

MALE AND FEMALE ALTERNATIVE REPRODUCTIVE BEHAVIORS IN FISHES: A New Approach Using Intersexual Dynamics

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KEY WORDS: alternative reproductive behaviors, sexual conflict, game theory, mating systems,
fish

ABSTRACT

The study of alternative reproductive behaviors in fishes has contributed to our general understanding of reproductive strategies and mating systems. Despite extensive research on the mechanisms and patterns of alternatives, two important factors have not been addressed, and both may strongly influence the evolution of alternative reproductive behaviors. First, alternative female reproductive behaviors exist and should be considered in theoretical and empirical work. Second, interactions between the sexes will influence the evolution of alternative reproductive behaviors. In this review, we explore these two points and suggest the development of a more comprehensive theory of alternatives that will increase our ability to make predictions regarding the existence and expression of alternative reproductive behaviors in both sexes.

INTRODUCTION: WHAT DO WE MEAN BY ALTERNATIVE REPRODUCTIVE BEHAVIORS?

In fishes, an amazing diversity in mating patterns exists within and across species. Interspecific variation in mating systems ranges from pelagic group spawning to monogamy with biparental care (7, 67). Diversity within species is no less impressive. For example, in the ocellated wrasse, *Symphodus ocellatus*, four distinct male reproductive behaviors exist simultaneously within one

population (66, 81). In this species, large males build nests and provide parental care (43). The smallest males sneak into the nest to parasitize the mating between the nesting male and a female (66, 81). Meanwhile, intermediate-sized males defend another male's nest from sneakers and court females while sneaking spawns themselves. Finally, the largest males, called pirates, temporarily take over another male's nest by force (66). Such diversity is not unique to this species (65), and studies of variation in fish mating systems have played an important role in our general understanding of reproductive strategies (67, 78).

The relatively recent realization that differences within a species can represent evolutionarily adaptive patterns has led to a large number of studies on alternative reproductive patterns in a variety of taxa (46). A multitude of examples exist of both within- and between-individual differences in reproductive behavior, and variation may be more the rule than the exception. Separate populations of a species will often experience different habitats and selective pressures, and, as a result, may exhibit different reproductive strategies. Single populations may also exhibit changes in phenotype distributions through time due to environmental variation and selection. Finally, reproductive behavior may vary within a population at one point in time.

The study of alternative reproductive behaviors has focused mainly on discrete male alternatives within a population (e.g. 2, 15, 17, 22, 30, 33, 60, 65, 73). For a number of well-studied examples of male alternative reproductive behaviors in fishes, we know the pattern of expression, life-history pathways, relative fitness, and in some cases even the underlying physiology and genetic basis of these differences (e.g. 5, 6, 15, 16, 29, 30, 32, 61, 62, 68, 74, 78, 80). Although these well-known patterns are very striking, two other important aspects of alternative reproductive behaviors have been virtually ignored (but see 11, 57, 75). First, female alternative reproductive behaviors clearly exist and should be considered. Second, there is a need to treat the effect of interactions between the sexes on the evolution of alternative reproductive behaviors. One of our major goals is to include consideration of these factors, since they enrich the topic considerably and should enhance our understanding of the evolution of alternative reproductive behaviors in both sexes.

In order to have a meaningful discussion of alternative reproductive behaviors, it is necessary first to ask the question "What do we mean by alternatives?" For this review, we focus on situations in which distinct reproductive behaviors exist within a sex, within a population, at one point in time. While distinction is often made between the underlying rule (termed a strategy) and the expression of that rule (termed a tactic: 2, 14, 17, 30, 33), we avoid the use of this terminology and focus on observed differences in reproductive behavior within or between individuals.

We briefly review some general types of alternative reproductive behaviors in males and females, and we discuss whether there are consistent differences between the sexes in the types and patterns of alternatives. Although we discuss only a few illustrative examples, it is important to realize that numerous other species exhibit alternative reproductive behaviors. We then review the mechanisms that can maintain alternatives and ask what factors might determine the presence of alternative reproductive behaviors and their pattern of expression. Finally, we discuss some limitations of current theory and argue that not only do alternative female reproductive behaviors exist, but that females play an important role in the expression and evolution of male alternative behaviors. Males will play a corresponding role in the evolution and expression of female alternatives. In essence, we argue that interactions both within and between the sexes must be considered. This will increase our understanding of observed alternatives and our ability to make predictions about expected patterns of mating behavior in both sexes.

EXAMPLES OF OBSERVED VARIATION

Male Alternative Reproductive Behaviors

Male alternative reproductive behaviors in fishes have been well documented, as exemplified in the comprehensive review of Taborsky (65). This extensive diversity falls into three broad categories. Males are usually in competition for access to mates or resources, and existing alternatives often represent different solutions to the problem of obtaining mates (e.g. males may differ in their tendency to engage in male-male competition). Males may also vary in mating mode (e.g. males may mate singly with females or they may spawn en masse), and in degree of investment in parental care. Alternatives can exist in each of these three main components of the mating system. Although the exact details differ among species, a few examples demonstrate both the basic trends and the variation in these patterns.

