Chapter 7
Sex Steroid-Dependent Modulation of Acoustic Communication Systems in Fishes

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Abstract Acoustic communication is widespread among fishes, the largest extant group of vertebrates, and in many vocal teleost species it is essential for their reproductive and social behaviors. Recent evidence suggests that a fish's internal hormonal state can profoundly influence its ability to produce and perceive social acoustic signals. Here, we review the current knowledge of how sex steroids can influence the auditory capabilities and vocal motor production of acoustic social signals in two incipient model teleosts, the plainfin midshipman fish *Porichthys notatus* and the African cichlid *Astatotilapia burtoni.* Studies of these model systems show that steroid-mediated improvements in vocal-acoustic processing are typically associated with reproductive readiness. This especially holds true for species that rely heavily on acoustic signaling during seasonal breeding such as the midshipman fish, as well as non-seasonally breeding species like cichlids that appear to use sound production as one component of a more complex multimodal courtship repertoire. Evidence for reproductive-state dependent plasticity in midshipman and cichlids is supported by changes in gonadal state, circulating sex-steroids (testosterone, 11-ketotestosterone, and estradiol), and steroid receptor expression in peripheral and central auditory structures that are concurrent with changes in auditory sensitivity and vocal motor production. This form of steroid-dependent vocal-acoustic plasticity is proposed to be an evolutionary labile solution for enhancing the detection and production of social acoustic signals. The abundance and diversity of vocal fish present unique future opportunities to explore how this solution may have shaped sexual selection and the evolution of acoustic communication systems in fishes.

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7.1 Introduction—Sex Steroids and Acoustic Communication Systems in Fishes

Sex steroids are a class of hormones that have profound organizational and activational effects on the vertebrate central nervous system (CNS) and are known to shape the expression of many social behaviors including those involved in courtship, reproduction, parental care, aggression, and communication. Sex steroids are derived from cholesterol and are synthesized in the brain, adrenal gland, and gonads (Schlinger and Remage-Healey 2012). Recent work suggests that the CNS may be modulated by both brain-derived steroids or "neurosteroids" and peripherally synthesized steroids or "neuroactive steroids". These activating hormones can regulate behavior by inducing an array of physiological and morphological changes in the CNS to shape the expression of behaviors such as those used in social communication.

Sex steroids such as androgens and estrogens are well-known modulators of vocal motor behaviors used during social and reproductive communication. These same steroid hormones are also known to greatly influence the production and reception of social acoustic signals leading to a more efficient exchange of information during communication. This steroid-dependent form of auditory plasticity is proposed to be an evolutionary labile solution for enhancing the detection of social acoustic signals during reproductive cycles in fishes (Sisneros et al. 2004a; Maruska et al. 2012). However, sensory plasticity related to reproductive-state and sex steroid levels is known to be widespread among vertebrates, including humans (Sisneros et al. 2004a; Walpurger et al. 2004; Hau et al. 2008; Arch and Narins 2009; Caras 2013).

Our review focuses on sex-steroid induced plasticity of the vocal-motor production and auditory reception of social acoustic signals during the reproductive cycle of fishes to enhance acoustic communication. We primarily report on recent evidence in two vocal teleost species, the plainfin midshipman fish (*Porichthys notatus*) and the African cichlid (*Astatotilapia burtoni*).

7.2 Reproduction, Sex Steroids, and the Midshipman Auditory System

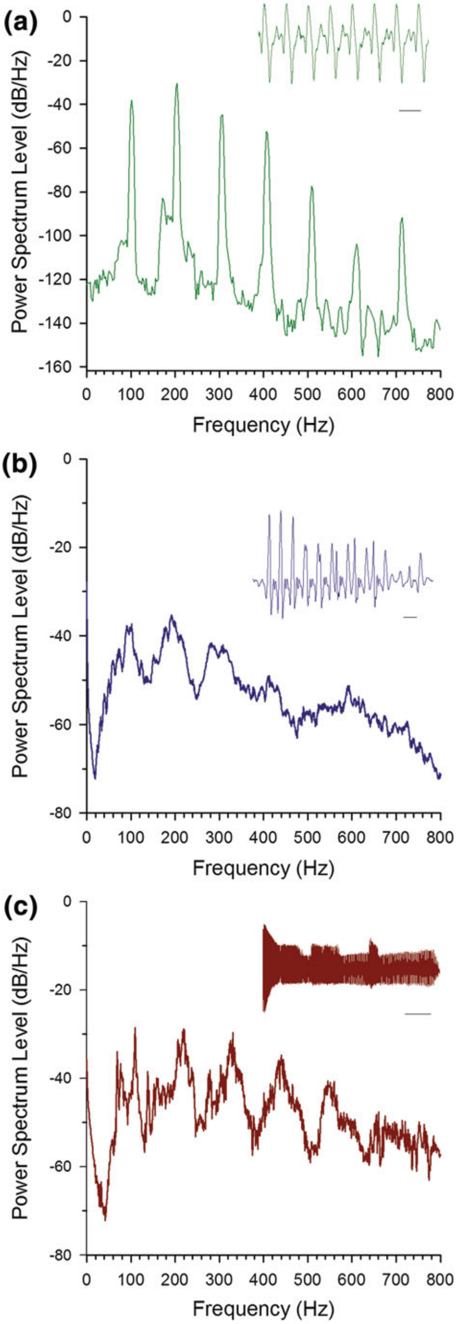
7.2.1 Reproduction and Acoustic Communication in the Plainfin Midshipman Fish

