

Courtship and Mate Choice in Fishes: Integrating Behavioral and Sensory Ecology¹

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SYNOPSIS. Sexual selection theory predicts a coevolution between male sexual ornamentation and female preference. The implication of this prediction for sensory ecology is that there should be a tight coupling between the physiology of male signal production and the physiology of female signal reception. Indicator models of sexual selection predict that male ornamentation is correlated with male condition, and that female preference is correlated with male ornamentation. Indicator models of sexual selection have a conceptual overlap with resource acquisition and investment models of behavioral ecology. Empirical studies with fishes, particularly with guppies (*Poecilia reticulata*) and threespine sticklebacks (*Gasterosteus aculeatus*), suggest a strong connection between acquired resources, male condition, male ornamentation, male courtship, and female preference.

INTRODUCTION

Whereas behavioral ecology focuses on how major categories of behavior such as avoiding predators, feeding, mating, parental care, contribute to fitness (Krebs and Davies, 1987; Sargent, 1990), sensory ecology focuses on the sensory adaptations to accomplish these classes of behavior (Dusenbery, 1992). If the behavior of interest involves intraspecific interaction and communication, such as courtship and mate choice, then integrating these two approaches can reveal insights into how and why signalers and receivers are coadapted.

Since Darwin's (1871) landmark treatise, evolutionary biologists have been fascinated by the phenomena of sexual dimorphism and sexual selection. Darwin was particularly intrigued by his observation that the males of most species have elaborate ornaments that are ostentatiously displayed during intrasexual competition and courtship; thus, he proposed his theory of sexual

selection, which can be defined as the differential ability of different phenotypes to obtain mates and reproduce, due to two forms of intraspecific interaction: 1. competition within a sex for access to mates or to resources for mating (intrasexual selection); and, 2. mate choice between the sexes (intersexual selection). Morphology and behavior conducive to fighting ability (*e.g.*, antlers in deer) are thought to have evolved through intrasexual selection; whereas, morphology and behavior involved in courtship (*e.g.*, the peacock's tail) are thought to have evolved through intersexual selection (see Andersson, 1994, for review). In most species, females are the limiting sex; that is, female reproduction is limited primarily by resources, whereas male reproduction is limited primarily by the number of females with whom they mate (Bateman, 1948; Williams, 1975). Consequently, most studies of sexual selection have focused on males.

Darwin (1871) himself recognized that these ornaments must have survival costs for their bearers; thus, he hypothesized that the survival costs of male ornamentation are offset by benefits in obtaining mates. An implication of Darwin's theory of sexual selection is that male ornaments act as signals to rival males, females, or both. There has been relatively little analytical modeling of intrasexual selection; however,

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genetic models of intersexual selection illustrate that through assortative mating, male ornaments and female preferences may coevolve (*e.g.*, Fisher, 1915, 1930; O'Donald, 1980; Lande, 1980, 1981; Kirkpatrick, 1982). This coevolutionary process, between signaler and receiver, has profound implications for sensory ecology. Not only would one predict a correlation between male ornament and female preference, but also a coupling of the underlying physiologies of male signal production and female signal reception.

We are intrigued by a particular class of sexual selection models, which are collectively referred to as indicator models (see Andersson, 1994, for review). In these models, male ornaments evolve to "indicate" or "honestly signal" some aspect of male phenotypic quality, genetic quality, or both, and female preference evolves to be correlated with the degree of male ornamentation (*e.g.*, Zahavi, 1975, 1977; Hamilton and Zuk, 1982; Hasson, 1989, 1997; Grafen, 1990*a, b*; Folstad and Karter, 1992; Price *et al.*, 1993; Wolf *et al.*, 1997). These models provide a conceptual basis for understanding what is being signaled by males. In addition, these models provide a conceptual link to the dynamics of resource acquisition, and subsequent investment of acquired resources into components of fitness (*e.g.*, Houston and McNamara, 1988; Mangel and Clark, 1988).

Animals acquire resources throughout their lives. Although these resources are incorporated into the phenotype in a variety of different ways, they ultimately contribute to an animal's fitness, or lifetime reproductive success (*e.g.*, Houston and McNamara, 1988; Mangel and Clark, 1988; Williams, 1992; Sargent, 1990; Sargent *et al.*, 1995). Behavioral ecologists use the term "condition" to refer to an animal's overall quality in terms of acquired resources, with the implicit assumption that higher condition leads to higher fitness. Within the paradigm of dynamic optimization, "condition" can be thought of as all axes in the state space that are relevant to fitness (*e.g.*, body size, energy reserves, immunocompetence). However, fisheries biologists have traditionally used the term, "condition," to refer to

an estimate of energy reserves by scaling weight to length (see Bolger and Connolly [1989] for review). This is the definition of "condition" that we will adopt here; however, other state variables are clearly important determinants of fitness as well.