Many species possess males that compete for territories as well as males that are nonterritorial. Although in some species nonterritorial males are not reproductively active, in others these males have mating success that is measurable, if not equal to that of territorial males (e.g. 30, 32, 62, 81). For example, in the bluegill sunfish, *Lepomis macrochirus*, large males build nests and defend territories (29, 30, 34). Other males in the population adopt alternative nonterritorial behaviors (15, 16, 29, 30, 32). Intermediate-sized males mimic females in order to gain access to the nest for spawning (29, 30). Smaller males hide nearby and use stealth to reach nests and to spawn with females ("sneaking": 29, 30). Although females will spawn only in nests, they do not appear to differentiate between male alternatives (30, 32). In this species, territorial and

nonterritorial males may have completely separate life-history pathways with different growth rates and reproductive spans (15, 16, 29, 30, 32). Nonterritorial males mature early and reproduce at a lower rate for a longer time period, while territorial males delay maturity in exchange for higher eventual mating success. Despite all these differences, male alternative behaviors appear to have equal lifetime reproductive success on average (30, 32). In this species, male types vary in all three components: how they obtain mates, mating mode, and parental investment.

In other species, individual males adopt both territorial and nonterritorial behavior at different times of life. For example, in the bluehead wrasse, *Thalassoma bifasciatum*, young males on large reefs do not defend territories but spawn in groups at mating sites. Older males defend territories around other mating sites and are involved in pair-spawns with females (80). Males appear to switch from nonterritorial to territorial behavior when they are large enough to compete for a territory (36). An individual male, if it survives long enough, will be both nonterritorial and territorial. Although the mating success of territorial males is higher, males achieve a higher lifetime reproductive success by initially reproducing as nonterritorial males than by delaying sexual activity until they are large enough to compete for a territory (74, 80). Males of this species have two alternatives in access to mates and mating mode, but in neither alternative do males provide parental care.

In threespine sticklebacks, *Gasterosteus aculeatus*, most males build nests, defend territories, and provide parental care (4). However, nesting males often sneak at neighboring nests (37). Although a male's success is higher while spawning in its own nest, a male loses little by sneaking at nearby nests when the opportunity arises. An individual male switches between sneaking and territorial behavior throughout its lifetime, depending on mating success at its own nest. In this species, all males can provide parental care and defend territories, but the two alternatives differ in the way males obtain access to mates.

In many species of salmon, male size appears to be bimodally distributed (30, 31). Large males compete for the opportunity to guard females, while smaller males employ sneak matings. Males of these two types also appear to have separate life history pathways. Large males grow for many years before reproducing, while small males mature early. Individuals do not switch between types. It appears that males of the two types have approximately equal lifetime fitness, although success per breeding season is lower for small males (30, 31). This lower success is compensated for by earlier reproductive age and higher survival rate to reproduction. Males that grow quickly during the juvenile period become early-maturing, noncompetitive types, whereas males that were slower-growing juveniles eventually become males that compete directly for access

to females; there may be a genetic component to these differences (30, 51). If early growth rate indicates general fitness, this comparison points out that larger males are not necessarily of better quality, or higher fitness.

Although we have focused our discussion on the territorial/nonterritorial male dichotomy, other patterns exist. Another common alternative is between males that court and those that coerce females into mating. This difference may depend on the female's choosiness, the male's quality, or even the local environment. For example, in guppies, *Poecilia reticulata*, individual males can either perform courtship displays or attempt to copulate without courtship (25, 26). Males adopt courtship more in the absence of predators and coercion more in the presence of predation risk (23, 26, 59). Alternatives also occur within species in degree of male parental investment; differences may represent differing life-history pathways, ontogenetic changes, or opportunistic switching. In many species, territorial males provide care for offspring while nonterritorial males do not (e.g. 29, 30, 43, 69, 70). In contrast, nonterritorial males of the cichlid *Lambrologus brichardi* help territorial males care for the offspring even if the nonterritorial male is unrelated to the young (63, 64).

Given the variety of basic patterns, it would be helpful to be able to predict the circumstances under which alternatives might evolve, and what the pattern of expression of alternatives might be. In order to do this it is necessary to understand what maintains the alternatives as well as the factors that determine pattern of expression. Classically, most male alternative reproductive behaviors have been assumed to arise as a consequence of "winner-take-all" situations in which a few individuals in the population accrue most of the mating success. In these cases, selection is expected to be very strong on other individuals to achieve matings through other means. For example, in mating systems in which only the few largest or oldest males win competitions for access to mates, smaller males will be selected to adopt reproductive behaviors that do not involve direct competition, such as sneaking. Although a "winner-take-all" situation clearly can lead to the evolution of alternatives, it is not the only or even the most common situation.

Female Alternative Reproductive Behaviors

Although the existence of alternative reproductive patterns is well established, there has been very little discussion of such alternatives in females. Females do not typically compete directly for resources or mates, and many of the classic male alternatives appear to be the result of direct competition between males. However, females are active participants in the mating process, and female choice and parental investment can be complex strategies. As in males, if female access to mates is limited, then we might expect behaviors to evolve to circumvent this limitation. Similarly, if costs and benefits change ontogenetically,

we would expect behavior to differ with age or size. We present here some examples.