The plainfin midshipman is a marine teleost species that has become a productive neuroethological model for investigating the neural and endocrine mechanisms of acoustic communication among vertebrates, in part because the reception and production of social vocalizations is essential to their reproduction. Plainfin midshipman are vocal fish from the Family Batrachoididae (order Batrachoidiformes) that migrate seasonally during the spring and summer from the deep ocean off the west coast of British Columbia and the United States into the sub-tidal and shallow rocky intertidal zones where they breed (Miller and Lea 1972; Bass 1990, 1996). This species is known to have three adult morphs that include two types of males (types I and II) and females; each male morph employs a different reproductive tactic (Brantley and Bass 1994; Bass et al. 1999). Type I or "singing" males build and defend nests that are constructed under rocky shelters in the sub-tidal and rocky intertidal zones during the spring and summer breeding season (May–July). At night from their nests, type I males produce long-duration advertisement calls also known as "hums" to attract potential mates for spawning (Bass et al. 1999). This seasonal advertisement call is a multiharmonic social acoustic signal with a fundamental frequency (F_0) that is established by the contraction rate of the sonic muscles attached to the swim bladder, which acts as a resonant structure in the midshipman fish to help propagate the vocal-acoustic signals. The advertisement calls are relatively long in duration on the order of several minutes to 1 h with a F_0 of 90–100 Hz at temperatures of 15–16 °C (Ibara et al. 1983; Bass et al. 1999), however the F_0 is temperature dependent and is known to vary linearly with ambient temperature (Bass and Baker 1991; Brantley and Bass 1994). The harmonics of the advertisement call extend up to 800 Hz (Fig. 7.1a) and are very stable (Bass et al. 1999). Typically the hum's dominant harmonics range up to approximately 400 Hz, can contain more or equal spectral energy as the F_0, and have been hypothesized to be used by females in the localization of male advertisement calls during the reproductive season (Sisneros and Bass 2003; Sisneros 2009a). McKibben and Bass (1998) showed that females can respond selectively in two-choice tests and are capable of differentiating and choosing between acoustic signals that differ in duration, frequency, amplitude, and spectral/temporal content. Taken together, the results from McKibben and Bass (1998, 1999, 2001a, b) suggest that females could potentially utilize acoustic information in male advertisement calls to access mate quality and facilitate mate-choice decisions.

Type I males are also known to produce "grunt" trains and "growls". While all adult morphs (females and both male types) are capable of producing "grunts" (Fig. 7.1b) or short duration ($\sim$50–200 ms) broad band acoustic signals during agonistic interactions (Ibara et al. 1983; Brantley and Bass 1994), only type I males produce grunt trains or rapid succession of single grunts at a rate that ranges from 97 to 110 Hz (Brantley and Bass 1994; Bass et al. 1999). Type I males often use grunt trains to ward off nest intruders during the reproductive season. "Growls" are also agonistic calls and are often used in the defensive of a nest. Like the advertisement call, "growls" are only produced by type I males and are long-duration multiharmonic calls. Growls (Fig. 7.1c) begin with a grunt-like signal component followed by a multiharmonic component with a F_0 of 59–116 Hz that changes over that duration of the call (Bass et al. 1999). Type I males often produce growls during the early breeding season when these males are highly aggressive and territorial as they establish their nest sites.

