Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

by Robert Craig Sargent, Victor N. Rush, Brian D. Wisenden and Hong Y. Yan

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.

© COPYRIGHT 1998 Society for Integrative and Comparative Biology(SICB)

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 Anderson, 1994, for review). In most species, females re 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 re 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, 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; Kirk-patrick, 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, 1990a, 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;

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 that 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, 1997; Kodric-Brown and Brown, 1984;

Grafen, 1990a, 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; Frischknecht, 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.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 run 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

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 is 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 sonic 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 he 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 ([is greater than] 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

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 responses 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 into 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), three-spine 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

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 [Beta], 2 [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 Crapona 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 17 [Alpha], 2 [Beta] - 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

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 different 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

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

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 libidum, 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 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.

ACKNOWLEDGMENTS

(1) From the Symposium Animal Behavior: Integration of

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Ultimate and Proximate Causation presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 26-30 December 1996, at Albuquerque, New Mexico.

REFERENCES

Andersson, M. 1994. Sexual selection. Princeton university Press, Princeton.

Archer, S. N. 1988. A microspectrophotometer study of visual pigment polymorphism in the guppy, Poecilia reticulata. Ph.D. Thesis, University of Bristol. England.

Atema, J., R. R. Fay, A. N. Popper, and W. N. Tavolga. 1988. Sensory biology of aquatic animals. Springer-Verlag, New York.

Bakker, T. C. M. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. Nature 363:255-257.

Bakker, T. C. M. and M. Milinski. 1991. Sequential mate choice and the previous male effect in sticklebacks. Behav. Ecol. Sociobiol. 29:205-210.

Bakker, T. C. M. and B. Mundwiler. 1994. Female mate choice and male red coloration in a natural stickleback population. Behav. Ecol. 5:74-80.

Barber, S. B. and W. H. Mowbray. 1956. Mechanisms of sound production in the sculpin. Science 124:219-220.

Basolo, A. L. 1990a. Female preference predates the evolution of the sword in the swordtail fish. Science 250:808-810.

Basolo, A. L. 1990b. Female preference for mate sword length in the green swordtail, Xiphophorus helleri (Pisces: Poeciliidae). Anim. Behav. 40: 332-338.

Basolo, A. L. 1995a. A further examination of the pre-existing bias favouring a sword in the genus Xiphophorus. Anim. Behav. 50:365-375.

Basolo, A. L. 1995b. Phylogenetic evidence for the role of a pre-existing bias in sexual selection. Proceedings of the Royal Society of London B 259: 307-311.

Basolo, A. L. 1998. Shift in investment between sexually selected traits: Tarnishing of the silver spoon. Anim. Behav. (In press)

Bass, A. H: and M. A. Marchaterre. 1989.

Sound-generating (sonic) motor system in a teleost fish (Porichthys notatus): Sexual polymorphism in the ultrastructure of myofribils. J. Compar. Neurol. 286:141-153.

Bass, A. H. amid R. Baker. 1990. Sexual dimorphisms in the vocal control of system of a teleost fish: Morphology of physiologically identified neurons. J. Neurobiol. 21:1155-1168.

Bass, A. H. and R. Baker. 1991. Evolution of homologous vocal control traits. Brain, Behav. Evol. 38: 240-254.

Bateman. A. J. 1948. Intra-sexual selection in Drosophila. Heredity 2:349-368.

Baube. C. L. 1998. Manipulations of the signalling environment affect male competitive success in threespine sticklebacks, Gasterosteus aculeatus. Anim. Behav. (In press)

Bell, M. A. and S. A. Foster 1994. The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford.

Bjerselius, R., K. H. Olsen, and W. Zheng. 1995a. Behavioural and endocrinological responses of mature male goldfish to the sex pheromone 17-alpha, 20-beta-dihydroxy-4-pregnen-3-one in the water. Exper. Biol. 198:747-754.

Bjerselius, R., K. H. Olsen, and W Zheng. 1995b. Endocrine, gonadal and behavioral responses of male crucian carp to the hormonal pheromone 17-alpha 20-beta-dihydroxy-4-pregnen-3-one. Chem. Senses 20:221-230.