MATE CHOICE AND COPYING Female choice of males before mating occurs in many species, and has gained attention as an important component of female reproductive strategies (1). Both theory and experimental studies suggest that some females may copy the mate choice of others in the population (18, 21, 38, 41, 45, 57, 73). This can be an evolutionarily adaptive behavior if females either differ in their ability to assess males or if assessment carries high costs (45, 57, 73), and younger or less experienced females do appear more prone to copy (20). Clearly, females can copy only the actual mate choices made by other females, and thus copying can exist only in the presence of another behavioral alternative. Copy or independent choice behaviors represent a good example of female alternative reproductive behaviors. In guppies, females copy the mate choice of other females when given the opportunity to observe another female's choice (18). Older females are not influenced by the decisions of younger females, while young females commonly copy the choice of older females (19). Individual females will both copy and choose depending on the circumstances, so both opportunity and age seem to influence female decisions.

RESISTANCE TO COERCION Females may also differ in the degree to which they require male courtship or resist coercion. In guppies, females usually experience extensive courtship before they are willing to mate (24, 25, 49). Males often attempt to force copulations without courtship, which females usually resist (25, 26). However, in the presence of a predator, females are willing to copulate without courtship (27, 49). It has been argued that females avoid increased risk of predation by accepting copulations without courtship (56). Individual females within a population express both alternatives, and their tendency to require courtship is mediated by differences in predation risk.

MODE OF MATING Females differ in the way they evaluate mates and may also choose between mating modes. Females of some species choose between pair- or group-mating modes. In the bluehead wrasse, both group-spawning and pair-spawning sites exist within a single population, and females are free to spawn at either type of site (74, 80). Some females tend to mate consistently at a group spawning site, where they mate with many males, while other females tend to visit a pair-spawning site, where they mate with only a territorial male (76, 77). While there appear to be no life-history differences between pair- and group-spawning females, nearly all females switch to pair-spawning when they reach large sizes (75). It is not known why some females choose one mode over the other, but these consistent differences persist between individual females within a single population.

In the damselfish *Chromis multilineata*, female sneaking occurs. Many individuals of this species carry the isopod ectoparasite *Anilocra multilineata*. A healthy male appears to deny parasitized females access to its nest. As a result, parasitized females rush into the nests of successful males to deposit their eggs and are quickly chased out (39). While these observations are preliminary, they indicate that sneaking may not be only a male behavior, and as in males, it is found in circumstances wherein access to mating is denied to a particular class of individuals.

PARENTAL CARE Females may also differ with respect to their choice of post-mating care of eggs. A striking example of female alternatives is found in the peacock wrasse, *Symphodus tinca*, in which parental care is facultative (69, 70). A female tends to mate with territorial males that care for her eggs (43). However, the same females will also mate outside of territories with males that do not provide parental care (69, 82). While egg survival is always higher in a nest, for females that cannot find suitable nests in which to lay their eggs, the cost of searching can outweigh the lower survival of untended offspring (82). The relative abundance of the two behaviors changes through the season as the availability of nests and the chance of egg survival out of the nest change (82). Females may either mate with a parental male or non-parental male, and female choice varies both between and within individual females.

Thus, distinct alternatives may occur within and between individual females in the same population. As in males, alternatives appear in all three components of reproductive fitness: access to mates, mating mode, and parental care (summarized in Table 1). While males commonly differ in the degree to which they enter into male-male competition, territoriality, or parental care investment, females tend to differ more in exercising choice in pre-mating, mating, and post-mating situations. As with males, some female alternatives depend on the existence of another alternative in the same or opposite sex, while in other cases alternatives can exist independently. Male alternatives in these species would not exist independent of female alternatives. There is a need to develop theory relevant to the expression and maintenance of female alternatives and to consider the links between male and female alternative reproductive behaviors.

UNDERLYING MECHANISMS

Mechanisms for the Maintenance of Alternative Reproductive Behaviors

The variety of mechanisms that have been postulated to allow the stable coexistence of alternative reproductive behaviors (2, 10, 14, 17, 22, 30, 40, 44, 47, 52, 53) have been reviewed elsewhere (2, 8, 22, 30, 33, 60). Alternative behaviors

Table 1 Examples of alternative reproductive behaviors in males and females

Species	Three main components of reproductive behaviors		
	Alternative access to mates	Mating mode alternatives	Parental investment
<i>Oncorhynchus kisutch</i> (coho salmon)	M: compete for access to females or sneak F: none	none none	none none
<i>Lepomis macrochirus</i> (bluegill sunfish)	M: territorial/nonterritorial F: none	pair spawn or sneak spawn none	care/no care none
<i>Gasterosteus aculeatus</i> (threespine stickleback)	M: none F: none	spawn in own nest or neighbor's nest none	none none
<i>Poecilia reticulata</i> (guppy)	M: coerce or court F: copy or choose	coerce or court resist or accept coercion	none none
<i>Thalassoma bifasciatum</i> (bluehead wrasse)	M: territorial/nonterritorial F: none	group or pair spawn group or pair spawn	none none
<i>Symphodus ocellatus</i> (ocellated wrasse)	M: territorial/nonterritorial F: none	spawn in own nest or sneak spawn none	care/no care none
<i>Symphodus tinca</i> (peacock wrasse)	M: territorial/nonterritorial F: none	spawn in territory or out of territory none	care/no care choose parental or nonparental male