Type II males also known as "sneaker" males employ an alternative reproductive and behavioral tactic during the breeding season. Type II males do not produce

Fig. 7.1 Power spectra and waveforms (insets) of representative vocalizations of the plainfin midshipman fish (*Porichthys notatus*) that include the hum, grunt, and growl recorded at 16°C from a nesting type I male. **a** The advertisement call or “hum” (inset, bar = 10 ms). **b** Grunt (inset, bar = 10 ms). **c** Growl (inset, bar = 500 ms)



advertisement calls or court females but instead satellite and/or "sneak" spawn in competition with type I males (Brantley and Bass 1994). Sneaker males invest less energy in body growth and instead invest more energy in the development of their gonads. Type II males can have testes as large as 15–20 % of their body mass which can presumably result in greater sperm production (Bass 1996; Brantley and Bass 1994; and JAS personal observation).

Reproductive females do not produce grunt trains, growls, or advertisement calls but instead are passive listeners that use audition to locate "singing" type I males to mate with during the breeding season. After a gravid female (full of eggs) has spawned with a type I male and has deposited all her eggs, she will then leave the intertidal nesting environment and return to deep offshore sites. Type I males remain with the fertilized eggs in the nest and will then continue to court and spawn with additional females over the course of the breeding season until their nests are filled with multiple clutches of eggs and developing larvae (DeMartini 1988; Brantley and Bass 1994; Bass and McKibben 2003; Sisneros et al. 2009a). The nesting type I males provide all the parental care of the nest eggs and larvae which include fanning and brushing the fertilized eggs to keep them free of detritus and bacteria. Nesting type I males vigorously defend and guard their nests from predators until the developing larvae have absorbed their yolk, detached from the nest, and become free swimming after approximately 50–60 days post fertilization at a relatively constant temperature of 15 °C (Alderks and Sisneros 2013).

The primary end organ used for hearing in the midshipman is the saccule. The midshipman inner ear, like other teleost fishes, includes three semicircular canals and three otolithic acoustic end organs: the utricle, lagena, and saccule. All three otolithic end organs are innervated by cranial nerve VIII, but the saccule serves as the main hearing organ in most teleost fishes (Popper 2011). The sensitivity and frequency response of the midshipman auditory peripheral nervous system (PNS) including the hair cells and afferents of the saccule have been extensively quantified (McKibben and Bass 1999, 2001a; Sisneros and Bass 2003, 2005; Sisneros 2009b). In general, the hair cells and afferents of the saccule are broadly tuned with peak frequency sensitivity at low frequencies (<150 Hz) associated with midshipman vocalizations (McKibben and Bass 1999; Sisneros and Bass 2005; Sisneros 2007). Ontogenetic comparisons of saccular afferent data from adult and juvenile midshipman indicate that the saccular primary afferents of juveniles, like those of nonreproductive adults, are best adapted to temporally encode the low frequencies within midshipman vocalizations (Sisneros and Bass 2005).

7.2.2 Seasonal Plasticity of the Midshipman Auditory System

Behavioral studies of the midshipman's spawning behavior and acoustic playback responses showed that reproductive females (full of eggs) exhibit strong phonotaxis to natural and synthetic advertisement calls, whereas recently spawned females (void of eggs) do not respond to the advertisement call (McKibben and Bass 1998, 2001b;

Zeddies et al. 2010, 2012). Based on these experiments and the fact that nocturnally-active females rely on audition to locate mates, Sisneros and Bass (2003) tested the hypothesis that seasonal reproductive state (gravid vs. non-gravid) influenced the frequency response and sensitivity of the auditory system (Sisneros and Bass 2003). Results from Sisneros and Bass (2003) showed that saccular afferents from summer reproductive females exhibited greater phase-locking accuracy to frequencies of 120–400 Hz and had higher peak frequency sensitivity than that recorded for winter nonreproductive females. In addition, Sisneros (2009b) showed that in reproductive females saccular hair cells were more sensitive (i.e., lower thresholds, $\sim$8–13 dB or 2.5–4.5 times lower) than nonreproductive females to frequencies 75–385 Hz. Together these studies showed that the sensitivity of the midshipman's peripheral auditory system was related to the female reproductive cycle such that breeding females were better adapted than non-breeding females to perceive the dominant harmonic frequencies in the male's mate call (Sisneros and Bass 2003; Sisneros 2009b).