Bleckmann, H. 1993. Role of the lateral line in fish behaviour. In T. J. Pitcher (ed.), The behaviour of teleost fishes, pp. 201-246. Chapman and Hall, London.

Bolger, T. and P. I. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. 34:171-182.

Brantlley, R. K. and A. H. Bass. 1994. Alternative male spawning tactics and acoustic signalling in the plainfin midshipman fish, Porichthys notatus. Ethology 96:213-232.

Brantley. R. K., M. A. Marchaterre, and A. H. Bass. 1993b. Androgen effects on vocal muscle structure in a teleost fish with inter and intrasexual dimorphisms. J. Morphol. 216:305-318.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Brantley. R. K., J. Tseng. and A. H. Bass. 1993a. The ontogeny of inter- and intrasexual vocal muscle dimorphisms in a sound-producing fish. Brain, Behav. Evol. 42:336-349.

Cardwell, J. R., N. E. Stacey, E. S. P Tan, D. S. O. McAdam, and S. L. C. Lang. 1995. Androgen increases olfactory receptor response to a vertebrate sex pheromone. J. Comp. Physiol. A 176: 55-61.

Chellapa. S., F. A. Huntingford, R. H, C. Strang, and R. Y. Thomson. 1989. Annual variation in energy reserves in male three-spined stickleback, Gasterosteus aculeatus L. (Pisces, Gasterosteidae). J. Fish Biol. 35:275-286.

Cole. K. S. and R. J. E Smith. 1992. Attraction of female fathead minnows. Pimephales promelas, to chemical stimuli from breeding males. J. Chem. Ecol. 18:1269-1284.

Connaughton, M. A. and M. H. Taylor. 1995. Effects of exogeous testosterone on sonic muscle mass in the weakfish Cynoscion regalis. Gen. Comp. Endocrinol. 100:238-245.

Connaughton, M. A. and M. H. Taylor. 1996. Drumming, courtship and spawning behavior in captive weakfish, Cynoscion regalis. Copeia 1996:195-199.

Crapon de Crapona, D.-M. and M. J. Ryan. 1990. Conspecific mate recognition in swordtails, Xiphophorus nigrensis and X. pygmaeus (Poeciliidae): Olfactory and visual cues. Anim. Behav. 39:290-296.

Crawford, J. D. 1986. Acoustic communication in an electric fish, Pollimyrus isidori (Mormyridae). J. Comp. Physiol. 159:297-310.

Crow, R. T. and N. R. Liley. 1979. A sexual pheromone in the guppy, Poecilia reticulata. Can. J. Zool. 57:184-188.

Crowley, P. H., S. E. Travers, M. C. Linton, S. L. Cohn, A. Sih, and R. C. Sargent. 1991. Mate density, predation risk, and the seasonal sequence of mate choice: A dynamic game. The American Naturalist 137:567-596,

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

DeFraipont, M. and P. W. Sorensen. 1993. Exposure to the pheromone 17-alpha, 20-beta-dihydroxy-4-pregnen-3-one enhances the behavioural spawning success, sperm production and sperm motility of male goldfish. Anim. Behav. 46:245-256.

Degani, G. and M. P. Schreibman. 1993. Pheromone of mate blue gourami and its effect on vitellogenesis, steroidogenesis and gonadotropin cells in pituitary of the female. J. Fish Biol. 43:475-485.

Dittman, A. H. and T. P. Quinn. 1994. Avoidance of a putative pheromone 17-alpha, 20-beta-dihydroxy-4-pregnen-3-one, by precociously mature chinook salmon (Onchorynhchus tshawytscha). Can. J. Zool. 72:215-219.

Dulka, J. G. and N. E. Stacey. 1991. Effects of olfactory tract lesions on gonadotropin and milt responses to the female sex pheromone, 17-alpha, 20-beta-dihydroxy-4-pregnen-3-one, in male goldfish. J. Exper. Zool. 257:223-229.