classically have been divided into two categories. Discrete behavior differences that are the result of frequency dependence are often termed evolutionarily stable strategies (ESS: 50). Therefore, there is no single "best" behavior. For example, territorial and nonterritorial behaviors in the bluegill sunfish are postulated to be maintained by frequency-dependent fitness (32). Female choice may create frequency-dependence if females tend to choose rare males (42). If female fitness depends on the number of other females using a mating mode, the resulting frequency-dependence could give rise to alternative female behaviors. These behavior types are expected to have equal fitness at equilibrium (Figure 1; also 30, 60). The fitness of a frequency-dependent behavior is affected by the number of other individuals adopting the same behavior.

The other important mechanism facilitating the existence of alternatives is condition-dependent fitness (2, 17, 30). This occurs where the fitness of a behavior is dependent upon some characteristic of the individual or the environment. If two alternative behaviors each has a different relationship of fitness with condition, alternatives can be maintained (see Figure 2). For example, male behavior may depend on juvenile growth rate (30) in Pacific salmon, and female copying in guppies may depend on predation risk. Condition-dependence

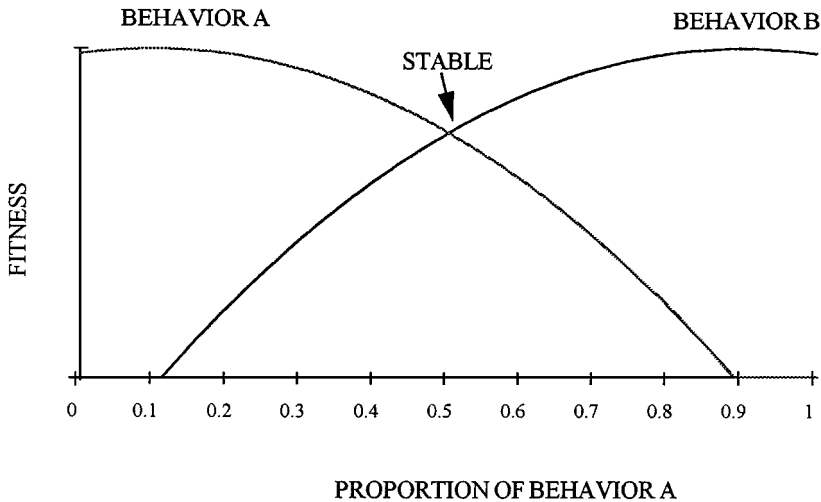


Figure 1 Negative frequency dependence can maintain alternative reproductive behaviors. At equilibrium (the ESS) alternatives have equal but suboptimal fitness. The proportion of alternatives in the population will be determined by the form of frequency-dependence. The stable solution occurs where the two fitness curves cross.

occurs if only individuals of high quality obtain most of the mating success. If individuals compete for access to mates or resources, and success in competition depends on age, experience, energy reserves, or size, then condition-dependent alternatives could result. For example, fecundity usually increases with size in fishes, and the cost of searching may decrease with experience.

A comprehensive theory does not currently exist regarding the relative importance of these two mechanisms in the maintenance of alternative behaviors. In reality, populations will often experience frequency-dependent selection and condition-dependent fitness simultaneously (33). Furthermore, complex interactions may occur among factors that influence the fitness of reproductive behaviors. For example, territorial males may compete for mating sites, while simultaneously competing with nonterritorial males using sperm competition tactics; territorial defense may be condition-dependent whereas sperm competition may be frequency-dependent. If males must allocate energy between sperm production and defense, maximizing fitness for one will not maximize it for the other. The best pattern of energy allocation may depend not only on social interactions, but also on total energy available and long-term tradeoffs between growth and reproduction. Female choice among males will affect the