The detection of male advertisement call harmonics by reproductive females likely increases the probability of mate localization due to the sound transmission properties of shallow water acoustic environments like those where plainfin midshipman court and breed. The harmonics of the advertisement call have been proposed to provide enhanced signal detection of the advertisement call for females because the call's dominant harmonics (200–400 Hz) will propagate farther than the lower F_0 ($\sim$80–100 Hz) in shallow water environments due to an inverse relationship between water depth and the cutoff frequency of sound transmission (Fine and Lenhardt 1983; Roger and Cox 1988; Sisneros and Bass 2003; Sisneros 2009c) (see also Chap. 6 by Lugli this volume). In very shallow water (<3 m), substrate composition (e.g., rocky substrate like that found in the midshipman's nesting environment) also becomes an important factor that is likely to affect the cutoff frequency of signal propagation and attenuate the transmission of acoustic signals less than 150 Hz (Roger and Cox 1988; Bass and Clark 2003). In addition, the harmonics of the mate call produce by males may also affect the receiver's detection of the signal when near the source of the advertisement call. McKibben and Bass (2001a) showed that saccular afferent detection of a tone at or near the F_0 of the mate call was improved when tones similar to harmonics were added to the presentation stimuli. In sum, this seasonal enhancement of auditory sensitivity likely represents an adaptation of the teleost auditory system to facilitate the detection of advertisement calls and enable females to acquire acoustic information needed for the recognition, identification, and localization of potential mates.

Recently, Coffin et al. (2012) showed that females undergo seasonal changes in hair cell sensitivity that were concurrent with changes in hair cell density in the midshipman saccule. Summer reproductive females were found to have greater hair cell receptor density in the saccule than winter nonreproductive females (Fig. 7.2a), but this change in receptor density did not occur in the other two inner end organs, the utricle, and lagena. The seasonal change in hair cell addition was not dependent on fish body size and the increase in saccular hair cell density was consistent across the size range of fish sampled. Coffin et al. (2012) also observed a seasonal increase

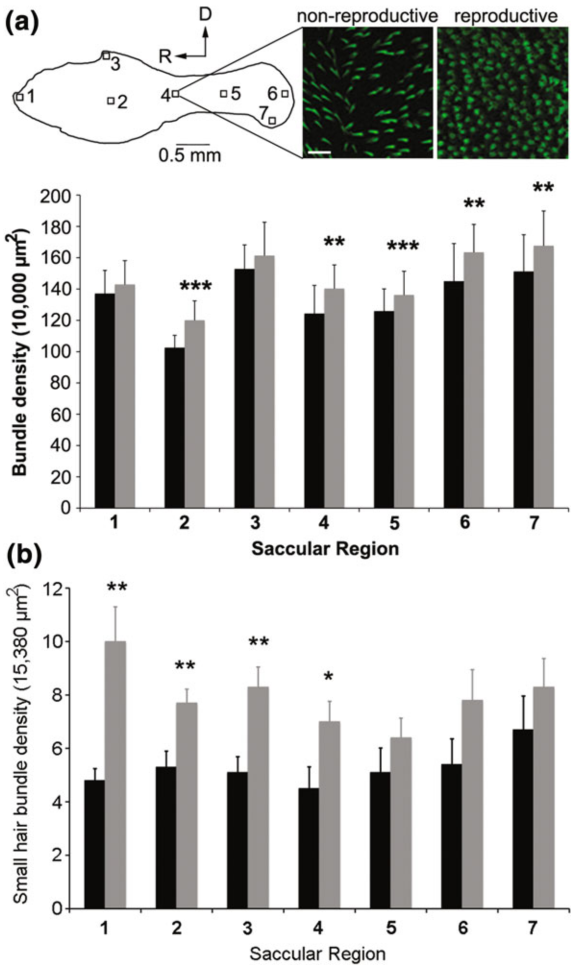


Fig. 7.2 Seasonal differences in hair bundle density and in the number of small hair bundles in the saccule of female midshipman (*P. notatus*). All data are plotted as means + 1 SE. **a** Phalloidin-labeled hair bundles were counted in 10,000 μm^2 areas from seven regions across the saccule, as indicated by the numbered boxes on the line drawing (*top portion of figure*). The micrographs (*top right*) show representative images from the *middle* of the saccule from a nonreproductive and reproductive female. Hair bundle quantification from these seven saccular regions (*bottom portion of figure*) shows significantly more hair cells in noted regions (** $p < 0.01$; *** $p < 0.001$). Note: *black bars*, nonreproductive females; *gray bars*, reproductive females. (Modified from Coffin et al. 2012). **b** Small hair bundles were counted in seven 15,380 μm^2 regions of ten saccules from both reproductive (*gray bars*) and nonreproductive (*black bars*) females. There were significantly higher densities of small hair bundles between reproductive and nonreproductive females in the noted saccular regions (* $p < 0.05$; ** $p < 0.01$). (Modified from Coffin et al. 2012)

