

Lecture 17. Breeding systems

Class Business

- Handout for polygyny threshold model

Reading for this lecture

Required. Gill: pg. 359 through Chapter 13

1. Introduction

A wide variety of different breeding systems are found in birds, but there is less variety than is found in animals in general. Various things go into determining the breeding system of a species, but two fundamental issues are the **mating system** (the pattern of pair-bond relationships) and the means by which **parental care** is provided to the young. These two issues are closely related.

The type of breeding system found in birds is influenced by their evolutionary history and other aspects of their biology. Several things constrain the types of breeding systems found in birds:

- **Internal fertilization**: because eggs are fertilized inside the female it is difficult for a male to “assure paternity” and this can mean that he is less invested in the young than if he were certain they were his.
- **Heterogamy** (= gametes are different sizes in the two sexes): because eggs are big and costly to produce and sperm are small and cheap, females usually have a much bigger investment in any particular offspring than do males. This imbalance has various effects, e.g., it means that females are typically less likely to abandon their young than are males.
- **High body temperature**: this means that young birds (a) need a lot of calories and (b) need a lot of brooding from their parents in order to stay warm enough. Hence, birds require a lot more parental care than some other types of animal.
- **Relatively big, helpless young**: in general young birds are not well equipped to survive on their own when they first hatch. Again, this means they need a lot of parental care.
- **Flight**: as mentioned previously, the reliance on flight in birds may be part of the reason why **viviparity** has not evolved in the class.

2. Types of mating systems

A) PAIR BONDS

- i) Mating systems are typically defined in terms of **pair bonds**, which in turn are defined as an association between members of opposite sexes for the purposes of reproduction.
- ii) Note that pair bonds can form for variable time periods, ranging from very short term to lifelong relationships.

B) MONOGAMY

- i) A **monogamous** relationship is one in which each bird has only one partner.
- ii) Historically, most birds have been thought to be monogamous. As we learn more about the genetic relationships between young birds and the adults that care for them, our understanding of monogamy has shifted (see below). But, it remains true that the majority of bird species form **socially monogamous** pair bonds.
- iii) Note that it is not straightforward what we mean by “having only one partner”. Some birds mate for life, only replacing their mates if they die, and literally only have one mate. Many others, however, form pair bonds with a different partner every year. Typically species are referred to as monogamous if they only have one breeding partner each year.

C) POLYGAMY

- i) A **polygamous** relationship is one in which at least one individual has multiple mates. There are several different forms of polygamy: **polygyny** (male forms pair bonds with multiple females), **polyandry** (female forms pair bonds with multiple males), **polygynandry** (both males and females form pair bonds with multiple members of the opposite sex),

promiscuity (birds mate more or less indiscriminately without ever forming real pair bonds. There are examples of each of these in the text book.

- ii) Polygyny tends to be the most common form of polygamy. Polyandry is less common and is found in about 1% of all bird species.

D) ASSIGNING MATING SYSTEMS IS COMPLEX

- i) People typically refer to a particular species as having a certain mating system. This approach can greatly oversimplify reality because there is often a range of mating systems present within any one species. For example, phalaropes are typically said to be polyandrous, and many female phalaropes do mate with more than one male. But, studies of phalaropes also have shown that there are lots of females that only mate with one male; these individuals are therefore monogamous.
- ii) The timing of different relationships also complicates things. For example, some species have multiple mates at the same time, which clearly counts as polygamy, but others have multiple mates sequentially. A polyandrous phalarope, for example, typically cycles through males in series: they form a pair bond and mate with one, lay him a clutch of eggs, and then leave him with the eggs and go in search of another male. This system is not too different from that of many species (including humans) that we tend to think of as monogamous. In general, ornithologists will refer to this system as **sequential polygamy** if pair bonds are formed with multiple mates in a single breeding season.

3. Parental care needs largely determine the mating system

A) GENERAL PATTERNS

- i) The ubiquity of social monogamy seems to be a direct result of the need in most birds for two parents to take care of the young. In these cases, if either parent were to desert the young would die and that parent would fail to get its genes into the next generation. This in turn would result in selection against desertion as a behavior and favor social monogamy.
- ii) Polygamy, therefore, tends to occur in situations where it is possible for one parent to raise the young on their own. For example, when young are able to take care of themselves (at least partially) at birth, when resources are very abundant, or both. Polygamy (both polygyny and polyandry) is relatively common in both the shorebirds and rails. It is, therefore, no surprise to learn that both these groups have **precocial** chicks and live in habitats where food is extremely abundant.