There is considerable empirical support for the importance of energy reserves for reproductive success in fishes (see Sargent [1997] for review). First, it is well known that energy reserves decline during the breeding season, and that fishes that have not reproduced have higher energy reserves at the end of the breeding season than fishes that have reproduced (*e.g.*, Unger, 1983; Sargent, 1985; Reznick and Braun, 1987; Chellapa *et al.*, 1989; FitzGerald *et al.*, 1989; Sabat, 1994). Second, many studies manipulate diet or ration, and these studies show that individuals that receive more supplemental food have higher reproductive success, survival between brood cycles, or both (*e.g.*, Townshend and Wootton, 1984; Ridgway and Shuter, 1994). Third, Sargent (unpublished) found with fathead minnows (*Pimephales promelas*) that "condition index" (*i.e.*, weight scaled to length) at the beginning of the breeding season is positively correlated with the amount of stored neutral lipids, and with the number of offspring produced during the breeding season. Thus, acquired resources are clearly tied to reproductive output in fishes.

Behavioral strategies are said to be "condition-dependent" if an individual's best strategy depends on its condition, or on its condition relative to that of other members of the population. For example, during male-male competition for females in fishes, larger males court females, whereas smaller males attempt to mate forcibly or sneakily (see Gross, 1984, 1996 and Farr 1989, for reviews). Females may benefit by mating with high condition males directly (*i.e.*, phenotypic benefits such as more resources for offspring, lower levels of pathogens that could infect the female or offspring), or indirectly (*i.e.*, genetic benefits inherited by the offspring, *e.g.*, Moore, 1994). If females do benefit by mating with high condition males, then sexual selection theory predicts that males will "honestly signal" their overall quality to prospective

females, and that females will base their mate choice on these male signals (Zahavi, 1975, 1977; Kodric-Brown and Brown, 1984; Grafen, 1990*a, b*; Price *et al.*, 1993). Honest signaling theory assumes that signals are costly to produce, and that a given level of signal is more costly for low-condition than high-condition males. Many of the predictions of honest signaling have been supported in fishes (see below). Thus, sexual selection theory potentially has broad implications for sensory ecology and intraspecific communication.

TWO MODEL SYSTEMS: THE GUPPY AND THE THREESPINE STICKLEBACK

Although there are many excellent studies of sexual selection on a wide spectrum of fish species, two species stand out as being especially appropriate for this review: 1. the guppy, *Poecilia reticulata*, which has internal fertilization and females that give birth to fully independent juveniles (see Meffe and Snelson [1989] for review); 2. the threespine stickleback, *Gasterosteus aculeatus*, which has external fertilization and male parental care of the developing eggs and newly hatched fry (see Wootton [1976] for review). Although these two species have very different mating systems and reproductive biology, they share much in common in terms of sexual selection and signaling between the sexes. We caution that these species exhibit enormous geographical variation (guppies, Endler, 1977, 1978; sticklebacks, Bell and Foster, 1994), so the results that we cite here are not true for all populations within a species; we discuss some of these "exceptions" below.

In both species, males develop a carotenoid-based, orange to red breeding coloration (guppies, Houde, 1987; sticklebacks, Wootton, 1976), and this breeding coloration is positively correlated with carotenoids in the diet (guppies, Kodric-Brown, 1989; sticklebacks, Bakker, personal communication, see also Frischnecht, 1993); positively correlated with condition index (weight scaled to length: guppies, Nicoletto, 1991, 1993; sticklebacks, Milinski and Bakker, 1990; Frischnecht, 1993; Bakker and Mundwiler, 1994); positively correlated with courtship intensity (guppies, Nicoletto,

1993; sticklebacks, Bakker and Milinski, 1991); and positively correlated with female preference (guppies, Houde, 1987; Endler and Houde, 1995; sticklebacks, Bakker, 1993). Finally, if males of both species are experimentally infected with parasites, parasitized males have reduced breeding coloration and are less preferred by females than non-parasitized controls (guppies, Houde and Torio, 1994; sticklebacks, Milinski and Bakker, 1990). A clear pattern has emerged; male breeding coloration, energy reserves, courtship display rate, parasite load, and attractiveness to females are all interrelated.