Dulka J. G., N. E. Stacey, P. W. Sorensen, and G. J. Van Der Kraak. 1987. A steroid sex pheromone synchronizes male-female spawning readiness in goldfish. Nature 325:251-253.

Dusenbery, D. B. 1992. Sensory ecology. WH Freeman, New York.

Endler, J. A. 1977. Natural selection on color patterns in Poecilia reticulata. Evolution 34:76-94.

Endler, J. A. 1978. A predator's eye view of animal colors. Evol. Biol. 11:319-364.

Endler, J. A. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Research 31:587-608.

Endler, J. A. and A. E. Houde. 1995. Geographic variation in female preferences for male tratis in Poecilia reticulata. Evolution 49:456-468.

Farr, J. A. 1989. Sexual selection and secondary sexual differentiation in poecillids: Determinants of male mating success and the evolution of female choice. In G. K. Meffe and F. F. Snelson (eds.), Ecology and evolution of livebearing fishes, pp. 91-124 Prentice Hall, Englewood Cliffs, New Jersey.

Fine, M. L. 1978. Seasonal and geographical variation of the mating call of the oyster toadfish Opsanus tau L. Oecologia 36:45-57.

Fine, M. L., D. McElroy, J. Rafi, C. B. King, K. E. Loesser, and S. Newton. 1996. Lateralization of the pectoral stridulation sound production in the channel catfish. Physiol. Behav. 60:753-757.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Fine, M. L., H. E. Winn, and B. L. Olla. 1977. Communication in fishes. In T. A. Sebeok (ed.), How animals communicate, pp. 472-518. Indiana University Press, Bloomington.

Fisher, R. A. 1915. The evolution of sexual preference. Eugenics Rev. 7:184-192.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

FitzGerald, G. J., H. Guderley, and P. Picard. 1989. Hidden reproductive costs in the threespine stickleback (Gasterosteus aculeatus), Exp. Biol. 48: 295-300.

Folstad, I. and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139:603-622.

Folstad, I., A. M. Hope, A. Karter, and A. Skorping. 1994. Sexually selected colour in male sticklebacks; a signal for both parasite exposure and parasite resistance? Oikos 69:511-515.

Frischknecht, M. 1993. The breeding colouration of male three-spined sticklebacks (Gasterosteus aculeatus) as an indicator of energy investment in vigour. Evol. Ecol. 7:439-450.

Gandolfi, G. 1969. A chemical sex attractant in the guppy Poecilia reticulata Peters (Pisces: Poecilidae). Monitoire Zool. Ial. (N. S.) 3:89-98.

Grafen, A. 1990a. Sexual selection unhandicapped by the Fisher process. J. Theor. Biol. 144:473- 516.

Grafen, A. 1990b. Biological signals as handicaps. J. Theor. Biol. 144:517-546.

Gross, H. P. and D. Franck. 1979. Sexual selection in sticklebacks: Resource prediction [abstract]. Second biennial conference on the ethology and behavioral ecology of fishes, Normal, Illinois.

Gross, M. R. 1984. Sunfish, salmon and the evolution of alternative reproductive strategies and tactics in fishes. In G. W. Potts and R. J. Wootton (eds.), Fish reproduction strategies and tactics, pp. 55-75. Academic Press, London.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: Diversity within sexes. Trends In Ecol. Evol. 11:92-97.

Gross, M. R. and R. C. Sargent. 1985. The evolution of male and female parental care in fishes. Am. Zool. 25:807-822.

Hagedorn, M. and W Heiligenberg. 1985. Court and spark: Electric signals in the courtship and mating of gymnotoid fish. Anim. Behav. 33:254-265.

Hamilton, W. D. and M. Zuk. 1982. Heritable true fitness and bright birds: A role for parasites? Science 218:384-387.

Hasson, O. 1989. Amplifiers and the handicap principle in sexual selection: A different emphasis. Proc. Royal Soc. London, B235, 383-406.

Hasson, O. 1997. Towards a general theory of biological signaling. J. Theor. Biol. 185:139-156.

Hawkins, A. D. 1993. Underwater sounds and fish behaviour. In T. J. Pitcher (ed.), The behaviour of teleost fishes, pp. 129-169. Chapman and Hall, London.

