornaments and brighter plumage, females may be indirectly selecting males that convey good genes for future offspring, such as pathogen-resistant genes. In such cases, females may evolve to be extremely choosy despite receiving no material benefits whatsoever from chosen males, as presumably occurs in lek-breeding species.

Male secondary sexual traits are important signals to advertise the quality of an individual. This can occur through traits that imply sort of male handicap - such as extremely long tails and brightly colored plumage - which may be an honest advertisement of the male’s quality. Individuals exhibiting such physiologically costly traits may be “handicapped” to a certain extent, but prove to have significant vigor. Thus females copulating with them will “gather” genes that favor overall viability for their offspring, although choosing them in an indirect way. It has also been suggested that costly trait genes can “hitchhike” with other viability-improvement genes.

Although some traits may enhance the survival of the male and future offspring, other chosen features may be ecologically non-adaptive, eventually diminishing the male’s actual viability. For instance, if female preference for long tails keeps producing progressively longer-tailed males each generation, even higher physiological costs and physical constraints may arise, such as the energy required for molting and low flight efficiency. However, such costs are counterbalanced by the persistent female preference itself, which ends up increasing the fitness of males and results in offspring bearing such traits (“sexy son” hypothesis), in an adaptive fashion. This is called runaway selection, a process where arbitrary or random features become the basis of female preference, even though the choices result in no direct benefits at all to the female, or to offspring survival and viability.

It is generally expected that three different types of sexual differences arise from sexual selection: size dimorphism; dichromatism, a result of differences in adult plumage color; and sexual diethism, translated into differences in adult sex role behaviors such as egg incubation, territory defending, and vocalizations. The level of these components can vary independently among species. Sex role divergence and sexual selection often reinforce each other in a feedback fashion. The sex more intensely linked to parental care tends to be the choosy gender, competing intrasexually for high quality partners, thus further increasing the degree of sexual divergence in a species. If both parents provide care to the young, sexual convergence might evolve, because both sexes are expected to be equally choosy. Although there are few studies on this matter, sex role divergence is regarded as low among tropical birds, i.e. there are presumably similar sexual selection pressures for both sexes, so males and females have similar “tasks”: both usually sing, defend territories and share parental duties. On the other hand, among temperate zone birds, there is markedly higher sex role divergence, which implies high sexual selection pressure for one sex. Males sing, defend territories and compete for extra-pair fertilizations. Paternal care is limited to nest defense and feeding the young, while females rarely sing or defend territories, but instead provide high parental care by building nests and incubating eggs alone.

Once female choice tendencies are established, the evolution of secondary sexual traits is expected to arise with more intensity in polygynous species than in monogamous ones, due to higher selection pressures for one gender, which may result in higher sexual dimorphism and/or dichromatism. For instance, in lek-breeding species such as the birds of paradise (Paradisaeidae), males usually evolve to have extremely conspicuous sexual secondary traits, which are meticulously inspected by females.

However, sexual selection may operate in monogamous species as well. When a population has unbalanced sex ratios with more males than females, for example, some males may be unable to obtain mates, which in turn can lead to increased variation in male reproductive success, resulting in higher sexual selection pressure for males. Also, if individuals differ in regard to the time they commence breeding, early breeding females (which are assumed to be in a better breeding condition) may be able to increase their own fitness by choosing the most vigorous males or those more inclined to help rear the young. Another possibility is the existence of exceptionally attractive males, which vary in regard to their parental effort, for instance, and which may stimulate females to increase their reproductive effort. Males of the tropical Buff-breasted Wren (*Thryothorus leucotis*) invest heavily in nest building, which may be a sexually selected trait that indicates a male's future feeding effort. But little is still known about monogamous tropical birds relative to sex-specific roles, mate choice and parental care.

Intersexual selection poses important issues such as the nature of the traits that attract females. In the tropics, most bird species pair year-round, so mate assessment may be continuous, although their period of reproduction is usually restricted to certain months. The cues females use to assess mate quality are still relatively unknown, and may include song, plumage coloration, or even parental effort. An important cue tropical females may use is the quality of the year-long territory potential mates occupy. It has been suggested that the quality of a mate is highly correlated with the quality of its territory. Individuals of tropical species such as the Dusky Antbird (*Cercomacra tyrannina*) may move to new territories, deserting its past mate to pair with another mate in a new territory, probably because of the quality of the territory itself.

Many visual traits may also play a crucial role in male advertisement quality. In a species of polygynous pheasant (*Phasianus colchicus*), for instance, tarsal spur length, which is a sexually selected male trait, was correlated with harem size, phenotypic condition of males, and overall estimated viability. Also, in the tropical lek-breeding Jackson's Widowbird (*Euplectes jacksoni*), it was found that tail length is positively correlated with female assessment. Males with experimentally shortened tails received less visits from females than did control males. Thus, it is expected that, in this species, such a trait is an honest visual indicator of male viability and quality for females. In many other species, as well, females use ornamental feather length traits as cues to choose their mates, such as in the bird of paradise Lawes' Parotia (*Parotia lawesii*), the Long-tailed Widowbird (*Euplectes progne*) and the Queen Whydah (*Vidua regia*). It has also been found that females of some monogamous species, such as the House Finch (*Carpodacus mexicanus*), choose more colorful males, indicating that selection for colorful patterns is not exclusive to polygamous birds.

As an alternative to producing physical secondary sexual traits, males of some polygynous tropical species such as bowerbirds (Ptilonorhynchiidae) have evolved to create “signal posts” in their environment. These birds use various resources from their surroundings to build variably decorated flamboyant constructions, called bowers, which are then vigorously defended. The degree of bower ornamentation may provide indirect cues for females to evaluate male quality and dominance status.

As previously mentioned, avian mating systems depend upon multiple factors that determine different evolutionary pathways of tropical birds. Besides sexual selection, ecological components may be determinant. Female reproductive success is not limited by male availability, but instead by resources important for successful egg development, such as food and nest sites, and predator pressure is also an important factor. Males, on the other hand, try to control access to females whenever possible, a strategy that ultimately varies according to the distribution of fertile females (i.e. whether or not they are gregarious), and with competition for mates, which in turn is related to the sex ratio of receptive females versus sexually active males. Thus, a species’ mating system emerges from this myriad of differential selective pressures, and therefore can be extremely variable across taxa and ecological contexts.

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Biographical Sketches

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