Considerable information is also known about the spectral sensitivities and the visual ecologies of each species. For example, based on microspectrophotometry of visual pigments, both species have four sets of retinal cone cells (guppies, Archer, 1988; Rush, 1995; sticklebacks, Baube, 1998; Baube, personal communication), which includes a set of ultraviolet cones, and three sets of cones in the "human-visible" wavelengths. In sticklebacks, both spectral sensitivity and male breeding coloration have been shown to correlate with the photic environment.

In "tea-stained" lakes in British Columbia, Canada, the short wavelengths attenuate rapidly, which creates a "reddish" photic environment; whereas, in mesotrophic lakes there is a broader spectrum of wavelengths of light (McDonald and Hawryshyn, 1995; McDonald *et al.*, 1995). There is a tendency for male breeding coloration to be black (rather than red) in these tea-stained lakes (Reimchen *et al.*, 1985). Using optic nerve recording, McDonald and Hawryshyn (1995) found that sticklebacks in tea-stained lakes have their peak spectral sensitivity shifted to longer wavelengths relative to fish in mesotrophic lakes. McDonald *et al.* (1995) hypothesized that black breeding coloration may be favored in tea-stained lakes, due to its higher contrast against a red background than would be the case for red breeding coloration. They tested this hypothesis with females from a mesotrophic lake, where males have the more typical red breeding coloration. They examined female preference for red or

black male video images against a red or blue background, which roughly approximated the two photic environments. They found that females preferred red males against a blue background, but black males against a red background, which supports their hypothesis (McDonald *et al.*, 1995). Thus it appears that photic environment can affect spectral sensitivity and female preference of male breeding coloration. It would now be interesting to examine condition dependence and honest signaling in non-red or black males from these tea-stained lakes.

In guppies, it appears that geographic variation in male coloration depends more on predation regime than on photic environment (Endler, 1977, 1978). Basically, orange breeding coloration is negatively correlated among populations with the intensity of predation on guppies. Female preference for male orange coloration is stronger in populations with lower predation intensities (Endler and Houde, 1995). In addition, Endler and Houde (1995) also found that male orange coloration correlates with the photic environment; orange coloration increases with the water orange ratio (*i.e.*, the relative transmission of long wavelengths through the water, which is calculated as the integral of 400–550 nm absorbance divided by the integral of 550–700 nm absorbance; see Endler and Houde 1995) among populations. Interestingly, this appears to be the opposite trend found in sticklebacks. In sticklebacks, redder photic environments are correlated with black breeding coloration, and female preference for black males over red males (McDonald and Hawryshyn, 1995; McDonald *et al.*, 1995; Reimchen *et al.*, 1985). In guppies, a redder photic environment is correlated with stronger preference for orange colored males (Endler and Houde, 1995). A possible resolution to this disparity is that tea-stained stickleback habitat attenuates the short wavelengths more completely than comparable guppy habitat (guppy habitat, Endler, 1991; stickleback habitat, McDonald *et al.*, 1995). In both guppies and sticklebacks, when the color of the ambient light is manipulated to coincide with male breeding coloration (thus reducing color

contrast of the male ornament), female preference for male coloration disappears (guppies, Long and Houde, 1989; sticklebacks, Milinski and Bakker, 1990). It would be interesting to conduct artificial selection experiments where photic environment is manipulated, and to look for evolutionary responses in spectral sensitivity, female preference and male coloration.

A common feature of all the above cited studies on condition dependence and honest signaling in guppies and sticklebacks is that they are all based on visual cues. It would be interesting to see if other sensory modalities play a role in honest signaling in these species.

OTHER SENSORY MODALITIES

It is well known that fishes send and receive acoustical, low frequency mechanosensory, chemical, and electrical signals, in addition to visual signals (see Atema *et al.*, 1988, for review). Moreover, cues other than visual cues are known to play a role in courtship and agonistic encounters in many species. However, it is not known whether these other sensory cues act as condition indicators. Because the active production of electrical signals is relatively restricted taxonomically in fishes, we choose not focus on this sensory modality; however, there are many excellent examples and reviews of courtship and mate choice using electrical cues (*e.g.*, Hagedorn and Heiligenberg, 1985; Heiligenberg, 1993; Moller, 1995; Tricas *et al.*, 1995). Instead, we briefly review literature on acoustical cues, low frequency mechanosensory cues, and chemical cues, and discuss their potential relevance to the phenomena of condition dependence and honest signaling.