in the number of small saccular hair bundles in reproductive females (Fig. 7.2b) that were hypothesized to be either mature hair cells with a distinct subtype of morphology or potentially immature hair cells. One possible explanation suggested by the authors was that the smaller hair bundles in breeding females represented immature saccular hair cells that were the product of increased hair cell proliferation that occurred earlier in the spring during the pre-nesting period (Sisneros et al. 2004b). The seasonal increase in saccular hair cell density observed in reproductive females occurred concurrently with increases in the magnitude of the evoked potentials of the saccule and had a corresponding decrease in the auditory thresholds of saccular hair cells (Fig. 7.3). This recent demonstration of concurrent seasonal change in hair cell receptor density and auditory sensitivity may represent one of the mechanisms that contribute to the increased saccular sensitivity observed seasonally in reproductive female midshipman.

In addition to seasonal changes in female auditory sensitivity, seasonal auditory plasticity is also known to occur in type I nesting males. Rohmann and Bass (2011) showed that the saccular hair cell thresholds of reproductive type I males were significantly lower than that of nonreproductive type I males at frequencies greater than 145 Hz. This seasonal frequency-dependent change in auditory sensitivity was most apparent at frequencies that were associated with the dominant harmonics in the male advertisement call (approx. 180–400 Hz) (Rohmann and Bass 2011).

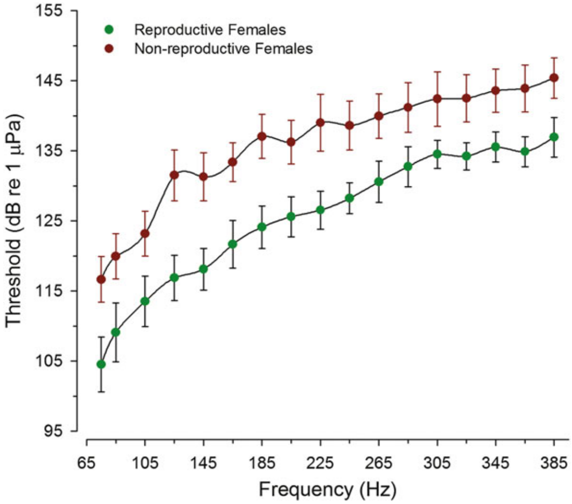


Fig. 7.3 Auditory threshold tuning curves for reproductive and nonreproductive female midshipman (*P. notatus*) based on the evoked potentials recorded from the saccule. All data are plotted as means ±95 % CL. The sample size for the reproductive females (*green circles*) was 12 animals (16 recordings) while the sample size for the nonreproductive females (*red circles*) was 12 animals (20 recordings). Auditory threshold at each stimulus frequency was determined as the lowest stimulus intensity in decibels (re 1 μPa) that evoked a saccular potential that was at least 2 SD above the background noise measurement. (Modified from Coffin et al. 2012)

One adaptive function for this seasonal enhancement of hearing in type I males may be to assess other males during intraspecific male competition and during nest establishment in the breeding season. The future work needs to determine whether or not seasonal changes in auditory sensitivity also occur in type II sneaker males. There is no reason to expect that such changes would be limited to females and type I males. One could hypothesize that the seasonal increase in auditory sensitivity would also benefit type II males in their ability to detect and assess calling type I males for the selection of cuckoldry sites during the breeding season.