Heiligenberg, W. 1993. Electrosensation. In D. H. Evans (ed.), The physiology of fishes, pp. 137-160. CRC Press, Boca Raton.

Houde, A. E. 1987. Mate choice based on naturally occurring color pattern variation in a guppy population. Evolution 41:1-10.

Houde, A. E. and A. J. Torio. 1994. Effect of parasite infection on male color pattern and female choice in guppies. Behav. Ecol. 3:346-351.

Houston, A. I. and J. M. McNamara. 1988. A framework for the functional analysis of behaviour. Behav. Brain Sci. 11:117-163.

Jacobs, J. 1992. Ultraviolet vision in vertebrates. Amer. Zool. 32:544-554.

Johnstone. R. A., J. D. Reynolds, and J. C. Deutsch. 1996. Mutual mate choice and sex differences in choosiness. Evolution 50:1382.

Kennedy, C. E. J., J. A. Endler, S. L. Poynton, and H. McMinn. 1987. Parasite load predicts mate choice in guppies. Behav. Ecol. Sociobiol. 21: 291-295.

Kenyon, T. N. 1994. The significance of sound interception to males of the bicolor damselfish, Pomacentrus partitus, during courtship. Environ. Biol. Fishes 40:391-405.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1-12.

Knapp, R. A. and J. T. Kovach. 1991. Courtship as an honest indicator of male quality in the bicolor damselfish, Stegastes partitus. Behav. Ecol. 2:295-300.

Kodric-Brown, A. 1989. Dietary carotenoids and male mating success in the guppy: An environmental component to female choice. Behav. Ecol. and Sociobiol. 25:393-401.

Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. Amer. Zool. 38:000-000.

Kodric-Brown, A. and J. H. Brown. 1984. Truth in advertising: The kinds of traits favored by sexual selection. Am. Nat. 124:309-323.

Kratochvil, H. 1977. Sound organ of the croaking gourami. Naturwissenschaften 64:592-593.

Krebs, J. R. and N. B. Davies, 1987. An introduction to behavioral ecology. Blackwell, Oxford.

Ladich, F. 1989. Sound production by the river bullhead, Cottus gobio L (Cottidae, Teleostei) J. Fish Biol. 35:531-538.

Ladich, F. 1998. Agonistic behaviour and significance of sounds in vocalizing fish. Mar. Freshw. Behav. Physiol. (In press)

Ladich, E and H. Y. Yan. 1998. Hearing sensitivity in vocalizing anabantoid fish. J. Comp. Physiol. A. (In Press)

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292-305.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. U.S.A. 78:3721-3725.

Liley, N. R. 1982. Chemical communication in fish. Can. J. Fish. Aq. Sci. 39:22-35.

Long, K. D. and A. E. Houde. 1989. Orange spots as a visual cue for female mate choice in the guppy (Poecilia reticulata). Ethology 82:316-324.

Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton.

McDonald, C. G. and C. W. Hawryshyn. 1995. Intraspecific variation in spectral sensitivity in threespine stickleback (Gasterosteus aculeatus) from different photic regimes. J. Comp. Physiol. A. 176:255-260.

McDonald, C. G., T. G. Reimchen, and C. W. Hawryshyn. 1995. Nuptial color loss and signal masking in Gasterosteus: An analysis using video imaging. Behaviour 132:963-977.

Meffe, G. K. and E E Snelson. 1989. Ecology and evolution of livebearing fishes. Prentice Hall, Englewood Cliffs, New Jersey.

Meyer, A., J. M. Morrissey, and M. Schartl. 1994. Recurrent evolution of a sexually selected trait in Xiphophorus fishes inferred from a molecular phylogeny. Nature 368:539-542.

Milinski, M. and T. C. M. Bakker. 1990. Female stick-lebacks use male coloration in mate choice and hence avoid parasitized males. Nature 344:330-333.

Moller, P. 1995. Electric fishes: History and behavior. Chapman and Hall, London.

