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Mechanisms of sexual selection: insights from fishes

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Studies of mating systems of fishes provide important insights into the types of male traits affected by sexual selection and the interaction of sexual and natural selection in the elaboration of male secondary sexual traits. Here I examine studies which test predictions of current models of sexual selection, document common trends in sexually selected traits, and show how models of adaptive female choice provide insights into the evolution of complex, multi-function male traits.

1. Introduction

1.1. "Adaptive" and "arbitrary" models of sexual selection

Darwin (1871) proposed the operation of intrasexual and intersexual selection to explain the evolution of exaggerated male traits. Although intrasexual selection has been accepted as a mechanism by which males evolve elaborate secondary sexual traits which signal social dominance and are used in aggressive contests, the importance of intersexual selection as a mechanism by which males have acquired exaggerated traits to display to females during courtship and mating was less readily accepted. It is currently the focus of a major controversy. The controversy concerns the types of male traits elaborated through intersexual selection, the nature of the benefits gained by females that choose mates with exaggerated characteristics, and the mechanisms underlying the interaction between female preferences and the expression of male traits.

One of the crucial issues to be resolved is whether female choice is arbitrary or adaptive. Arbitrary female choice would select for the elaboration of any male trait which confers a mating advantage to male offspring expressing genes for that particular trait. It is considered arbitrary, since sexual selection could potentially act to amplify any male trait for which there is an initial female preference and sufficient additive genetic variance in the population. Models of arbitrary female choice (e.g. Lande 1981, Kirkpatrick 1982) predict the establishment of a genetic correlation between a male trait and female preference for this trait, which then results in rapid and often extreme exaggeration of the male trait. Such a process eventually may lead to a reduction in population fitness, if the trait decreases the survivorship of sons, or lowers the viability and/or fertility of daughters (Lande 1981, Kirkpatrick 1982). These models focus solely on the sexually selected trait, its effect on male reproductive success through female choice of mates, and its cost in terms of male survivorship. They make no predictions regarding the relationship between the sexually selected trait and other male traits which are subjected to natural rather than sexual selection, and which enhance fitness in a Darwinian sense through viability and/or fertlity.

Models of adaptive female choice postulate the evolution of secondary sexual traits that indicate a male's high genetic quality (Kodric-Brown & Brown 1984, Andersson 1986, Pomiankowski 1987, Hasson 1989). They assume that the size of the ornament within a species is positively correlated with the overall genetic fitness of the male. Females mating with more highly ornamented males would pass on superior genes that would enhance the viability and/or fecundity of both their sons and daughters. Secondary sexual traits elaborated through adaptive female choice should be conditionally expressed and phenotypically plastic; they should vary with a male's physical condition and social status. They should be costly to produce and maintain. Otherwise they would be subject to cheating and replacement by low-cost signals of low information content. Adaptive female choice should favor those traits that most accurately reflect a male's phenotypic and genotypic quality. In the adaptive or "good genes" models of female choice the emphasis is shifted from the sexually selected traits themselves, to correlations between these traits and other traits reflecting a male's vigor and vitality, such as foraging efficiency, age, growth rate, body size, physical condition, resistance to parasites and disease, and social status.

Models of adaptive female choice provide insights into three important processes. First, the models make empirically testable predictions regarding the interactions between sexual and natural selection on male traits. They postulate a positive phenotypic correlation and a positive genetic correlation between the expression of a secondary sexual trait and the components of male fitness. Males with the most exaggerated sexual traits should be the most vigorous, healthiest, oldest, or most dominant individuals, and they should also secure most matings. Thus sexual selection should reinforce the effects of natural selection.

Second, models of adaptive female choice potentially also offer insights into the evolution of complex, multi-function signals used in aggressive contests, courtship, and mating. Since adaptive female choice should favor the elaboration of traits that are condition-dependent, costly, and high in information content, sexual selection should favor the evolution of a suite of traits, that may be either positively or negatively correlated and may serve a variety of functions. Such complex signals should reflect the interaction of complementary or antagonistic functions, such as courtship of females and nest guarding.

Finally, adaptive female choice models also provide insights into the interaction between intra- and intersexual selection, because the same male traits may function both in attracting females and in signalling dominance to potential rivals. The latter will act to reinforce their honesty through constant challenging and aggressive contests.

Recent quantitative genetic and analytical models of intersexual selection have presented theoretically plausible mechanisms by which both adaptive and arbitrary female choice may result in elaboration of certain male traits into ornaments (Anderson 1982, 1986, Lande 1981, Kirkpatrick 1982, Pomiankowski 1987, Hasson 1989). Many assumptions and predictions of both types of models are not empirically testable according to Andersson (1987). However, even those that are testable remain, for the most part, untested on real systems.