Acoustical cues

Most research on fish acoustical communication focuses on the mechanisms of sound production and detection (see Tavolga *et al.*, 1981; Hawkins, 1993, for reviews). Acoustical communication is taxonomically widespread in fishes. Here we focus on a small set of species for which there are data on acoustical cues and courtship.

Vocalization in fishes requires modification of the swimbladder, pectoral fins or

pharyngeal teeth (Tavolga, 1971; Sand and Hawkins, 1973; Schwartz, 1974; Kratochvil, 1977; Crawford, 1986; Ladich, 1989; Hawkins, 1993; Connaughton and Taylor, 1996; Ladich, 1998). Low frequency sounds are produced by drumming muscles attached to the swimbladder (Tavolga, 1971; Brantley and Bass, 1994; Connaughton and Taylor, 1996). High frequency sounds are produced by bony attachments to the pectoral fin, or scraping of the pharyngeal teeth (Schwartz, 1974; Kratochvil, 1977; Torricelli *et al.*, 1990; Fine *et al.*, 1996). The specialization of the sound production organs are usually confined to males and may vary intrasexually based on size, and possibly age. In water, low frequency sounds travel farther and are more easily localized than high frequency sounds (Dusenbery, 1992). This suggests that low frequency sounds should be used to court at a distance, whereas high frequency sounds should be used during interactions that involve close contact between individuals. However, such bimodal sound production has never been reported. One possibility is that it is costly to possess dual structures (drumming muscles and stridulation of pectoral fin or pharyngeal teeth) for sound production. Another possibility is that if fish were to produce an intense sound type at a long distance and another less intense sound type when the receiver is nearby (Kenyon, 1994), then the signal sender can attract mates at both long and short distance without investing in dual structures for two specific types of sound production. Finally, the energy required to produce a low frequency sound of equal intensity is greater than that for a high frequency sound (Dusenbery, 1992). This suggests that the cost of sonic communication among fishes may vary depending on the type of sound producing organ.

Let us first consider drumming. Sonic muscle size is tightly associated with body size in larger males; immature males show very little enlargement of sonic muscles, whereas adult males in season show radically enlarged muscle tissue (Templeman and Hodder, 1958; Bass and Marchaterre, 1989; Brantley *et al.*, 1993a; Connaughton and Taylor, 1995). The enlargement of son-

ic muscle is induced by steroid hormones (Brantley *et al.*, 1993b; Connaughton and Taylor, 1995). One might expect sound production to be constrained by body size, because, in general, larger fish will have larger swimbladders with lower resonant frequencies (Fine *et al.*, 1977). Thus one might expect the fundamental frequency of a fish vocalization to be negatively correlated with body size. Interestingly, this appears not to be the case for drumming. With drumming, the fundamental frequency depends on sonic muscle contraction rate (Fine *et al.*, 1977), which in turn is controlled by a central nervous system vocal circuit (Bass and Baker, 1990, 1991). In the midshipman (*Porichthys notatus*), there two types of sexually mature males: large, territorial, egg-guarding males (*i.e.*, Type-I males), and smaller males that "sneak" fertilizations (*i.e.*, Type-II males, Brantley and Bass, 1994). The larger Type-I males have much larger sonic muscles, have much larger motoneurons and pacemaker neurons in their vocal sonic circuits, and produce *higher* fundamental frequencies than do the smaller Type-II males (Bass and Marchaterre, 1989; Bass and Baker, 1990). Although it appears that fundamental frequency is independent of body size for Type-I males (Bass and Baker, 1990, Figure 2), it would now be interesting to see if fundamental frequency, or the duration of the call (*e.g.*, Fine, 1978), is correlated with condition (weight scaled to length) or some other index of energy reserve.

Unlike drumming muscles, pharyngeal teeth and pectoral fin structures may not have the same relationship between body size and signal capabilities. However, it is likely that larger pectoral fins or larger pharyngeal teeth will produce higher amplitude sounds as well. It is possible that high frequency communication might be an example of sensory drive or sensory bias while lower frequency communication is an example of condition-dependent mate-choice. More work needs to be done on the relationship between body size and frequency of stimuli. Kratochvil (1977) and Ladich and Yan (1998) report that high frequency sound production in croaking gouramis is correlated with body size, with smaller fish

producing higher frequency sounds than larger fish. Furthermore croaking gouramis have relatively larger sonic muscle mass for their body size (Kratochvil, 1977).