Moore, A. J. 1994. Genetic evidence for the `good genes' process of sexual selection. Behav. Ecol. Sociobiol. 35:235-241.

Myrberg, A. A. 1981. Sound communication and interception in fishes. In W. N. Tavolga, A. N. Popper, and R. R. Fay (eds.), Hearing and sound communication in fishes, pp. 395-425. Springer, New York.

Myrberg, A. A., S. J. Ha, and M. Shamblott. 1993. The sounds of the bicolor damselfish (Pomacentrus partitus): Predictors of body size and a spectral basis for individual recognition and assessment. J. Acoust. Soc. Amer. 94:3097-3070.

Myberg, A. A., M. Mohler, and J. D. Catala. 1986. Sound production by males of a coral reef fish (Pomacentrus partitus): Its significance to females. Anim. Behav. 34:913-923.

Nelissen, M. H. J. 1991. Communication. In M. H. A. Keenleyside (ed.), Cichlid fishes: Behaviour, ecology and evolution, pp, 225-240, Chapman and Hall, London.

Nicoletto, P. F. 1991. The relationship between male ornamentation and swimming performance in the guppy, Poecilia reticulata. Behav. Ecol. Sociobiol. 28:365-370.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Nicoletto, P. F. 1993. Female sexual response to condition-dependent ornaments in the guppy, Poecilia reticulara. Anim. Behav. 46:441-450.

Noble, G. K. 1939. Sexual selection in fishes. Am. Mus. Nat. Hist. 133-158.

O'Donald, P. 1980. Genetical models of sexual selection. Cambridge University Press, Cambridge.

Olsen, K. H. and N. R. Liley. 1993. The significance of olfaction and social cues in milt availability, sexual hormone status, and spawning behavior of male rainbow trout (Ochorynchus mykiss). Gen. Comp. Endocrin. 89:107-118.

Popper, A. N. and R. R. Fay. 1973. Sound detection and processing by teleost fishes: A critical review. J. Acoust. Sec. Amer. 53:1515-1529.

Price, T. D. Schluter, and N. E. Heckman. 1993. Sexual selection when the female directly benefits. Biol. J. Linn. Sec. 48:187-211.

Reimchen, T. E., E. M. Stinson, and J. S. Nelson. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. Can. J. Zool. 63:2944-2951.

Resink, J. W., P. K. Voorthuis, R. Van den Hurk, H. G. B. Vullings, and P. G. W. T. Van-Oordt. 1989. Pheromone detection and olfactory pathways in the brain of the female African catfish, Clarias gariepinus. Cell Tiss. Res. 256:337-346.

Reznick, D. N. and B. Braun. 1987. Fat cycling in mosquitofish (Gambusia affinis): Fat storage as a reproductive adaptation. Oecologia 73:410-413.

Ridgway, M. S. and B. J. Shuter. 1994. The effects of supplemental food on reproduction in parental male smallmouth bass. Env. Biol. Fishes 39:201-207.

Ridley, M. 1986. Animal behaviour. A concise introduction. Blackwell, Oxford.

Rowland, W. J. 1982. Mate choice by male sticklebacks, Gasterosteus aculeatus. Anim. Behav. 30: 1093-1098.

Rowland, W. J. 1989. The ethological basis of mate choice in male threespine sticklebacks, Gasterosteus aculeatus. Anim. Behav. 39:112-120.

Rowland, W. J. 1995. Do female stickleback care about male courtship vigour? Manipulation of display tempo using video play back. Behaviour 132: 951-961.

Rowland, W. J., C. L. Baube, and T. T. Horan. 1991. Signalling of sexual receptivity by pigmentation pattern in female sticklebacks. Anim. Behav. 42: 243-249.

Rush, V. N. 1995. The role of light, visual behavior and phylogeny on the evolution of visual pigments in the poeciliid fishes. Ph.D. Diss., University of California, Santa Barbara.

Ryan, M. J. and W. E. Wagner. 1987. Asymmetries in mating preferences between species: Female swordtails prefer heterospecific males. Science 236:595-597.

Sabat, A. M. 1994. Costs and benefits of parental effort in a brood-guarding fish (Ambloplites rupestris Centrarchidae). Behav. Ecol. 5:195-201.