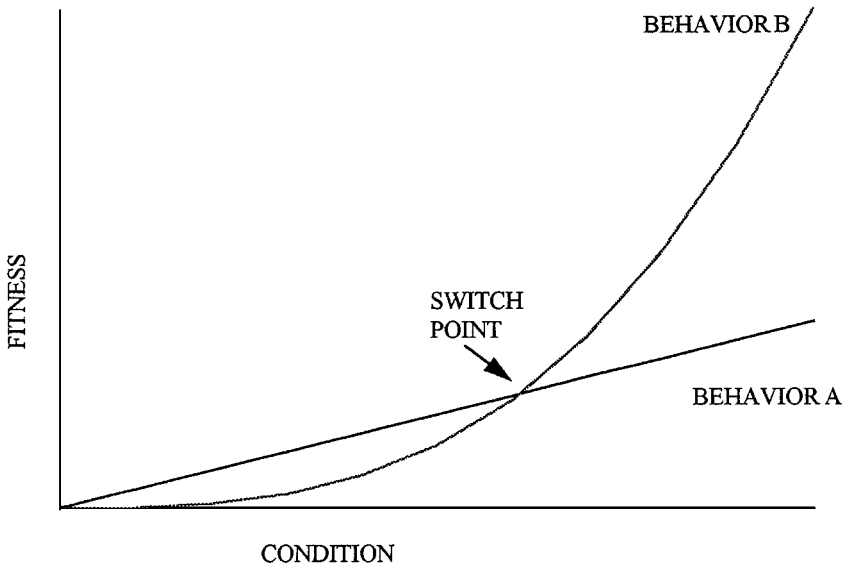


Figure 2 Condition-dependence can maintain alternatives. Two fitness curves are shown as a function of increasing condition. A particular individual is predicted to switch between behavior A and B at the point where the two functions cross. Different individuals are not predicted to have equal fitness.

fitness of each male reproductive tactic as well, and that choice may depend simultaneously on individual condition, male behavior, environmental state, and frequency of other females choosing the same site or male.

Genetic Basis of Alternatives

Alternative reproductive behaviors are sometimes classified with respect to underlying genetics. Alternatives maintained by frequency-dependence may be the result of either a genetic polymorphism or phenotypic plasticity. Condition-dependence can maintain alternatives only when variation in condition is independent of genotype.

In the swordtail, *Xiphophorus nigrensis*, size is sex-linked and determined by a single locus (61, 62, 83). Small males sneak behind a female to copulate, while large males display in front of a female before copulation, and intermediate-sized males adopt both behaviors. Male behavior is correlated with size, which is genetic in origin. In contrast, male guppies adopt both alternatives, and behavior choice appears to be determined by predation risk (59). Most of the examples of female alternatives mentioned above could

occur within individuals and therefore are likely to result from conditional responses.

If alternatives are expected to evolve under predictable circumstances, is it also possible to predict their underlying genetics? As mentioned above, frequency-dependent alternatives can result from either a genetic polymorphism or phenotypic plasticity. Since these two mechanisms can lead to the same phenotypic distributions, they may in some circumstances be equivalent. However, if individuals switch between alternatives, then only behavioral plasticity can be responsible. While simple genetic polymorphisms may evolve easily and adjust to changes in the equilibrium frequency, the fitness of the individual genotype will be greater if it can adapt to changes in the optimal frequency of each alternative.

Patterns of Expression

Alternative reproductive behaviors may occur either between or within individuals (Figure 3). In the bluegill sunfish, differences occur between males, which act either as nonterritorial or as nesting males. In contrast, male peacock wrasses facultatively switch between nesting behavior and spawning out of nests, and individual male sticklebacks switch between spawning in their own and their neighbor's nest. Clearly, if alternatives are expressed within individuals, the only possible mechanism is phenotypic plasticity, while alternatives occurring between individuals allow the possibility of a genetic polymorphism as well. Either frequency-dependence or condition-dependence can lead to alternatives occurring between and within individuals. For example, if bluegill alternatives are the result of frequency-dependence, then either genetic polymorphism or plasticity could be responsible. However, in peacock wrasse females, switching between alternatives depends on the availability of nests and thus likely does not represent a genetic polymorphism.

Do any factors exist that would predict one type of expression over another? Regardless of origin, the cost of switching will influence the pattern of expression. Although it has been suggested that, if alternatives involve morphological differences, they are likely to be irreversible, whereas solely behavioral variation may enable switching (5, 6, 8, 52). However, costs of switching between behavior types, as might occur if individuals must learn new behaviors or accrue territories, can be high. In the bluehead wrasse, males not only change anatomically by decreasing allocation to testes and changing color patterns, but they must also compete for a territory. Males in this species switch only once to territorial behavior (36). In peacock wrasse females, switching from searching for nests and spawning out of nests is relatively free of costs because nonterritorial males are always available to spawn with females of either inclination (82).

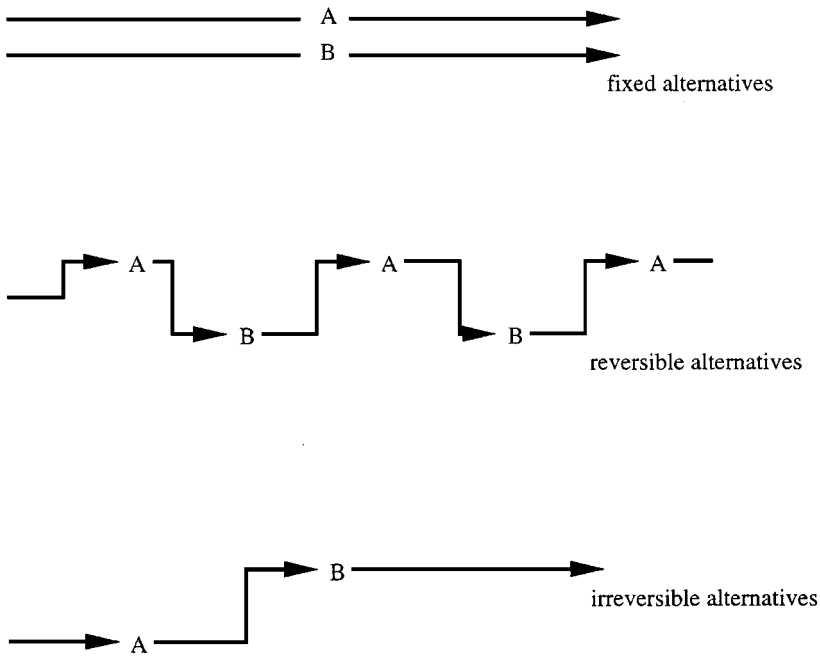


Figure 3 Alternative reproductive behavior patterns may be fixed, reversible, or irreversible within individuals. Redrawn with permission from Gross (30). Condition (age, size, or experience) increases from left to right.