7.2.3 Steroid-Dependent Plasticity of Midshipman Auditory System

In natural populations of plainfin midshipman, sex steroids levels are known to fluctuate seasonally with the reproductive cycle and correspond to seasonal changes in reproductive biology and behavior (Brantley et al. 1993; Knapp et al. 1999; Sisneros et al. 2004b). There are four time periods that correspond to the annual reproductive cycle in the plainfin midshipman: the nonreproductive, prenesting, nesting, and postnesting periods (Sisneros et al. 2004b). The nonreproductive period occurs in the winter from December to February when females have a low gonadal somatic index (GSI, ratio of gonad to body mass) with ovaries containing undeveloped oocytes and low estradiol (E_2) and testosterone (T) plasma levels, whereas type I males have a similar low GSI with no sperm present and low T and 11-ketotestosterone (11-KT) plasma levels. The prenesting period occurs in the spring (March–April) when both females and type I males exhibit seasonal development of the ovaries and testes, respectively, with females exhibiting a brief spike of E_2 and T plasma levels in April about 1 month prior to the summer breeding season while type I males continue to show a gradual increase in T and 11-KT plasma levels during gonadal recrudescence. The nesting period occurs in late-spring and summer (May–August) when breeding females have high GSI with well-developed eggs ($\sim$5 mm diameter) and low T and E_2 levels while type I males exhibit an intermediate GSI with T and 11-KT levels that peak at the start of the summer nesting season (May–June). During the nesting period, "humming" type I males have significantly higher plasma levels of 11-KT than non-humming males (Genova et al. 2012). The postnesting period occurs in the fall months (September–October) when females and type I males show a marked decrease in GSI and in E_2, T, and 11-KT plasma levels.

The spring prenesting peak of circulating blood levels of E_2 and T exhibited by females, which occurs approximately 30 days before the reproductive season begins, led Sisneros et al. (2004a) to hypothesize that E_2 and T could induce seasonal changes in peripheral auditory sensitivity via enhancements in phase-locking accuracy and changes in peak frequency sensitivity of saccular afferents in nonreproductive individuals. Sisneros et al. (2004a) showed that ovariectomized

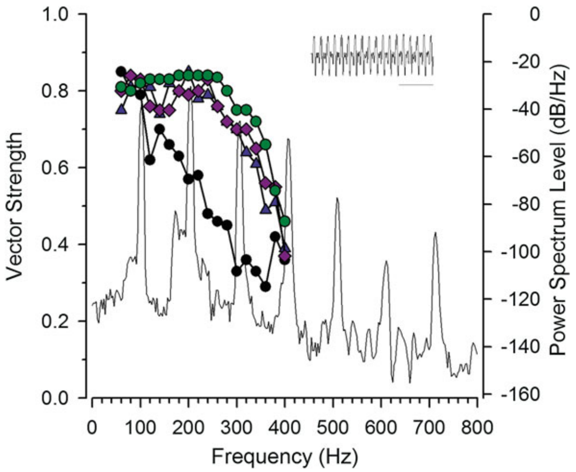


Fig. 7.4 The adaptive coupling between the frequency encoding of saccular afferents and the dominant harmonic components in the male advertisement call of the plainfin midshipman fish (*P. notatus*). The type I male midshipman advertisement call or "hum" recorded at 16 C is shown in the *inset* (bar = 10 ms) above the main combined plot of the phase-locking precision of saccular afferents as a function of the vector strength of synchronization (*VS, left y-axis*) and the power (*amplitude*) spectrum level of the hum (*right y-axis, in relative dB values*) from a nesting type I male. Plotted are the median Vector Strength values of the saccular afferents emphasizing the overlap in frequency sensitivity between testosterone-treated (*blue triangles*) and 17β-estradiol-treated (*pink diamonds*) nonreproductive females and wild-caught reproductive females (*green circles*). Steroid-treated and wild-caught reproductive females show robust encoding of the fundamental frequency (~100 Hz) and the second (~200 Hz) and third (~300 Hz) harmonics of the hum. In contrast, winter nonreproductive females (*black circles*) show comparable encoding only for frequency close to the fundamental frequency at approximately 100 Hz. Adapted from Sisneros et al. (2004b)

nonreproductive females implanted with either E_2 or T capsules to produce prenesting steroid levels resulted in an improvement of phase-locking accuracy of saccular afferents at higher frequencies within the midshipman hearing range. These steroid induced changes improved the encoding of saccular afferents at frequencies that corresponded to the major harmonic components of the advertisement call and was similar to the female reproductive auditory phenotype (Fig. 7.4). Furthermore, an estrogen receptor alpha (ERα) specific for midshipman was cloned and identified by real-time reverse transcription polymerase chain reaction in the sensory macula of the saccule and provides further evidence for direct effects of sex steroids on the peripheral auditory system of teleosts (Sisneros et al. 2004a).