Sand, O. and A. D. Hawkins. 1973. Acoustic properties of the cod swimbladder. J. Exp. Biol. 58: 797-820.

Sargent, R. C. 1985. Territoriality and reproductive tradeoffs in the threespine stickleback, Gasterosteus aculeatus. Behaviour 93:217-226.

Sargent, R. C. 1990. Behavioural and evolutionary ecology of fishes: Conflicting demands during the breeding season, Annales Zoologici Fennici 27:101-118.

Sargent, R. C. 1997. Parental care. In J-G. Godin (ed.), Behavioural ecology of teleost fishes, Oxford University Press, Oxford.

Sargent, R. C., P. H. Crowley, C. Huang, M. J. Lauer, D. A. Neergaard, and L. Schmoetzer. 1995. A dynamic program for male parental care in fishes: Brood cycling and filial cannibalism. Behaviour 132:1059-1078.

Sargent, R. C., M. R. Gross, and E. P. van den Berghe. 1986. Male mate choice in fishes. Anim. Behav. 34:545-550.

Sargent, R. C. and J. B. Gebler. 1980. Effects of nest site concealment on hatching success, reproductive success, and paternal behavior of the threespine stickleback, Gasterosteus aculeatus. Behav. Ecol. Sociobiol. 7:137-142.

Sargent, R. C., P. D. Taylor, and M. R. Gross, 1987. Parental care and the evolution of egg size in fishes. Am. Nat. 129:32-46.

GALE GROUP

Information Integrity

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Satou, M., H.-A. Takeuchi, K. Takei, T. Hasegawa, T. Matsushima, and N. Okumoto. 1994a. Characterization of vibrational and visual signals which elicit spawning behavior in the male hime salmon (landlocked red salmon, Oncorhynchus nerka). J. Comp. Physiol. A 174:527-537.

Satou, M., H.-A. Takeuchi, K. Takei, T. Hasegawa, T. Matsushima, and N. Okumoto. 1994b. Behavioral and electrophysiological evidences that the lateral line is involved in the inter-sexual vibrational communication of the hime salmon (landlocked red salmon, Oncorhychus nerka). J. Comp. Physiol. A 174:539-549.

Schuster, S. 1989. The volume of air within the swimbladder and breathing cavities of the anabantoid fish, Colisa lalia (Perciformes: Velontiidae) J. Exp. Biol. 144:185-198.

Schwartz, A. 1974. Sound production and associated behavior in a cichlid fish, Cichlasoma centrarchus. I. Male-male interactions. Z. Tierpsychol. 35:147-156.

Scott, A. P. N. Liley, and E. L. M. Vermeirssen. 1994. Urine of reproductively mature female rainbow trout, Onchorynchus mykiss (Walbaum), contains a priming pheromone which enhances plasma levels of sex steroids and gonadotrophin II in males. J. Fish Biol. 44:131-147.

Segaar, J., J. P. C. De Bruin, A. P. Van Der Meche, and M. E. Van Der Meche-Jacobi. 1983. Influence of chemical receptivity on reproductive behaviour of the male three-spined stickleback (Gasterosteus aculeatus L.). Behaviour 86-1/2:100-166.

Skarstein, F. and I. Folstad. 1996. Sexual dichromatism and the immunocompetence handicap: An observational approach using Arctic charr. Oikos 76:359-367.

Sorensen, P. W. 1992. Hormonally derived sex pheromones in goldfish: A model for understanding the evolution of sex pheromone systems in fish. Biol. Bull. 183:173-177.

Sorensen, P. W. and A. P. Scott. 1994. The evolution of hormonal sex pheromones in teleost fish: Poor correlation between the pattern of steroid release by goldfish and olfactory sensitivity suggests that these cues evolved as a result of chemical spying rather than signal specialization. Acta Physiol. Scand. 152:191-205.

Sorensen, P. W., A. P. Scott, N. E. Stacey, and L. Bowdin. 1995. Sulfated 17 [Alpha], 20 [Beta] -dihydroxy-4-pregnen-3-one functions as a potent and specific olfactory stimulant with pheromonal activities in the goldfish. Gen. Comp. Endocrinology 100:128-142.

