

MATING SYSTEMS AND STRATEGIES OF TROPICAL FISHES

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Summary

Ecological factors influencing the temporal distribution of resources and/or mates (e.g. breeding synchrony, dispersal, and population density) will affect the potential for mate monopolization, resulting in the different types of mating systems we observe in nature. Mating patterns and parental care are also interrelated: parental care tends to limit the potential for multiple matings, but sometimes mating opportunities is what limits the amount of care provided. The optimal mating system may be different for each sex and how this conflict is resolved also affects the resulting mating system. Polygyny, where one male mates with several females, is the most common mating system among

tropical fishes, and comes in four different forms: resource defense polygyny, common among substrate brooders, female defense polygyny, scramble competition, found in species with mass spawning events and lek polygyny. Polyandry, where females mate with more than one male, tends to occur in species where sex roles are reversed and dominant females mate with multiple males to acquire good genes, or direct benefits such a spawning sites or parental care. The need for biparental care seems to be an important factor promoting true monogamy, and there are several well documented cases of monogamy among tropical fishes. Genetic evidence indicates that promiscuous mating systems, in which both sexes have multiple mates, are more common than previously suggested by observation of social interactions alone. Alternative reproductive strategies and tactics among individuals of the same sex are also common in many tropical fishes, and expected to evolve when sexual selection is strong. Furthermore, the flexibility of the reproductive organs in fishes has allowed them to evolve strategies that include sex change and hermaphroditism. Finally, tropical fishes are among the few vertebrates that have asexual reproduction, adding further to the incredible mating system diversity tropical fish exhibit.

1. Introduction

The theory of evolution by natural selection proposed by Charles Darwin and Alfred Wallace is widely accepted as the central paradigm in biology. A key point in this theory is that, within a population, some individuals are better at surviving and reproducing; thus their genes will be disproportionately represented in the next generation. Furthermore, sexual selection (the advantage which certain individuals have over others of the same sex and species in exclusive relation to mating success) is very often an important component of the selection process. In this chapter, we will review how tropical fishes undergo the very important process of acquiring mates. During this chapter we will consider tropical fishes as those species with a geographical distribution that includes, but is not restricted, to the tropics.

A mating system can be formally defined as the species-specific pattern of male-female associations (Shuster and Wade 2003). However, in a broad sense, mating systems not only represent the numbers of mates individuals acquire, but also include a description of how those mates are acquired, the characteristics of pair bonds and patterns of parental care by each sex, and thus ultimately reflect how the conflicting interests of the two sexes are resolved (Davies 1991; Berglund 1997). For the first part of the chapter, we will describe the factors that affect mating systems in general. For the second part we will describe the different types of mating systems. During this process we will use tropical fish species as examples. However, this chapter does not intend to be a comprehensive list of all the tropical fish species in every type of mating systems; instead, with every section we try to emphasize how the factors and conditions that exist in the tropics have an effect on the presence of the different types of those mating systems.

1.1. Ecology and Dispersion

In a seminal paper, Emlen and Oring (1977) proposed one of the first attempts of a unified theory of mating system evolution. Under their hypothesis, ecological

constraints on mate monopolization attempts lead to the specific mating systems. Mate monopolization can be direct (by exclusion of other members of the same sex from potential mates) or indirect (by controlling resources that are critical for mate attraction and/or successful reproduction), and the environment affects the potential for monopolizing one (monogamy, but see below) or several mates (polygamy, but see below). Specifically, the spatial and temporal distribution of mates and/or resources will result in how the potential monopolization of mates is realized. When mates and/or resources are highly clumped, the opportunity for monopolizing multiple mates increases. Alternatively, when mates and/or resources are distributed uniformly, the opportunity for monopolization of multiple mates is low. Clearly, the degree at which mates become sexually receptive has important and obvious implications on the temporal distribution of mates. Thus, when mates become receptive in synchrony, potential mates would be common and the opportunity for polygamy would be high; on the other hand, when mates become receptive in asynchrony, potential mates would be rare and the opportunity polygamy would be low.

Based on the previous premises, Emlen and Oring also proposed a classification of mating systems, for this chapter we will use this “traditional” mating system classification with some modifications. We refer the reader to a revision by J. Reynolds (1996) for a more recent view of what is now consider “a breeding system”. We would also like to note that some authors would describe a mating system from the perspective of both sexes independently. Thus, a species where males mate with only one female, but females mate with several males would be monogamous from a male perspective, but polyandrous from a female perspective. In this chapter the terms we use to describe the mating systems apply to both sexes within a species. Therefore, we classify a species where both males and females mate with several partners as promiscuous, rather than polygynous (from the male perspective) and polyandrous (from the female perspective).