One mechanism that could explain the seasonal change in hair-cell frequency sensitivity (Sisneros 2009b; Rohmann et al. 2011) is a reproductive-state dependent change in ion channel expression of midshipman saccular hair cells (Rohmann et al. 2013), which is almost certainly linked to seasonal fluctuations in steroid hormone levels. Rohmann et al. (2013) recently demonstrated that reproductive midshipman show increased abundance of Ca^+-activated potassium (BK) channels in saccular hair cells which are thought to enhance the midshipman's ability to "hear" social acoustic signals during the reproductive season. The large conductance BK channels are known to underlie the primary outward hair cell current and influence the electrical resonance and frequency tuning of hair cells in nonmammals (Fettiplace and Fuchs 1999). Rohmann et al. (2013) showed pharmacological manipulation that reduced BK currents replicated the natural range of hair cell sensitivity of the saccule in midshipman. These pharmacological manipulations targeting BK channels, together with the increased measures of BK transcript abundance, could explain the observed seasonal increase in auditory sensitivity to the higher harmonics of the midshipman vocalizations (Rohmann et al. 2013).

In addition to their effects on the midshipman auditory system, sex steroids are also known to have both rapid and long-term effects on the vocal motor behavior and activity of the central pattern generator of the vocal motor system in type I males. Androgens (T and 11-KT) and estrogen have been shown to regulate vocal motor output and call production in the midshipman and the closely related Gulf toadfish (*Opsanus beta*). For a more detailed review of the sonic motor behaviors and the effects of sex steroids on the associated neural mechanisms of the vocal motor system in midshipman and toadfish see Bass et al. (Chap. 2 in this volume), Bass and McKibben (2003), and Bass and Ladich (2008).

The distribution of estrogen and androgen receptors has been described extensively for the vocal and auditory networks in the midshipman (for more detailed descriptions see Forlano et al. 2005, 2010; Fergus and Bass 2013). In sum, Forlano et al. (2005) described the distribution of ERα mRNA in the saccule and brain of reproductive females and type I males and identified transcripts in liver and ovary, the CNS, and in the VIII nerve branches of the saccule proximal to the sensory epithelium. More recently, Fergus and Bass (2013) identified estrogen receptors ERβ1 and ERβ2 in midshipman vocal–acoustic networks of the CNS and in the saccule. In that study, Fergus and Bass (2013) developed antibodies to localize protein expression in the vocal-acoustic areas of the peripheral and central nervous systems and showed that ERβ1 and ERβ2 receptors were expressed in the telencephalon, hypothalamus, and in other vocal–acoustic brain regions shown previously to exhibit expression of ERα and aromatase. In addition, both ERβ1 and ERβ2 were expressed within the hair cells of the saccular epithelium with ERβ1 being expressed in a very small region at the apical end of hair cells immediately adjacent to the hair bundle while ERβ2 was expressed more broadly within hair cells and within the ganglion cells of the VIII nerve proximal to the sensory macula of the saccule (Fergus and Bass 2013). Forlano et al. (2010) described the distribution of androgen receptor mRNA throughout the CNS with transcripts found in the vocal pre pacemaker nucleus, dorsal periphery of the vocal motor nucleus, and in the saccule.

An additional candidate site for sex steroid effects on the auditory system may include the saccular efferents that project from hindbrain and diencephalic efferent nuclei to the base of saccular hair cells (Forlano et al. 2014). Saccular efferent neurons provide inhibitory input to the saccular afferents and their hair cells from the CNS and can modulate the sensitivity or gain of the saccule (Furukawa and

Matsura 1978; Lin and Faber 1988). Xiao and Suga (2002) showed that auditory neurons in the mammalian cortex are able to modulate the frequency response and sensitivity of hair cells in the cochlea. Future work that examines the steroid-dependent effects of efferent modulation of the midshipman PNS may prove fruitful. In sum, the distribution of estrogen and androgen receptors in the inner ear saccule and brain strongly supports the role of these sex steroids as neuromodulators of behaviorally defined auditory, vocal, and neuroendocrine circuits in the midshipman and teleost fishes in general.

7.3 Sex Steroids and the Cichlid Auditory System

7.3.1 Acoustic Communication in Cichlids

Cichlids represent a large and diverse group of freshwater fishes, well-known for their flashy coloration patterns and visually conspicuous behavioral displays. Recently, however, the importance of non-visual signaling (acoustic, chemosensory, mechanosensory, tactile) during social interactions such as aggression and mating has come to the forefront. Previous studies suggest that single traits, such as those involved in visual signaling, are often insufficient to explain phenotypic diversity in cichlids, and that species richness is a function of the number of traits involved in diversification (i.e., the "multifarious selection" hypothesis) (Blais et al. 2009; Nosil and Harmon 2009; Nosil et al. 2009). Thus, the use of multimodal communication systems for social interactions provides more traits on which sexual selection can act, possibly contributing to the high diversity of cichlid fishes (Blais et al. 2009; Sturmbauer et al. 2011). Consequently, there has been significant recent interest in understanding the function and diversity of acoustic signaling in cichlids, with sound production and/or hearing abilities now described for a number of African, American, and Asian cichlid species (Yan and Popper 1992; Ripley et al. 2002; Amorim et al. 2004; Amorim 2006; Simoes et al. 2008; Maruska et al. 2012; Schulz-Mirbach et al. 2012).