If fitness is condition-dependent, the dynamics of the state of the individual or environment are expected to determine whether alternatives are fixed, reversible, or irreversible (Figure 3). For example, if fitness is size-dependent, but size is determined by factors in the juvenile stage, individuals may not be able to change size after maturity and thus can adopt only one behavior. In contrast, individuals may change behavior through ontogeny if growth continues after maturity. If absolute size determines behavior choice, switches need not be reversible. In contrast, relative size differences might select for reversible alternatives. If energy reserves or the current environment determine fitness, individuals may adopt reversible tactics. Stickleback males switch constantly between sneaking and nesting determined by mating opportunity (28), and female guppies switch between avoiding and accepting coercion based on predation risk (48, 49).

While Table 2 outlines some basic situations that will lead to one pattern over the other, predictive ability is clearly a weak link in our understanding

Table 2 Underlying mechanisms of alternative reproductive behaviors

	Frequency-dependence	Condition-dependence
Genetic basis	<ul style="list-style-type: none"> ● genetic polymorphism or phenotypic plasticity 	<ul style="list-style-type: none"> ● phenotypic plasticity
Pattern of expression (fixed, reversible, or irreversible alternatives)	<ul style="list-style-type: none"> ● any pattern possible ● switches occur with a fixed probability ● influenced by the cost of switching 	<ul style="list-style-type: none"> ● any pattern possible ● condition determines switching ● influenced by the cost of switching and the condition dynamics

of alternative reproductive behaviors in fishes. Future theory and experimental work should focus on the biological factors that determine the underlying mechanism, genetic basis, and pattern of expression of alternatives. Ideally, theory should allow both explanation of observed variation in mating system and prediction of the existence and pattern of alternative reproductive behaviors.

INTERSEXUAL DYNAMICS: A NEW VIEW OF THE EVOLUTION OF ALTERNATIVE REPRODUCTIVE BEHAVIORS

Traditionally, alternative reproductive behaviors have been thought to result from competition between males for access to mates or resources. We have argued that not only do females have alternative reproductive behaviors, but many factors interact to determine the evolution of alternatives in both sexes. An important factor that has been ignored is the effect that conflict between the sexes might have on the evolution of alternatives. Intersexual conflict is now recognized as an important factor in determining mating systems (e.g. 1, 9, 12, 13, 49), and a comprehensive theory on alternative reproductive behaviors must consider the simultaneous effect of both intra- and inter-sexual conflict interactions.

As an example, note that males often compete among themselves for territories, but the territory connected with the highest mating success will be determined by female mating strategies. The degree of female choosiness will dictate the distribution of success between males and thus the degree to which males must compete for territories. Correspondingly, female choosiness will be affected by the variation in male and territory quality. Female willingness to mate with a male may also be affected by the presence of other females on the

territory. The existence of male alternatives depends on female willingness to mate with either male type, and female alternatives often differ in their choice between males. Thus, within-sex interactions may set the stage for between-sex conflict. Just as easily, mate choice can determine the degree of competition between males, and female choice can nullify predictions made, when only the interactions between males are considered. In order to have a complete understanding of the evolution of alternatives in either sex we must also consider the influence of the other sex on the existence of alternatives.

The Influence of Females on the Evolution of Male Alternatives

Females of some species exhibit a strong preference for one type of male, while females of other species show no choice between male behavior types. For example, females of the ocellated wrasse attempt to avoid nonterritorial males (71), while bluegill sunfish females seem indifferent (32). We would expect female choice to depend on whether male alternatives differentially affect female fitness. Furthermore, the cost of female choice and the ability to discriminate between males may also differ between species.

If male choices of alternatives have no direct effect on female fitness or offspring survival, then females should choose between alternatives only if indirect genetic benefits correlate with the alternative reproductive behaviors. However, mechanisms for the maintenance of genetic polymorphisms predict that at equilibrium male alternatives will have equal fitness. Thus, it is unlikely that females will choose between male alternatives maintained by frequency-dependence unless direct effects occur on female or offspring fitness. In support of this idea, females in the bluegill sunfish and Pacific salmon (in which male alternatives are proposed to be maintained by frequency-dependence) do not appear to choose actively between male alternatives (30, 32).