In general, where males only provide sperm to females, female reproductive success is limited by access to resources (i.e. the more resources females get the more offspring they can produce). In contrast, males tend to have the (physiological) potential to sire offspring at a faster rate than a female can produce them. Therefore, male reproductive success is generally limited by access to females (i.e. the more mates males can have the more offspring they can produce). As a consequence, males tend to be the sex that searches for females, initiates courtship, fights for mates, ultimately trying to monopolize as many mates as possible. This difference in the factors limiting the reproductive success of the sexes causes female dispersion to be primarily influenced by resources while male dispersion is primarily influenced by female dispersion. A clear example occurs in the blue-headed wrasse, *Thalassoma bifasciatum*, where through experimental manipulations, it was shown that females choose the spawning sites and males compete to defend sites which females prefer. However, a lot of tropical fishes provide male parental care, in such cases males become a resource important for female reproductive success and female dispersion is not only influenced by resources but also by males. We will further consider this complication of the simple previous scheme in the next section.

Ecological factors also determine the movement of young animals from their place of

birth to that of their first breeding attempt (i.e. natal dispersal). Sex-biased dispersal of birds and mammals has been shown to be closely linked to their mating system, but few studies have examined the relationship between mating systems and dispersal in fishes. A recent study by Croft and collaborators (2003) has shown that male Trinidadian guppies (*Poecilia reticulata*) disperse at higher rates than females. A higher rate of male dispersion in the guppy was interpreted as a strategy to acquire more females. Thus sex-biased dispersal may be also related to mating systems in fishes; however, the evidence is limited and further studies should test this possibility more explicitly.

Finally, it has been recently proposed that the effects of population density on several aspects of mating systems have been neglected and deserve further analysis (Kokko and Rankin 2006). Specifically, density would affect encounter rates, which in turn can have strong effects on competition for mates, mate choice or resistance, mate searching, mate guarding, parental care and the probability of divorce. Furthermore, changes in density can cause mating skew or changes in switch points between alternative mating strategies (see below). Most of the aforementioned consequences of changes in density have either been discussed in the previous paragraphs or will be discussed in the following sections.

1.2. Parental Care

In the classical theory of mating systems the potential for polygamy also depends in large part on the degree of parental care required for successful rearing of the offspring. In species where one sex does not provide parental care, this sex can spend more time and energy competing for resources and mates; thus, the opportunity for polygamy is higher. The predictions that result from these premises are that polygamy should be more common where one sex is predisposed to provide most of the parental care (e.g. territorial fish); parental care requirements are minimal; and resources are very abundant, enabling single parents to provide successful parental care. It is thus not surprising that differences between species in parental care are associated with differences in mating system. When contrasting fish to birds and mammals, a very broad generalization is that in those fish families that provide parental care, the males usually provide the care, and male parental care is associated with polygamy or promiscuity.

Further empirical and theoretical studies of mating systems (for a review see Reynolds 1996) uncovered that parental care and mating behaviors do not co-vary as clearly or as consistently as originally proposed. In addition to the effect that parental care has on sex differences in mating behavior, we now know that the relationship can go in the opposite direction with mating behaviors dictating parental care. It is now accepted that mating patterns, mating opportunities and parental care patterns are explicitly interrelated, thus Székely and collaborators (2000) suggest that their study requires an integrative approach. For example, Awata and collaborators (2006) found that in the African cichlid fish *Julidochromis transcriptus*, the size of the multiple fish involved in the breeding attempt results in either monogamous pairs or polygamy. In the resulting monogamous pairs both parents shared their parental tasks equally, while polygamous parents showed less parental care. Furthermore, Keenleyside (1983) found that males of the American rainbow cichlid (*Herotilapia multispinosa*) commonly share parental care duties with their single mate; however they desert their brood earlier when there are

more potential mates available. In contrast, males of the African cichlid *Eretmodus cyanostictus* did not desert their brood when Grüter and Taborsky (2005) experimentally increased their mating opportunities, thus the described response to potential mate availability cannot be generalized. However, the rainbow cichlid example illustrates that: (1) there is a feedback between mating behaviors and parental care, in that particular case the allocations are not fixed and competing for more females occurs at the expense of parental care; (2) the availability of each sex depends on adult sex ratios, yielding another important factor affecting mating systems, namely the overall ratio of available females to males (the operational sex ratio).