1.2. Fish mating systems

Breeding systems of many fishes are ideally suited to test not only the assumptions and predictions of the arbitrary and adaptive models of intersexual selection, but also the interactions between intersexual and intrasexual selection in the elaboration of male traits. Some breeding systems can be manipulated experimentally (e.g. Downhower & Brown 1980, Endler 1980, Hastings 1988a, Kodric-Brown 1988, Rowland 1989, McLennan & McPhail 1989a, b, Bisazza et al. 1989), thus providing unique opportunities for examining the precise nature of female choice and for testing specific predictions of the two types of models. Furthermore, a comparison between breeding systems within and between families of fishes for which sufficient data are available, not only will provide insights into the types of traits elaborated by intersexual and intrasexual selection operating within phylogenetic constraints, but also will address some fundamental issues regarding the interaction between natural and sexual selection.

The majority of breeding systems of fishes can be described as resource-based polybrachygamy (Selander 1965), where both males and females mate with several sexual partners during a breeding season, males aggressively defend a spawning substrate or nest, and provide either incidental or direct care of eggs and fry. These breeding systems are not directly suitable to test predictions of current models of intersexual selection sensu stricto, since under these conditions females should invariably select traits of males and/or their spawning sites which would maximize survivorship of eggs and fry. However, they are ideal for examining the complex relationships between natural, intrasexual, and intersexual selection, and their combined effects on the elaboration of exaggerated male traits. To date, most empirical studies of sexual selection have focused only on female choice, even though male-male competition may be equally important, since male traits appear to function both as signals of male dominance and to confer a mating advantage due to the attraction of females.

Here I review the literature on mating systems in fishes, with an emphasis on current manipulative studies of mate choice. I focus on the types of traits important in enhancing male mating success, either through social dominance or female choice, and document some general patterns in the types of traits elaborated by sexual selection. Furthermore, I attempt to interpret the results of mate choice experiments with guppies (*Poecilia reticulata*), sticklebacks (*Gasterosteus aculeatus*), and other less well studied species in terms of the predictions of the "arbitrary" (e.g. Lande 1981, Kirkpatrick 1982) and the "adaptive" (e.g. Kodric-Brown & Brown 1984, Andersson 1986, Hasson 1989) models of intersexual selection. Finally, I suggest several approaches for future empirical studies.

2. Types of sexually selected traits

Sexual selection could act on females in such a way as to maximize both their fecundity and the viability of their offspring. In species where females oviposit on substrates, predation on eggs and fry is usually high. Potential egg predators include invertebrates, other species of fishes, as well as conspecifics, and very often the male parent himself in species with direct or incidental paternal care. Thus in these species females should be under strong selection to minimize losses due to egg and fry predators by selecting suitable oviposition substrates and males with traits which would either directly indicate parenting ability, or be correlated with other traits enhancing offspring survivorship. Female choice should thus focus either on immediate material benefits, such as nest quality, type of substrate, paternal care (e.g. fanning of eggs Ridley & Rechten 1981) or traits such as a male's size, courtship vigor or intensity of nuptial coloration, which may indicate possession of a territory or social dominance (e.g. Hoelzer 1989) and thus the ability to aggressively exclude potential egg predators from the territory.

Both manipulative and correlative studies of mate choice in fishes (Table 1) indicate that characteristics of a male's territory, such as size, location, (e.g. Jones 1981, Schmale 1981, Sargent 1982, Kodric-Brown 1983, Warner 1987), and availability and quality of oviposition substrate (e.g. Downhower et al. 1983, deMartini 1988, Thompson 1986, Hastings 1988 a, b, Bisazza & Marconato 1988, Bisazza et al. 1989) are important criteria of female choice.

2.1. Size

Male body size is perhaps the most ubiquitous sexually dimorphic trait. In some species, where it functions in establishing male dominance (Table 1 and 2; Centrarchidae, Chaenopsidae, Cottidae, Cyprinidae, Gasterosteidae, Gobiidae, Hexagramidae, Labridae, Percidae, Pomacentridae, some species of Poeciliidae, Salmonidae and Tripterygiidae), it is apparently acted upon primarily by intrasexual selection. In other groups (Table 1) it is positively associated with other traits, and could also be acted upon by intersexual selection, especially in species where females actively select potential mates (e.g. Bleniidae, Chaenopsidae, Cottidae, Gobiidae). Large males typically are able to defend better quality territories with superior oviposition sites and thus to attract a greater number of females than smaller males (e.g. Labridae: Martel & Green 1987; Gobiidae: Bisazza et al. 1989). Often body size is positively correlated with other traits which are important to females, such as the quality and

Table 1. Sexually selected traits in fishes: function of male body size and other sexually selected traits in male dominance and female choice (symbols are as follows: a = male-male competition, b = female choice, c = male choice and * = experimental evidence).