4. Monogamy can be complex

A) A REVOLUTION IN UNDERSTANDING

- i) With the advent of genetic fingerprinting techniques in the last two decades our understanding of bird breeding systems has changed dramatically. The main discovery has been that many young birds are not raised by their genetic parents. It turns out that in many birds there are large numbers of **extra-pair copulations** (EPCs) and that many of these lead to **extra-pair fertilizations** (EPFs).
- ii) Consequently, many birds that are socially monogamous still have a lot of families in which the young are of mixed parentage. (Extra-pair interactions also occur in birds that are polygamous – it's just not as surprising when birds are already mating with several individuals.)

B) SOURCES OF MIXED PARENTAGE

- i) Both sexes are known to seek extra-pair copulations. Males can be very aggressive about seeking opportunities to mate with females with which they have not formed a pair bond (e.g., male Mallards often seem to rape female Mallards). Equally, mated females will often leave their home territory and seek out EPCs with neighboring males.
- ii) A consequence of all this is a behavior referred to as **mate guarding** in which males will follow females around to both guard them against the advances of other males and also to restrict their opportunities for surreptitious matings.

- iii) EPFs are not the only source of mixed parentage. In some species, females will engage in a behavior called **nest parasitism** or **egg dumping** in which they lay their eggs in the nest of another bird of the same species. In a minority of species this is very common (see lecture on parental care), but it is now known that it occurs at a low level in quite a lot of birds. (More on this in the lecture on parental care.)
- iv) How do you think you would detect and distinguish young that are the product of EPFs and those that result from egg dumping? Clue: the answer involves comparing the genetic fingerprint of the offspring with the social parents.

5. More on polygamy

A) WHAT DETERMINES THE FORM OF POLYGAMY?

- i) Incentive. Polygamy occurs when it pays one parent to desert the young more than it does the other. In these cases the type of polygamy will depend on who has the greatest incentive to desert. In general, females have a greater investment in their offspring. This is because eggs are expensive, sperm is cheap and because females have greater certainty that they are actually raising their own young than do males (because of internal fertilization).
- ii) Parental care costs. The incentive to leave also is influenced by the cost of parental care. If parental care is more costly to one parent, then that parent is more likely to desert. These costs can take the form of simple energetic needs, the risk of survival, or even the cost of losing future reproductive opportunities. In all cases the ultimate cost must be measured in terms of the number of offspring an individual gets into the next generation if they stay, vs. the number they would produce if they desert.
- iii) Opportunity. In general, males have better chances to desert. This is because eggs must be laid one at a time and it can take several days for a clutch to be laid. Consequently, the male can desert immediately after copulation, while the female cannot.
- iv) Sex ratio. Another component of opportunity is determined by the sex ratio. If there is no one else to mate with then there may be little point in deserting even if the opportunity arises. In general if you are a member of the limiting (i.e., rarer) sex, then it makes more sense to desert; if you are a member of the more common sex, then it makes better sense to invest time in the offspring you already have because you may not get to produce more even if you do desert. The greater the sex ratio skew, the greater the imbalance and the more likely it is that polygamy will occur.
- v) Resource availability and distribution. Another way in which polygamy can occur is if resources are sufficiently abundant, patchy, or both, that a bird can defend enough resources to attract more than one mate into their territory. Depending on the resource distribution it may pay an individual to choose to mate with an already mated bird with a great territory than to choose monogamy with a bird in a poor territory. The **polygamy threshold model** illustrates how this works.
- vi) So given all of that, why do you think polygyny is more common than polyandry? Also, which of these mechanisms are likely to result in serial polygamy vs. sequential polygamy?

B) POLYGAMY OFTEN LEADS TO SEXUAL DIMORPHISM

- i) When polygamy is an option there is often considerable variation in the reproductive success of individuals in the non-limiting sex (usually males). This creates a great deal of competition within that sex, which results in sexual selection for traits that increase reproductive success for members of the non-limiting sex.
- ii) Extreme sexual selection in only one sex can result in the development of **sexual dimorphism** – because the selection drives evolution in one sex only.
- iii) Consequently some of the most extreme forms of sexual dimorphism occur in polygamous species. (But note that dimorphism does still occur in monogamous species.)
- iv) Dimorphism can take several forms: size, plumage colors, ornamentation, etc. Typically, it is the males that are bigger, brighter, more ornamented. Why do you think this is? But in some cases there is **reversed sexual dimorphism** and females are bigger, brighter, etc. Under what conditions would you expect this to evolve?