Stacey, N. E., W. B. Zheng, and J. Cardwell. 1994. Milt production in common carp (Cyrinus carpio): Stimulation by a goldfish steroid pheromone. Aquaculture 127:265-276.

Sumner, I. T., J. Travis, and C. D. Johnson. 1994. Methods of female fertility advertisement and variation among males in responsiveness in the sailfin molly (Poecilia latipinna). Copeia 1994:27-34.

Tavolga, W. N. 1971. Sound production and detection. In W. S. Hoar and D. J. Randall (eds.), Fish physiology, pp. 135-205. Academic Press, New York.

Tavolga, W. N., A. N. Popper, and R. R. Fay. 1981. Hearing and sound communication in fishes. Springer-Verlag, New York.

Templeman, W. and V. M. Hodder. 1958. Variation with fish length, sex, stage of sexual maturity, and season in the appearance and volume of the drumming muscles of the swim-bladder in the haddock, Melonogrammus aeglefinus (L.). J. Fish. Res. Bd. Canada 15:355-390.

Torricelli, P, M. Lugli, and G. Pavan. 1990. Analysis of sounds produced by male Padogobius martensi (Pisces, Godiidae) and factors affecting their structural properties. Bioacoustics 2:261-276.

Townshend, T. J. and R. J. Wootton, 1984. Effects of food supply on the reproduction of the convict cichlid, Cichlasoma nigrofasciatum. J. Fish Biol. 23:91-104.

Tricas, T. C., W. M. Scott, and J. A. Sisneros. 1995. Electorsensory optimization to conspecific phasic signals for mating. Neuroscience Letters 202:129-132.

Turner, G. F. 1993. Teleost mating behaviour. In T. J. Pitcher (ed.), The behaviour of teleost fishes, pp. 307-331. Chapman and Hall, London.

Unger, L. M. 1983. Nest defense by deceit in the fathead minnow, Pimephales promelas. Behav. Ecol. Sociobiol. 13:125-130.

Waas, J. R. and P. W. Colgan. 1992. Chemical cues associated with visually elaborate aggressive displays of three-spine sticklebacks. J. Chem. Ecol. 18:2277-2284.

Werner, E. E. and J. E Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15:393-425.

Courtship and mate choice in fishes: integrating behavioral and sensory ecology.

Whang, A. and J. Janssen. 1994. Sound production through the substrate during reproduction in the mottled sculpin, Cottus bairdi (Cottidae). Env. Biol. Fishes 40:141-148.

Wiens, J. J. and M. R. Morris. 1996. Character definitions, sexual selection, and the evolution of swordtails. Am. Nat. 147:866-869.

Williams, G. C. 1975. Sex anti evolution. Princeton University Press, Princeton.

Williams, G. C. 1992. Natural selection: Domains, levels, and challenges. Oxford University Press, Oxford.

Wolf, J. B., E. D. Brodie, III, and A. J. Moore. 1997. The evolution of indicator traits for parental quality: The role of maternal and paternal effects. Am. Nat. 50:639-649.

Wootton, R. J. 1976. The biology of the sticklebacks. Academic Press, London.

Yamazaki, F. 1990. The role of urine in sex discrimination in the goldfish Carassius auratus. Bull. Fac. Fish. Hokkaido Univ. 41:155-161.

Yu, K. L. and R. E. Peter. 1990. Alterations in gonadotropin-releasing hormone immunoactivities in discrete brain areas of male goldfish during spawning behavior. Brain Res. 512:89-94.

Zahavi, A. 1975. Mate selection--selection for a handicap. J. Theor. Biol. 53:205-214.

Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). J. Theor. Biol. 67:603-605.

ROBERT CRAIG SARGENT(2), VICTOR N. RUSH, BRIAN D. WISENDEN(3), AND HONG Y. YAN (2) To whom correspondence should be addressed; E-mail: craig@ceeb.uky.edu (3) Current address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G-2E9.