Trait(s)	Funct.	References
Bleniidae		
Ohioblennius atlanticus		
size	b,c	Cote & Hunte'89
nest size	b	
paternal care	b	
Centrarchidae		
Ambloplites rupestris		
size	a b	Nolte & Keenleyside'86
Chaenopsidae		
Acanthemblemaria crockeri		
size x	a b*	Hastings'88a
residency x	b*	
paternal care	b*	
Coralliozetus angelica		
size x	a,b*	Hastings'88b
male condition x	b*	
spawning site	b*	
Cichlidae		
Cichlasoma nigrofasciatum		
size x	b*	Noonan'83
paternal care	b*	Keenleyside et al.'85
Cottidae		
Cotus bairdi, C. gobio		
size x	a b*	Downhower & Brown'80,
paternal care	b*	Bisazza & Marconato'88
C. hangiongensis		
size x	b*	Goto'87
paternal care		
Gobiidae		
Pomatoschistus minutus		
size x	a*	Lindström'88
nest size		
Amblyeleotris japonica		
size	a	Yanagisawa'82
paternal care		
Padogobius martensi		
size	a*	Bisazza et al'89
nest quality	b*	
Coryphopterus nicholsi		
size	a b*	Cole'82
courtship	b*	
Labridae		
Coris dorsomaculata		
courtship	b	Tribble'82
Tautogolabrus adspersus		
size x	a	Martel& Green'87
territory x	a b	
courtship x	b	
Pseudolabrus celidotus		
spawning site	b	Jones'81
courtship	b	
Thalassoma bifasciatum		
spawning site	b*	Warner'87
Pomacentridae		
Pomacentrus partitus		
size x	a b	Schmale'81
courtship	b	
sound	b*	Myrberg et al.'86
Hypsypops rubicundus		
spawning site	b	Sikkel'88
Malacoctenus macropus		
size x	a	Petersen'88
spawning site	b	
Glyphidontops biocellatus		
color x	b	Thresher & Moyer'83
display	b	
G. cyaneus		
size	a b	Thresher & Moyer'83
Stegastes rectifraenum		
size	a*	Hoelzer'89
courtship	b*	
spawning site	b*	
Salmonidae		
Oncorhynchus nerka		
size	a*c*	Foote'88
O. kisutch		
size	a c	Sargent et al.'86
Syngnathidae		
Nerophis ophidion		
size x	c	Berglund et al.'86
display x	c	
color	c	
Tripterygiidae		
Fosterygion varium		
size	a b*	Thompson'86
spawning site	a b*	

intensity of courtship displays (e.g. Gobiidae: Cole 1982; Pomacentridae: Schmale 1981; Poeciliidae: Constantz 1975, Hughes 1985, Ryan & Causey 1989; Gasterosteidae: Rowland 1984, 1989a, b), behaviors associated with egg guarding (e.g. aggression toward intruders: Cichlidae: Keenleyside et al. 1985; Labridae: Jones 1981), egg care (Cottidae: Goto 1987; Cyprinidae: Unger & Sargent 1988; Pomacentridae: Hoelzer 1989), or past reproductive success such as presence of eggs on a territory (e.g. Chaenopsidae: Hastings 1988a; Gasterosteidae: Ridley & Rechten 1981). In species with reverse sexual dimorphism (e.g. Syngnathidae: Berglund et al. 1986), male mate choice is based both on female size and intensity of courtship displays.

2.2. Nuptial coloration

Intensification of sexual dichromatism in permanently dichromatic species, or development of nuptial coloration during the breeding season is characteristic of many species of fishes (Table 2). The expression of nuptial coloration varies between males, and is positively correlated with a male's breeding condition, social status, and possession of a territory.

In polygynous or polybrachygamous species, nuptial coloration signals dominance or possession of a territory to males, and availability of resources, and/or past spawning performance to females. In *Cyprinodon pecosensis* nuptial coloration is associated with breeding status, since

Table 2. Sexually selected traits in fishes: function of nuptial coloration in male dominance and female choice (symbols: a = male-male competition, b = female choice, c = male choice and * = experimental evidence).