Sound reception in most teleosts is most efficient in the low frequencies, which correlates with the sound producing organ of the fishes (Popper and Fay, 1973). However several fishes have modifications of the acoustical system that increases sensitivity to high frequencies. In fish with swimbladders, air filled tubes or bones directly attached to the bladder increase the sensitivity of the ear to high frequency sounds (>1 khz) (Schuster, 1989; Hawkins, 1993). Similar air filled passages around the gill are used in anabantoid fish to increase their sensitivity to high frequency sounds. Removal of air filled bubbles produces a dramatic decline in the sensitivity of these fish (Yan, unpublished). Researchers have shown a general correlation between sound production organs and acoustical sensitivity in fishes for low frequency sounds. Ladich and Yan (1998) have shown a similar relationship for fish that produce high frequency signals. It would be interesting to see if the correlation between high frequency sound production and sound reception is also correlated with condition.

The function of sound production has received less attention than has its physiology. Work on sound production and sound interception in the bicolor damselfish (*Stegastes partitus*) indicates that vocalization in this fish is functionally similar to bird song. Males exhibit responses to "intruder vocalizations" and "stranger vocalizations" (Myrberg, 1981; Myrberg *et al.*, 1986; Myrberg *et al.*, 1993). Females are attracted to both the visual display and the acoustical signature of a male (Myrberg, 1981; Myrberg *et al.*, 1986). Sound production in midshipman (*Porichthys notatus*) is thought to have a similar function; the vocalizations of large calling males is attractive to females (Brantley and Bass, 1994). Substrate drumming is exhibited by the mottled sculpin (*Cottus bairdi*), which knocks its head against the substrate (Barber and Mowbray, 1956; Whang and Janssen, 1994). This low frequency signal, from a fish with no swimbladder travels rapidly

along the substrate with little attenuation. This channel would stimulate the upper reaches of the lateral line and the lower range of the auditory system.

In general the physiological, neurobiological, and morphological aspects of fish vocalization have outstripped research on the functional bases of communication, beyond a small set of specific examples (*e.g.*, Myrberg, 1981; Crawford, 1986; Brantley and Bass, 1994; Whang and Janssen, 1994; Ladich, 1998) that have been studied in detail. The functional relationship between sound production as a signal and the response of the receiver is unclear. Future research should focus on signal transmission through the environment, which is complicated by thermoclines and the body temperatures of the fish (both for sound production and hearing). Similarly, we need more field and laboratory studies of how fish use sound. Research in the future should examine the relationship between age, body size, and sonic muscle mass. Because signal production requires a large expenditure of energy to maintain and produce, they have the prerequisites to be honest signals of condition. Correlations between condition, sound production, and mate choice should be easy to acquire. It is clear that in the last few years the gap between functional and proximate mechanisms of acoustical communication has narrowed; now there is an opportunity to narrow the gap further.

Low frequency mechanosensory cues

A common feature in both courtship and agonistic encounters in fishes is lateral display and quivering (Bleckmann, 1993; Nelissen, 1991). A signaling fish aligns itself beside a recipient, often within a few centimeters, and vibrates its body with fins erect. Although it would appear that this behavior generates a low frequency mechanosensory stimulus that the recipient of the display could detect with its lateral line system, there have been surprisingly few tests of this hypothesis (see Bleckmann, 1993).

Satou *et al.* (1994a, b) have examined mechanosensory stimuli generated by female hime salmon (*Oncorhynchus nerka*) during spawning. They examined male re-

sponses to vibrational and visual components of female courtship and spawning behavior using dummy females. If both components were present, males spawned; however, if the dummies did not vibrate, then males did not spawn (Satou *et al.*, 1994a). If males' lateral lines were blocked with cobalt, which is known to interfere with the function of lateral line hair cells, then males failed to spawn to vibrating dummies (Satou *et al.*, 1994b). These experiments indicate the importance of the lateral line in perceiving vibrational cues. Now it would be interesting to examine male mechanosensory cues as potentially honest signals to females.

We have undertaken such a study with the green swordtail (*Xiphophorus helleri*). Our data are very preliminary; however, using posterior lateral line trunk nerve recording we found that the lateral line system of the female swordtail was most sensitive to frequencies between 20–50 Hz, and a high speed video analysis of male courtship suggests they generate a particle acceleration well within the peak of female sensitivity (Rush *et al.*, unpublished data). We suggest that some component of the male lateral display (*e.g.*, amplitude, frequency) in the green swordtail may be an indicator of condition, and we intend to pursue this further.