1.3. Operational Sex Ratio

In most sexually reproducing organisms the sex ratio at birth is 1:1 (50% males and 50% females), which Fisher (1930) explained theoretically by the fact that each offspring has one mother and one father. However, if either the time to reach adulthood (sexual maturity) or survival to adulthood is different for males as compared to females, the ratio of reproductively active males and females may not be 1:1. In addition, the rate of reproduction can be different between the sexes. So, for example, if females provide parental care and males do not, then females may have to wait until the young can survive on their own before they reproduce again, while males reproduce again more quickly. Both a biased sex ratio of adults and differences in the reproductive rate of females can lead to biases in the operational sex ratio (OSR), or the ratio of reproductively active males and females at a given time and place defined by Emlen and Oring in 1977.

Kvarnemo and Ahnesjö in 1996 reviewed how operational Sex Ratios can have a large impact on competition for mates, and consequently sex roles. For example, Forsgren and collaborators (2004) found that in the two spotted goby, *Gobiusculus flavescens*, male–male competition for mates is intense early in the season, but when the abundance of males drops later in the season, females start competing with one another for access to males. Due to the impact OSR has on the sex roles of males and females, it will also influence the mating systems we see in tropical fishes. The benefits of mating with one as compared to several individuals will in part depend on the number of potential mates that are available.

1.4. Sexual Conflict

Because the two sexes have different roles in reproduction, the optimal behaviors and traits for each are likely to be different. This sets up a situation where the sexes are likely to disagree on the optimal mating system. For example, Kokita and Nakazono (2001) found that in the longnose filefish, *Oxymonacanthus longirostris*, males gained higher reproductive success when mated with several females, but monogamy was advantageous to females because they produced fewer eggs when their mates mated polygynously. Parker defined sexual conflict in 1979 and this occurs when selection on one sex causes the other sex to pay a cost, and can influence traits related to everything from courtship, mate choice and fertilization to parental care. So, for example, sexual conflict can help explain why one sex provides more parental care than another. In the monogamous mouthbrooding cichlid *Eretmodus cyanostictus*, in which the clutch is

successively incubated first by the female and then by the male, if unmated females are present, males take the eggs later, extending the parental care period for the female.

Theory suggests that sexual conflict can lead to sexually antagonistic co-evolution, or in other words, an arms race, where an adaptation in one sex can lead to a counter-adaptation in the other. It is important to realize that in the case of any arms race, there will be situations where one side is winning and situations where the outcome appears equal, even though the conflict still exists. In addition, the conflict between males and females can be intertwined with sexual selection, which includes either male-male competition for mates and female mate preference. As Henson and Warner (1999) have shown for the Mediterranean wrasse, *Symphodus ocellatus* (Labridae), males are willing to reduce their immediate mating success by reducing spawning at the nest when there are many small male competitors present. This behavior causes a sexual conflict with females that are ready to mate with the nesting males, but is beneficial to the nesting male, as by postponing mating until there are fewer competitors nearby, he decreases mate competition. Therefore, sexual conflict, sometimes in combination with sexual selection, will be an important factor to consider as we examine the evolution of mating systems in tropical fishes.

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Biographical Sketches

Oscar Rios-Cardenas is a professor at the Instituto de Ecología, A.C. in Xalapa, Mexico. He received a PhD in Biological Sciences in 2003 from the State University of New York at Buffalo, USA. His previous work has involved studies of sex roles in cichlids with biparental care, the effect of paternity on parental care and alternative reproductive strategies in sunfish. Since his first postdoctoral position he has been working with swordtail fishes, studying female preferences, hybridization patterns and the maintenance of alternative reproductive strategies. His main research interests are sexual selection, the evolution of parental care and alternative mating strategies, and how these factors affect mating systems.

Molly Ruth Morris graduated from Indiana University, Bloomington IN, USA, with a PhD in Ecology, Evolutionary Biology and Behavior in 1987. For her dissertation, she worked on the mating behaviors of treefrogs in both Indiana and Costa Rica. Since then, she has worked on the mating behaviors of *Xiphophorus* fishes, conducting research in both Mexico and in her laboratory at the University of Ohio, Athens OH, USA. She has published over forty papers and reviews on the mating behaviors and reproductive biology of treefrogs, swordtail fishes, alternative mating strategies and the evolution of communication. In addition, she has served as the secretary and is currently the president of the Animal Behavior Society.