Trait(s)	Funct.	References
Cyprinidae		
Notropis leedsi		
color	a b	Rabito& Hines'85
size	a	
Pimephales promelas		
color	a b	Unger & Sargent '88
paternal care	b	
Cyprinodontidae		
Nothobranchius guentheri		
color	b	Haas'76
Cyprinodon pecosensis		
color x	a b	Kodric-Brown'83
territory quality	b	
Gasterosteidae		
Gasterosteus aculeatus		
size	a*b*c*	Rowland'84,'89
color	a*b*	Bakker & Sevenster'83
courtship	b*	McLennan & McPhail'89, Ward & Fitzgerald'87
paternal care	b	Ridley & Rechten '81
territory quality	b*	Sargent'82
Hexagrammidae		
Oxylebius pictus		
color	a b	DeMartini'85
courtship	b	
Percidae		
Etheostoma nigrum		
aggression	a b	Grant & Colgan '83
paternal care	b	
Etheostoma juliae		
color	a b	James & Taber'86
size	a b	
Poeciliidae		
Gambusia affinis		
size x	a*b*	Hughes'85
display	b*	
Gambusia hurtadoi		
color	a	McAlister'58
Poeciliopsis occidentalis		
size x	a b	Constantz'75
color x	b	
display	b	
Poecilia reticulata		
color patterns	b*	Endler'83, Houde '87
carotenoids	b*	Kodric-Brown'85, '89
display	a*b*	Kennedy et al.'87, Farr'76,'80
fin size	b*	Bischoff et al.'85
Poecilia latipinna		
fin size	b	Farr et al.'86
display	b	
Xiphophorus nigrensis		
size	a	Ryan & Causey '89
display	b*	
Limia zonata		
color	a	Farr'84
Limia melanogaster		
color x	a b	Farr'84
display	b	

only territorial males develop the bright blue breeding color (Kodric-Brown 1983). Nuptial coloration in this species is also condition-dependent and phenotypically plastic. The intensity of a male's breeding coloration depends on the quality of his territory, and also reflects his past mating success and agonistic encounters. Similarly in sticklebacks there is a positive interaction between the amount of red coloration on a male's body and his dominance (Bakker & Sevenster 1983, but see Rowland 1984). Nuptial coloration also functions in courtship, as well as in an agonistic context. Maintenance of a breeding coloration is costly, because males with a well-developed nuptial coloration engage in a greater number of agonistic interactions both with intruders and with neighboring territorial males. Thus the reliability of the signal is maintained through continuous testing by other males. Such multifunction signals should be particularly favored by sexual selection relative to single-function traits, such as those that operate only in epigamic selection. Thus it is not surprising that in many species of fishes, in which the function of nuptial coloration has been studied in some detail, (e.g. Cyprinidae, Cyprinodontidae, Gasterosteidae, Hexagramidae, Percidae, and Poeciliidae: *Poeciliopsis occidentalis*, and *Limia melanogaster*), breeding coloration functions in signalling dominance as well as in attracting females. However, the relative importance of intersexual and intrasexual selection in the evolution of such nuptial coloration has yet to be determined.

In species with brood cycles, a male's breeding coloration often is a complex signal which varies temporally, coinciding with whether he is in a courting or parenting phase. Since such functions as courting females and fanning or guarding eggs, are often mutually exclusive, they are frequently accompanied by changes in nuptial coloration, which apparently signal a change in role (e.g. Gasterosteidae). Females should be sensitive to temporal changes in a male's appearance and behavior, and clear, unambiguous signals which accurately reflect a particular stage of a male's brood cycle should be favored by sexual selection. Females misinterpreting such signals and laying eggs late in the brood cycle, when males already have switched to the parenting phase, would suffer higher egg predation due to male cannibalism (e.g. Petersen 1988, Hoelzer 1989). Thus females should continually test the accuracy and honesty of a male's nuptial signal by inspecting nests.