In contrast, females should exercise choice between male alternatives if direct fitness effects exist. For example, male alternatives might differ in their degree of investment in parental care and the resultant survival of offspring. In the peacock wrasse, *Symphodus tinca*, females prefer to spawn in nests where males provide parental care, spawning with nonparental males only if they are unable to find suitable nests within a limited period of searching (82). Equally, if females benefit from mate choice, they should prefer males that do not adopt coercive tactics. For example, in guppies, females actively avoid males that do not court, and they also benefit from choosing high-quality males (25, 58). Just as with the peacock wrasse, female choice between alternatives will depend on the costs, and in guppies, these costs seem to be mediated by predation risk (27, 49).

Clearly, if females choose directly between male alternatives, mate choice alone can either suppress or maintain alternatives in male behavior. Females can also influence the evolution of alternatives without actively choosing between male alternatives. For example, females can increase skew in reproductive success among males and thereby create a situation that favors the evolution of male alternatives. Thus, if females skew mating toward large males, sexual selection may lead to smaller males choosing other reproductive behaviors. In the end, this may not be to the female's benefit. One can imagine a situation in which females prefer to mate with males that are large because these males are able to obtain and defend the best territories. Smaller males may then be selected to attempt nonterritorial behaviors such as coercion of females or sneak spawning. If these small males are of lower quality, disrupt the mating, or decrease territorial male parental care through lowered paternity, female preference for large males may lead to a situation in which male alternatives actually lower female fitness.

The existence of alternatives in female choice could maintain male alternatives, or highly consistent female choice could lead to a situation in which a male alternative behavior has correspondingly consistent low fitness and does not persist. It is thus important to consider female behavior when attempting to make predictions about the evolution of male alternatives. Consider the basic predictions made by frequency- and condition-dependent fitness (Figures 1 and 2). By including female preference in the male fitness equation, we can ask what the equilibrium frequency of each alternative will be as a function of the degree of female preference for one alternative. Female choice can change the basic predictions drastically (Figure 4). The predicted frequency of male alternatives in the population increases as a function of female preference for that alternative. Sufficiently strong female choice can even suppress the existence of one alternative (Figure 4e). In the other extreme, female choice could conceivably maintain male alternative reproductive behaviors in the absence of either frequency- or condition-dependence. It is necessary to consider not only the benefits of a particular mate choice, but the costs as well, because these costs can create the opportunity for alternatives. Both female preferences and the ability to obtain a choice are important. For a complete understanding of male alternatives, male competition and female choice as well as the interactions between female choice and male behavior must be considered.

The Influence of Males on the Evolution of Female Alternatives

Female alternatives usually exist in terms of mate choice, and thus females often influence male fitness directly by determining male mating success. Males may

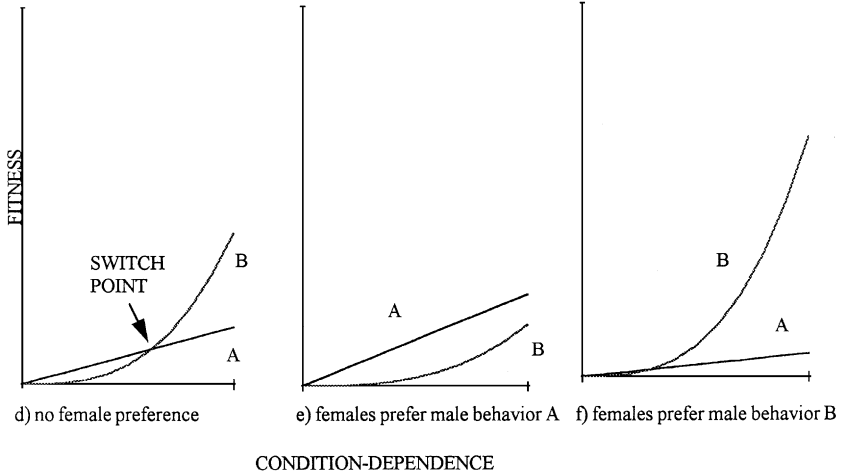
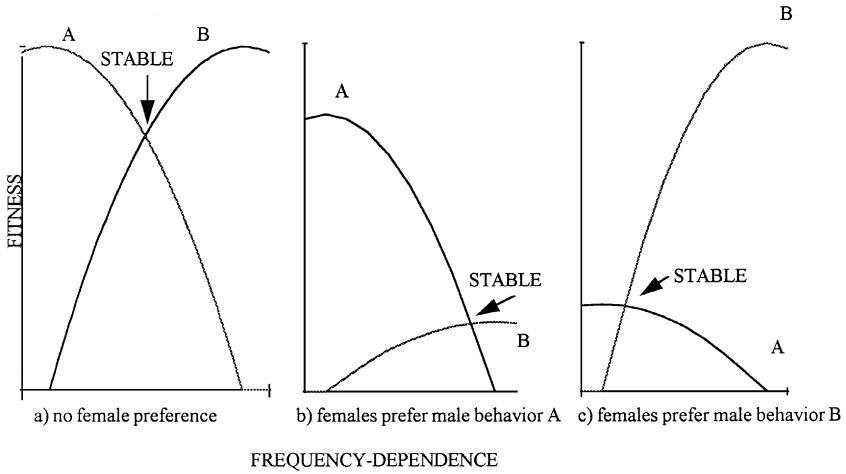


Figure 4 Female preference can influence predictions for male alternative reproductive patterns. Both frequency-dependence and condition-dependence can maintain alternatives within a sex. However, when female preference is included, predictions can change dramatically. Male distributions in the absence of female preference (left) can shift with female preference for male type A (center) or male type B (right). Female choice alone can change the frequency or even suppress the existence of either alternative.

not respond to female alternatives by being choosy themselves but may instead attempt to reduce a female's ability to choose through coercion or sneaking. Sneaking as an alternative to territorial behavior in many fishes may be the direct result of female choice to avoid spawning with small males.