It is noteworthy that male display rate (evaluated visually by human observers) is correlated with condition and female preference in guppies (*Poecilia reticulata*, Kennedy *et al.*, 1987; Nicoletto, 1993), threespine sticklebacks (*Gasterosteus aculeatus*, Gross and Franck, 1979; Ridley, 1986; but see Rowland, 1995), and bicolor damselfish (*Stegastes partitus*, Knapp and Kovach, 1991). Undoubtedly, much of the signaling during male courtship display in these species is visual; however, it would now be interesting to see if visual and mechanosensory stimuli in combination produce a larger female response than either stimulus alone.

Chemical cues

Chemical cues have been long suspected to have an important function in the reproductive behavior of fishes (Noble, 1939) and in the past decade the study of sex

pheromones in goldfish, *Carassius auratus*, has been an active area of research. Most research has focused on male detection of females, rather than vice versa.

Dulka *et al.* (1987) demonstrated that endogenous steroid hormones act also as sex pheromones that increase physiological and behavioral competence and synchrony of gamete release in goldfish. Sorensen (1992) and Sorensen and Scott (1994) envision three stages in the evolution of chemical sex signals, which require only minor reorganization of pre-existing compounds and receptors. First, reproductive hormones are released into the surrounding water as a mechanism for clearing them from the blood. At first, these water-borne hormones do not function as pheromones. Second, the expression of pre-existing receptors from the endocrine system on external chemosensory cells give the fish the ability to detect water-borne hormones. Thus, fish could 'spy' on the physiological state of conspecifics and respond accordingly. Third, true pheromonal 'communication' is achieved when controlled and reciprocal exchange of chemical signals occurs. Sorensen and Scott (1994) did not find a strong correlation between steroid production by female goldfish and their detection by males, which led them to conclude that hormonal sex pheromones are an example of chemical spying rather than a co-evolved system of reciprocal signal production and detection. Nevertheless, water-borne pheromones could serve as condition indicators.

The female preovulatory hormone, $17\alpha, 20\beta$ -dihydroxy-4-pregnen-3-one ($17\alpha, 20\beta$ -P) has received the most attention. Exposure to $17\alpha, 20\beta$ -P induces males to increase plasma levels of $17\alpha, 20\beta$ -P and gonadotropin, and to increase milt volume in salmonids (Olsen and Liley, 1993; Dittman and Quinn, 1994; Scott *et al.*, 1994) and cyprinids (Dulka *et al.*, 1987; Yamazaki, 1990; DeFraipont and Sorensen, 1993; Stacey *et al.*, 1994; Sorensen *et al.*, 1995; Bjerselius *et al.*, 1995a, b). The medial olfactory tract of the male seems to be the location of the pheromone receptors, without which the full complement of spawning behavior does not proceed (Yu and Peter,

1990; Dulka and Stacey, 1991; Resink *et al.*, 1989).

Cardwell *et al.* (1995) report that field-caught male minnows *Puntius schwanenfeldi*, bearing tubercles (a transient secondary sex character under androgen control developed by males during the breeding season) showed greater sensitivity to a female sex pheromone than males without tubercles. Further investigation with *P. gonionotus* revealed an important activational effect of androgen on olfactory receptors, leading to greater intensity of courtship behavior (Cardwell *et al.*, 1995).

Females in a number of poeciliid species release a sex pheromone (see Liley [1982] for review). Female guppies *Poecilia reticulata*, have a sex pheromone, probably hexestrol dipropionate, produced by the ovary shortly after parturition (Amouriq, 1967 in Liley, 1982; Gandolfi, 1969; Crow and Liley, 1979). Sex pheromones of female poeciliids generally stimulate male activity, attract males and increase male courtship. Sumner *et al.* (1994) found that chemical cues from female sailfin mollies, when in combination with visual cues, resulted in large males (but not small males) preferentially courting females that had recently giving birth (*i.e.*, fertile), over females that are gravid with embryos (*i.e.*, not fertile). Given that large males typically court females whereas small males "sneak," females may use chemical cues to reduce sexual harassment; large males attracted by the sex pheromone repel subordinate males.