In species with extended paternal care, females assess males by means of multiple criteria, thus the relative importance and rank of these male traits may change depending on the stage of the breeding cycle. Thus male nuptial coloration may initially attract females, since it may signal a competitive male capable of defending a territory with a suitable spawning site, but as the male acquires egg batches, the criteria of female choice may change. Nuptial coloration may become of secondary importance. Eggs and their stage of development may be a more reliable cue to females than a male's nuptial coloration, since the number and condition of eggs indicate a male's past reproductive success and his ability to attract females. In species with complex nuptial signals which vary sequentially within individuals, as well as between individuals, the function of such signals will only be apparent if they are considered as components of a "mosaic" (McLennan & McPhail 1989a). For example, the "red" body color of three-spined sticklebacks is highly variable both within and between individuals. A variable signal potentially has a higher signal value, because the information it conveys more accurately reflects a male's current social status, physical condition, or stage of the brood cycle. Other aspects of a male's nuptial coloration, such as the intensity of the blue eye color or the black pigmentation on the body, are less variable, thus their contribution to the information content of the signal is smaller. However, the contrast they provide with red, is probably important in attracting females and focusing their attention to the more variable components of the signal. Thus females may evaluate males at several levels. They may be sensitive to the variation of important components of the signal, the ones with the highest information content, but the other components of the signal "mosaic" may increase the accuracy of the information by increasing the conspicuousness of these important components. Thus such multiple signals are integrated wholes, whose function will only be understood when they are examined on two levels — the variability and signal value of their component parts, as well as the function of, and the dynamic changes in the entire "mosaic" signal.

3. Correlations between sexually selected traits

Both experimental and field studies of mate choice indicate that female mating decisions are based on multiple criteria. In some species (e.g. Labridae, Pomacentridae, Gasterosteidae), females inspect males and their territories several times before selecting a mate. Many examples are listed in Tables 1 and 2. Three types of commonly observed interactions are:

1) Positive correlations between male size, expression of nuptial coloration, and the frequency, intensity and duration of courtship displays, all of which are correlated with male mating success;
2) Positive correlations between male size and paternal care, especially in species with brood cycles and extended paternal care of eggs and fry;
3) Interactions between male size, aggressive behavior, territory quality, and male spawning success.

The pattern that emerges is that female choice of males is based on a combination of male traits. The relative importance of each in affecting a female's mating decision will depend on how sensitive a particular trait is to environmental variation. For example, in a population of guppies where males have ready access to diets high in carotenoids and there is virtually no competition among males for such food resources, the intensity of the orange and red spots should not vary among males, and females should not weigh this male trait very heavily in selecting a mate. Other traits, such as courtship intensity should become relatively more important. Females do show such threshold responses. For example, in a laboratory study with three-spined sticklebacks, where the quality of nest sites was controlled, females chose mates based on the development and intensity of the red component of their breeding coloration. Thus they discriminated against pale males and invariably mated with bright males. However, when given a choice between males with intermediate development of the red component of nuptial coloration, they ceased to discriminate, at least on the basis of this trait (McLennan & McPhail 1989b). Thus female choice selects for built-in redundancy of signals, and a multi-level decision process. Females should be especially sensitive to those traits that show the highest inter- and intramale variation, and are accurate indicators of a male's phenotypic and genotypic quality. Thus it is no longer profitable to think in terms of relatively simple, unimodal signals which are elaborated by sexual selection. Empiricists must keep in mind that females may be assessing mates and males may be evaluating competitors on an entire suite of traits which vary in their phenotypic plasticity. The relative importance of each will depend on how accurately it reflects a male's phenotypic, thus genotypic quality.

4. Interaction between intrasexual and intersexual selection

The relative importance of the two types of sexual selection on the elaboration of secondary sexual traits of males depends in part on the cost of mate choice. If cost is high, then females are less likely to be discriminating, and male interactions may become relatively more important. Predation on females, either by conspecifics or heterospecifics may limit female choice. In *Cotus bairdi*, a species with paternal care, females prefer to mate with large males. However, it is the relative, rather than absolute size that is the important criterion of female choice (Downhower & Brown 1980, Downhower et al. 1983), since large differences in size between the sexes tend to increase the possibility that the female will be preyed upon by the male. In species where both sexes are territorial (e.g. Pomacentridae), or where males defend breeding territories (e.g. Chaenopsidae, Gobiidae, Gasterosteidae), predation costs to females while searching for mates may be high. Thus intensity of predation may limit female choice. Predation risk may even eliminate female choice entirely, so that females would visit the territory of the closest male, as long as it had an appropriate shelter for the eggs (e.g. Lindström 1988). In such species or populations, intermale competition for suitable breeding territories would become the important selective pressure.