As with females, males will influence female alternatives if they actively choose between females. This will occur when female alternatives have differential effects on male fitness and males are limited in their spawning rate (39, 55). Even if males are not limited, female choosiness could result in the appearance of a class of males that force copulations, which in turn leads to female alternatives between accepting coercion or attempting active choice (as in guppies, see above). If variation exists in the degree to which male alternatives invest in providing parental care, females may also adopt alternatives between demanding or doing without care of their offspring, as in the peacock wrasse. Male behavior may also affect female alternatives even in the absence of male alternatives. For example, high-quality females may choose high-quality males; if these males are limited in their mating rate, low-quality females have no option but to accept low-quality males (79). Admittedly, it is often impossible to identify cause and effect when both sexes have corresponding alternatives, and it is more instructive to model their joint evolution (see below).

Multiple Game Interactions and Coevolutionary Dynamics

The effect of males on females and of females on males both need to be considered in order to have a complete understanding of the evolution of alternative reproductive behaviors (35, 54). Females will determine, to a great extent, the mating success of various male behaviors, and skew in mating success due to female choice may lead to the evolution of male alternatives themselves. Male alternatives may, in turn, lead to the evolution of variation in female choice or other forms of variation in female reproductive behavior. Conflict between the sexes will be an important factor in determining patterns of mating behavior. This does not mean that competition or conflict within a sex is not also an important factor in mating systems. Instead, the existence and pattern of alternative reproductive behaviors in either sex will be the result of interactions within and between the sexes, and female behavior cannot be viewed separately from male behavior or vice versa. Considering the coevolution of male and female reproductive behavior by examining the links between male behavior and female behavior will lead to a better understanding of alternative reproductive behaviors and mating systems in general and may explain observations that seem counter-intuitive in light of present theory.

Imagine a species in which intrasexual competition leads a few strong males to all of the mating success, while most small males are not able to reproduce.

In another species, male-male competition is very weak. Standard theory would predict that only the former species should exhibit male alternative reproductive behaviors. However, strong and consistent female choice could lead to the absence of male alternatives in the species with male-male competition, and conditional female mate choice could lead to male alternatives in the species with no direct intrasexual competition. In parallel although theory might predict that female fitness would be higher in mating with one alternative, male coercion or sneaking might lead to the evolution of female alternative reproductive behaviors.

Ideally, theoretical predictions should include not only the effect of intersexual dynamics, but also the interactive effects of intra- and inter-sexual interactions. It has been suggested that dynamic programming games should be used to study the simultaneous effects of frequency- and condition-dependence on the evolution of alternative male reproductive behaviors (3). These models can be extended to model female behavior as well so that the dynamics of both intra- and inter-sexual interactions can be assessed, and even simple game theoretical models can demonstrate the importance of interactions between the sexes on the evolution of alternative reproductive behaviors (Henson, unpublished).

A consideration of intersexual dynamics can often suggest the basis for otherwise counter-intuitive behavior. For example, in the peacock wrasse, small sneaking males do not interfere with the mating of large males at the beginning of their nesting cycle, even though mating rates can be very high, and mating is performed in plain view of the small males (Warner, personal observation). Females in this species do not prefer to spawn with sneaker males (71) but will do so if a nest is very attractive. Since egg load in a nest increases its attractiveness to females (71, 82), small males may allow a nest to gain eggs before initiating alternative reproductive behaviors there.

In the ocellated wrasse, nests with high mating rates attract sneaker males, but mating rate decreases as sneaker numbers increase (71). Usually, nesting males court females and chase sneaker males away from the nest (66). However, at times, when the number of sneakers at the nest becomes very high, nesting males will refuse to mate with willing females (SA Henson, personal observation). This counter-intuitive observation may be explained by the interactions between male alternatives. If mating rate decreases at the nests, sneaker males leave, thus increasing the later mating success of the nesting male. Consideration of both female choice and interactions between male alternatives is needed to understand this otherwise surprising observation.

In general, females will choose between male alternatives when direct fitness effects occur. Male alternatives should exist only if female fitness is not affected or if male alternatives circumvent female choice, as with sneaking behavior or forced copulations. Similarly, female alternatives will exist either when male

fitness is not affected by alternatives or when males have not been able to prevent females from exercising their options. Interactions between the sexes also can lead to counter-intuitive patterns of alternative reproductive behaviors, such as the absence of alternatives in a species where fitness is condition-dependent or the presence of alternatives in a system without any of the classical mechanisms for maintaining alternatives. To understand observed behavior and make predictions regarding the evolution and expression of alternatives, intersexual dynamics must be considered.

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