Information on male pheromones is much more limited. In swordtails (*Xiphophorus*), females appear to be able to use male chemical cues in species recognition (Crapon de Craona and Ryan, 1990). Chemical stimuli from male fathead minnows in breeding condition attract females to a greater degree than stimuli from regressed males or females (Cole and Smith, 1992). Male threespine sticklebacks (*Gasterosteus aculeatus*) release a sex pheromone during courtship displays that attracts gravid females and repels non-territorial males (Waas and Colgan, 1992). Also in sticklebacks, the olfactory nerve appears to play an important role in nest building behavior, onset of courtship, and suppressed

aggression against gravid females (Segaar *et al.*, 1983).

In several species of gouramis female pheromones attract males, initiate nest construction by males, and stimulate the development of male breeding coloration (Liley, 1982). A pheromone produced by males inhibits nest building behavior by subordinate males and also attracts females (Liley, 1982). Pheromones released by male *Trichogaster trichopterus* induce female ovarian maturation and increased plasma levels of steroid hormones, including 17α , 20β -P (Degani and Schreibman, 1993).

In summary, most chemical signaling during fish reproduction appears to originate from females; although, there is some evidence of male signaling as well. Although chemical cues seem to indicate reproductive state or receptivity, their potential role as condition indicators is unknown. It would be interesting to tease apart the separate effects of chemical cues from those of other sensory cues as determinants of the outcome of courtship and mate choice.

SUMMARY AND DIRECTIONS FOR FUTURE RESEARCH

Behavioral ecology theory, particularly sexual selection theory and resource acquisition theory, makes specific predictions on communication between the sexes during courtship and mate choice. If signals are costly to produce, then theory predicts that signalers should produce signals in direct proportion to their condition. Receivers should be well adapted to discriminate the level of signal being produced, and thus the signaler's condition. Sensory ecology provides a wealth of information on physiological mechanisms underlying signal production and signal detection; thus, a great deal remains to be learned by integrating behavioral and sensory ecology.

It appears that male visual cues do honestly signal condition to females in many cases; however, this issue has not been addressed explicitly for other sensory modalities. It seems plausible that acoustical and mechanosensory cues may also be condition dependent. However, chemical cues primarily seem to signal a fish's sex and reproductive state. It may well be that dif-

ferent sensory modalities signal different aspects of overall condition. It is clear, however, that integration of behavioral and sensory ecology, with regard to the question of sexual selection and resource acquisition, is still in its infancy. Below we make some specific suggestions for directions for future research.

1. Other measures of condition

Throughout this discussion, we have focused primarily on stored energy reserves (measured directly or estimated as being proportional to weight scaled to length) as our measure of condition; however, body size and immunocompetence may also be important determinants of lifetime reproductive success.

First, consider body size. It has been well documented in fishes that survival and fecundity depend more on body size (*i.e.*, mass) than on age (*e.g.*, Werner and Gilliam, 1984; Sargent *et al.*, 1987). Large fish have higher rates of fecundity, mating success, and survival than small fish (Werner and Gilliam, 1984; Gross and Sargent, 1985; Andersson, 1994). Thus, body size is clearly an important component of overall condition in fishes.

Second, consider immunocompetence (Hamilton and Zuk, 1982; Folstad and Karter, 1992). In many fishes, females avoid parasitized males (see Andersson [1994] for review). In guppies and sticklebacks, certain parasites result in a reduction of male orange or red, carotenoid-based breeding coloration (Houde and Torio, 1994; Milinski and Bakker, 1990; but see Folstad *et al.*, 1994), and in Arctic charr, male red breeding coloration is positively correlated lymphocyte density in the blood (Skarstein and Folstad, 1996). How one measures immunocompetence may be problematic, but future research on immunocompetence, sexual selection, and the potential role of carotenoids should be very rewarding. We suggest that empiricists explore how body size, energy reserves, and immunocompetence interact to determine lifetime reproductive success, and that theoreticians explore the implications of these interactions for multi-modality honest signaling.

2. Search for condition indicating traits

We suggest that empiricists determine whether or not any of the traits that they study (*e.g.*, morphology, signal production, signal detection) are correlated with condition (*e.g.*, weight scaled to length). Condition can be estimated as $Weight/Length^b$ where b represents the allometric coefficient between weight and length, which can be estimated by non-linear regression of W versus L , or by log-log regression (Bolger and Connolly, 1989). Alternatively, condition can be estimated as the residuals about a W versus L regression line, or one can compute partial correlations between potential condition indicators and weight, while holding the effects of length constant. Preliminary studies in our laboratories suggest that components of fin morphology and of breeding coloration may be correlated with condition, in some cases in both sexes of fishes. We are pursuing this further.