5. Correlations between sexually selected traits and fitness traits

The inheritance of fitness traits is still disputed, although there is increasing empirical evidence indicating that at least some fitness traits are heritable (Watt et al. 1986, Charlesworth 1987). Studies of heritablility of fitness traits are complicated by the fact that there are few systems where genetic markers are associated with fitness traits. Also, standard parent-offspring correlations for fitness traits are difficult to obtain, because fitness, unlike many sexually selected traits that show simple inheritance or are sex-linked (e.g. guppies: Farr 1983), must be measured in the context of a normal environment where both competition and predation can take place. Thus a laboratory setting, where at best predation may be absent and the intensity of intermale competition may be reduced, is not adequate to test heritability of fitness traits, or correlations between sexually selected traits and fitness traits. Under field conditions, offspring disperse before reaching sexual maturity. Thus it is difficult, and usually practically impossible, to determine maternity or paternity of offspring, and to measure various components of fitness such as growth rates, age of first reproduction, survivorship, fecundity, and reproductive success.

Since direct measurements of fitness are impossible under field conditions, and difficult to simulate under laboratory conditions, fitness can only be inferred, or at best measured indirectly. Thus fitness traits, per se are not measured. Instead, traits that are correlated with various components of fitness, such as male vigor, dominance, foraging ability, resistance to parasites (inferred from low parasite loads) are measured, and their relationship to male mating success is assessed. Both in guppies (Kennedy et al. 1987) and sticklebacks (Bakker & Milinski 1989) females discriminate against parasitized males. In guppies, display rate is a phenotypically plastic trait that reflects a male's physical condition. It is inversely correlated with degree of parasitism. Since male displays are an important component of female choice, and females select males, at least in part, based on the intensity and duration of the courtship displays, parasitized males should have lower mating success.

Thus the intensity and duration of courtship should be an indicator of male vigor. Vigor is affected by the response of a male's genome to social and environmental factors such as the availability of resources and the intensity of competition for these resources. Courtship will also be inversely correlated with susceptibility to parasites and predators. Male vigor is associated with virtually all aspects of a male's phenotype and behavior, including the intensity of agonistic behaviors, which will determine his social dominance or access to a territory, his physical appearance, the intensity of his nuptial coloration, his courtship behaviors, his parenting ability, his size, and his energy reserves. Thus variance among males in all aspects of breeding activities can potentially be explained by differences in the vigor, health, or physical condition of males relative to other males in the population. In *Pseudolabrus* (Jones 1981) female choice of males is based on courtship intensity, an indicator of male vigor, rather than male age, body size or coloration.

An indirect approach to studying the interaction between sexual selection and natural selection on the development and expression of male phenotypes and underlying genotypes, is to look for correlations between sexually selected male traits which are positively correlated with male mating success, and other male characteristics that have evolved by natural selection and may contribute to survival. If the subset of breeding males in a population truly represents individuals that have demonstrated better than average abilities to acquire resources for growth and reproduction, which would reflect their superior foraging tactics, resistance to disease and avoidance of predators, then sexual selection should reinforce the effects of natural selection and we should see the following pattern:

Males with the most exaggerated sexually selected traits (e.g. nuptial color, courtship displays) should also be near the optimum for the population in morphological traits. Furthermore, males showing the least variance in these quantitative morphological traits should have the highest mating success. Quantitative traits such as fin ray number, sensory pores, and scaling pattern are characteristic of populations or species, are used as taxonomic characters, and presumably have been acted upon by natural selection. If there are population optima for such meristic traits, then the degree of deviation from the population mean of each trait, summed over a large number of quantitative traits, should be a relative measure of overall fitness of an individual. Thus males that show large deviations from the population mean in a number of quantitative morphological characters, should represent less fit phenotypes than those with traits near the population mean. The assumption, of course is that such traits are under stabilizing selection, and that phenotypes near the population mean are selected, while those with deviant values are selected against. Wide variation in such morphological traits indicates lack of developmental homeostasis (Mitton & Grant 1984, Quattro & Vrijenhoek 1989, but see Zink et al. 1985). High variance in bilateral asymmetry for a number of meristic traits is associated with low heterozygosity for a number of species. Beardsmore & Shami (1979) showed that female guppies with intermediate lateral line scale counts had higher fecundity than those with extreme lateral line scale counts. Thus both number and size of broods is positively correlated with degree of heterozygosity. At least in this species, there is stabilizing selection for intermediate phenotypes, since these have a higher fitness than extreme phenotypes. Unfortunately, as yet no such data are available for males.