3. Honest signaling in both sexes

In most genetical models of sexual selection (*e.g.*, Lande, 1980, 1981; Kirkpatrick, 1982), the limiting sex exhibits the mating preference and the limited sex exhibits the ornament. For this reason, most empirical studies have focused on sexual selection in the limited sex, typically males (see Andersson [1994] for review). However, in recent game theoretical models, Crowley *et al.* (1991) and Johnstone *et al.* (1996) found that under certain conditions it pays both sexes (*i.e.*, the limiting and limited sexes) to be choosy. Even though females are the limiting sex in sticklebacks (*e.g.*, Sargent and Gebler, 1980), male sticklebacks do exhibit mate choice based on female body size and fecundity (Rowland, 1982, 1989; Sargent *et al.*, 1986), and females adopt a breeding coloration that signals when they are receptive to males (Rowland *et al.*, 1991). Furthermore, in several species of the biparental cichlid genus, *Cichlasoma*, females are the more colorful sex (Turner, 1993). Finally, most sex pheromone signals seem to be produced by females. We suggest that theoreticians develop genetical models of intersexual selection for both sexes simultaneously, and explore the co-

evolution of honest signaling in both sexes. We suggest also that empiricists look for condition dependence and honest signaling in both the limited and limiting sexes.

4. Sensory or pre-existing bias versus condition indicators

Throughout our discussion we have emphasized a coevolution between female preference and male ornament. There is evidence in swordtails (*Xiphophorus*) that the "sword" (*i.e.*, a ventral extension of the caudal fin that develops as males reach maturity) may have evolved through a sensory or pre-existing bias in female preference (Ryan and Wagner, 1987; Basolo, 1990a, b, 1995a, b). Female *Xiphophorus* prefer males with swords, whether or not the males of their species have swords; in addition, female *Priapella olmecae* (the outgroup genus to *Xiphophorus*) also prefer males with swords (Ryan and Wagner, 1987; Basolo, 1990a, b, 1995a, b), even though swords are not known in this genus. Whether or not phylogenetic comparative data within the genus, *Xiphophorus*, supports the pre-existing bias hypothesis is controversial (Meyer *et al.*, 1994; Basolo, 1995a; Wiens and Morris, 1996); however, Basolo's (1995b) recent demonstration of female preference for males with swords in the "sword-less" outgroup genus, *Priapella*, does favor this hypothesis. What about condition dependence in swordtails?

Basolo (1998) found that male green swordtails (*Xiphophorus helleri*) on restricted diets produced swords as large as males that were fed *ad libitum*, despite the fact that males on the restricted diet had reduced growth in body size. These data suggest that swords may not be honest indicators of male quality. To our knowledge, sword length has not been compared to condition index or energy reserves within a species. It appears that morphological traits such as fin size reflect the conditions that prevailed when their development was initiated. As such, they may be relatively fixed and less reliable as "instantaneous" condition indicators than an ephemeral color pattern (see Kodric-Brown, 1998), which can reflect more short-term fluctuations in condition. This is certainly worth further investigation.

Also, it would be interesting to see if the strength of female preference is correlated with mean male sword length among species of *Xiphophorus*, which may indicate a coevolution between female preference and male ornament in addition to the pre-existing bias.

5. Empirical studies that explore more than one sensory modality

Fish ethologists who study visual cues have traditionally separated their stimulus and focal fish with transparent glass or plastic partitions (*e.g.*, Sargent and Gebler, 1980). Users of transparent partitions are cautioned that not only do these partitions block chemical cues and the particle movement that is generated by low frequency mechanosensory cues (*e.g.*, during a lateral display), but most of them are also effective filters of ultraviolet light, and many fishes are known to be able to see ultraviolet light (Jacobs, 1992; Archer, 1988; Rush, 1995). In fact, we have preliminary data for a poeciliid that males have UV breeding coloration, and that females prefer males behind UV transparent over UV filtering partitions (Rush *et al.*, unpublished).

We suggest that empiricists who study communication between the sexes explore two or more sensory modalities in combination. For sensory ecologists, this may require collaboration among research laboratories; however, behavioral ecologists might approach the problem with simple factorial experimental designs. If factorial-design experiments of mate choice indicate that sensory cues from two sensory modalities produce a greater response in the receiver than either cue alone (either additively or multiplicatively), then it becomes interesting to investigate how these modalities interact at both ethological and physiological levels. Alternatively, sensory biologists who have already determined that two sensory modalities interact on a physiological level can set the stage for behavioral ecological experiments.

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