Kodric-Brown & Hohmann (1990) tested these predictions with pupfish (*Cyprinodon pecosensis*). They compared the variance in 8 morphological traits for three groups of fish: breeding males, non-breeding males and females. Unlike non-breeding males, breeding males were defending territories, had well-developed breeding coloration, and were spawning. Breeding males tended to be less variable than non-breeding males and females for 7 out of the 8 morphological traits. Thus sexual selection, operating through a combination of male-male competition for breeding substrates and female choice of males with best territories or most intense breeding coloration, reinforces the effects of natural selection by eliminating the most variable male phenotypes, which, presumably, are also the less fit genotypes. Thus sexual selection acts as a more stringent selective sieve than natural selection, because a large proportion of males with less-fit phenotypes are unable to breed, even though they have survived to reproductive maturity. It would be instructive to pursue such studies on a finer scale, and to examine the relationship between the degree of expression of sexually selected traits in males, variance in morphometric traits (e.g. degree of asymmetry in bilateral meristic characters), fitness-related traits (e.g. swimming endurance) degree of heterozygosity, and reproductive success. Such studies are crucial to our understanding of the interaction between sexually-selected traits, other male traits not directly affecting mate choice or male dominance, and fitness.

6. Sexual selection in the guppy (*Poecilia reticulata*): a model system

The breeding system of the guppy is unusual among fishes in several respects. Males do not contribute any material benefits to females or their offspring. Males are extremely variable in their breeding coloration. This variation is expressed both at the level of a population as well as between populations. Also, since male dominance seems relatively unimportant (Houde 1987, but see Farr 1980) in determining male mating success, intersexual selection is probably the dominant selection pressure responsible for the evolution of male secondary sexual traits in this species. Thus the breeding system of the guppy provides a unique opportunity to study the mechanisms of intersexual selection without the complicating effects of intrasexual selection, and is ideally suited to test predictions of the "adaptive" and "arbitrary" models of female choice.

Male color patterns are genetically determined, and except for the carotenoid pigments, are mostly y-linked (Winge & Ditlevsen 1947). The extreme male polychromatism in this species is maintained by a combination of sexual selection, favoring conspicuous males that contrast with their background, and natural selection for crypsis in heterogeneous environments (Endler 1980). Experimental studies have shown that female preference of males is based on the proportion of the area of a male's body covered by iridescent and carotenoid pigments. Such males are preferred by females and have a higher mating success than males with smaller amounts of these two types of pigments (Endler 1983, Kodric-Brown 1985, Houde 1987).

Iridescent colors show relatively little phenotypic plasticity, thus they would fit the criteria of "arbitrary" sexually selected traits, since they are sex-limited, and relatively invariant. They enhance equally the mating success of all males expressing them. They also reduce the survivorship of individuals in environments where there are predators, thus their expression is counteracted by natural selection (Endler 1980, 1987).

Carotenoid-based colors, on the other hand, are phenotypically plastic, because their intensity is affected by diet (Schiedt et al. 1985). Since carotenoids cannot be synthesized but must be ingested, the intensity of a male's red and orange coloration reflects the availability of carotenoids in the diet. If prey-items high in carotenoids are limiting, the intensity of red and orange pigments should reflect foraging and perhaps competitive ability of a male. Thus the intensity of a male's carotenoid pigments varies with physical condition, and is a good indicator of his phenotypic, thus presumably his genotypic quality. Manipulations of dietary carotenoids in an experiment where male genotypes were carefully controlled by using full brothers, indicated that females were very sensitive to the intensity of carotenoid pigments. They preferentially responded to and mated with males whose diets were enhanced with carotenoids (Kodric-Brown 1989).

Another criterion of female choice is the intensity and duration of a male's courtship displays. Display rates are heritable (Farr 1983), but also phenotypically plastic, since they show social facilitation (Farr 1976). Male mating success is positively correlated with courtship intensity (Baerends et al. 1955, Farr 1980, Kodric-Brown 1989). Courtship is a phenotypically plastic trait reflecting male vigor as well as motivation. Both the frequency and type of courtship displays and the intensity of carotenoid pigments are negatively correlated with parasite load (Kennedy et al. 1987). Physical condition, as measured by swimming endurance, is positively correlated with the intensity of carotenoid colors (P. Nicoletto, personal comm.).

Thus, both male behavior and aspects of the carotenoid component of breeding coloration are variable, phenotypically plastic traits. Both show variation between individuals as well as within individuals over time, and thus have a high information content. Both indicate not only the phenotypic and genotypic quality of prospective mates, but also short-term, environmentally-induced changes in a male's health or social status. Since female choice probably is relative, and is based on a sub-sample of the male population encountered, females using phenotypically plastic, condition-dependent male traits such as courtship intensity and carotenoid pigments, will insure that they are always choosing the best available phenotypes and genotypes.

A central role of carotenoid pigments in mate choice seems to be characteristic of many breeding systems of fishes. It is an important criterion of female choice in Gasterosteidae and Cyprinodontidae (e.g. *Nothobranchius guentheri*).

Most of the sexually selected traits of *Poecilia reticulata* meet the criteria of the "adaptive" female choice models. Although both the size and location of carotenoid pigment spots as well as display rates are heritable, the intensity of expression of both types of traits is phenotypically plastic, varies with a male's physical conditon, and reflects his phenotypic and presumably genotypic quality. Iridescent colors and tail shape and size, in contrast, do appear to conform to predictions of the "arbitrary" models of female choice. Both of these traits enhance the mating success of males and both are sex-linked, so that costs and benefits accrue only to the male sex; both appear to be uncorrelated with other attributes which may be indicative of fitness. However, iridescent colors and size, shape, and pigmentation of the tail (Bischoff et al. 1985) may enhance the effectiveness of courtship displays, enabling females to evaluate more easily the development of adaptive signals in potential mates. Thus these traits may represent correlated traits, which are only indirectly acted upon by sexual selection.

8. Geographic variation in sexually selected traits

In species with multiple, geographically isolated populations, female choice of male traits may differ between populations in ways that may reflect adaptation to local conditions. In guppies, female choice of male traits shows evidence of such adaptations (Luyten & Liley 1985, Endler 1980, 1987, Breden & Stoner 1987, Stoner & Breden 1988, Houde 1988). Behavioral observations of populations from high predation environments show a reduction in both the frequency and intensity of male courtship displays and in the development of carotenoid and iridescent colors. Thus in these populations both "adaptive" and "arbitrary" sexually selected traits are reduced. Experimental studies of female choice indicate that females from populations exposed to high levels of piscivore predation prefer males that are both drab and have low display rates (Breden & Stoner 1987, Stoner & Breden 1988, Houde 1988). The results of such studies suggest that female choice has evolved under these local conditions. Other experiments by Ryan & Wagner (1987) on swordtails, support the idea that female choice is conservative, and not so readily modified. Females of *Xiphoporus pigmaeus* a species with small males which have low display rates, prefer to mate with the males of *X. nigrens*, which have higher display rates. Thus females still retain a preference for high display rates, which have been lost in conspecific males, perhaps due to drift or local selection.

What is the underlying mechanism for these different patterns in female choice? Both the "adaptive" and "arbitrary" female choice models provide insights into possible mechanisms. According to the "adaptive" female choice models, females should use criteria which would maximize the fitness of both their sons and daughters. Thus it would be a maladaptive strategy to mate with brightly colored males in high-predation environments, since any advantage gained by mating with showy males would be couterbalanced by high predation on their sons. The "arbitrary" models of sexual selection predict that local populations vary in types of male secondary sexual traits that evolve, because each population represents an evolutionary equilibrium, determined by mutation-selection balance and random factors such as genetic drift (Lande 1981, Kirkpatrick 1982). So far, empirical studies have not discriminated between alternative hypotheses about what types of male traits females should select. Perhaps high predation risk decreases the advantage of choosiness, search costs to females increase due to low population density, and sexual selection ceases to be a very important selective force (Endler 1983, 1987).

9. A suggested approach: definitive rather than correlative testing of viability models of sexual selection

Another approach to understanding the interactions between sexually selected traits and viability traits would be to focus on traits that contribute to survival and reproduction of offspring, rather than on sexually selected traits per se. So far, the results of both experimental and field studies of mate choice in fishes indicate that female choice is based on multiple criteria, and that the relative importance of each male trait in a female's evaluation and selection of mates is facultative and contextual. For example, the relative importance of a particular male trait in the female's selection process may vary with operational and/or adult sex ratios, which reflect availability of prospective mates, or with the cost of mate choice, expressed either as increased predation risk to females while mating with a conspicuous male, or to increased predation of conspicuous offspring.

Now that we are learning from simple laboratory experiments how sexual selection operates in such model systems as guppies, it is important to approach a second level of complexity. We need to understand the context in which sexual selection operates on populations in their natural environments. In particular, we need to place increased emphasis on the interaction between sexual and natural selection, and on genotype/phenotype/environment interactions, such as the effects of predators and competitors on the expression of secondary sexual traits and mate choice. Although the controversy regarding mechanisms of epigamic selection was at times acrimonious and controversial, it has paved the way to a better understanding of the action of sexual selection in the context of both the past evolutionary history of a species, and its current environment.

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