Many cichlid fishes use sounds for species or individual recognition (Amorim et al. 2008; Verzijden et al. 2010; Bertucci et al. 2012a; Longrie et al. 2013), during territorial or agonistic interactions (Amorim 2006; Simoes et al. 2008; Bertucci et al. 2012b), and during reproductive courtship contexts (Amorim et al. 2003, 2008; Maruska et al. 2012). Cichlids are one of the most visually conspicuous groups of fishes, with complex coloration patterns and elaborate courtship behavioral displays. Thus, visual communication is extremely important in this group, and sounds are likely used as a supplement to this rich visual information, which differs from the case in batrachoidid fishes (toadfish, midshipman) that use acoustic signaling as a primary sensory channel. Descriptions of sound production in cichlids thus far show that sounds are not typically used alone, but are produced concurrent with visual display behaviors (Ripley and Lobel 2004; Maruska et al. 2012; Longrie et al. 2013).

For example, in the Lake Malawi cichlid *Metriaclima zebra*, sounds produced during male-male interactions reduced opponent aggression as a complement to visual displays, thereby potentially lowering the risk of escalated fights (Bertucci et al. 2010). In the Lake Victoria cichlid *Pundamilia nyererei*, playback experiments showed that while both males and females can discriminate conspecific sounds compared to noise controls, females do not display phonotaxis toward courtship sounds without the presence of a live male (Estramil et al. 2013). In the African cichlids *P. nyererei* and *A. burtoni*, however, playback experiments that consisted of visual and acoustic signals that were temporally uncoupled from each other showed that courtship sounds alone influenced a female's preference before she could see the male (Verzijden et al. 2010; Maruska et al. 2012). These experiments suggest that while a live male may be required to elicit receptive behaviors in a female and ultimately determine her mate choice decision, simply overhearing courtship sounds alone may provide the female with some valuable information such as the presence and relative quality of a courting male in the area. Nevertheless, sound production in cichlids is likely one component of a complex multimodal signaling system that complements visual, chemosensory, mechanosensory, and tactile cues.

7.3.2 Steroids and Acoustic Communication in the Model African Cichlid Astatotilapia burtoni

The African cichlid fish *A. burtoni* is an excellent and emerging model for studying the role of acoustic communication as part of a multimodal signaling system used during reproduction, and for investigating the role of internal hormonal state on auditory processing. Importantly, this species already has a wealth of available information on its social behaviors, reproductive physiology, steroid cycling, and communication modalities, as well as an understanding of the remarkable plasticity in behavior and physiology associated with changes in social status and reproductive state [reviewed in (Maruska and Fernald 2011a, 2013; Fernald and Maruska 2012)]. Further, genomic resources for *A. burtoni* are now available, along with those of four other African cichlid species, providing important molecular tools for understanding the mechanisms of putative steroid-induced plasticity in behavior and sensory processing in comparative and evolutionary contexts.

7.3.2.1 Natural History and Social Behavior of *A. burtoni*

Astatotilapia burtoni is endemic to Lake Tanganyika, the oldest, deepest, and most diverse lake within the rift valley system of Eastern Africa. This species lives primarily in shallow shore pools and river estuaries, where visual conditions are often variable, and environmental parameters are dynamic (Fernald and Hirata 1977).

Adult males exist in two distinct but reversible phenotypes, which differ in appearance, behavior, morphology, activity of their brain-pituitary-gonadal axis, and ultimately reproductive capacity [reviewed in (Fernald 2009; Maruska and Fernald 2011a, 2013; Fernald and Maruska 2012). Dominant (also called territorial) males represent a small percentage of the adult male population (~10–30 %), are brightly colored (blue or yellow) with a black stripe through the eye (eye-bar), an opercular black spot at the caudal tip of the gill cover, prominent egg-spots on the anal fin, and a red humeral patch on the side of the body. These dominant males hold territories that they defend vigorously from rival males, and spend significant amounts of time engaged in courtship displays and eventually spawning with females (Fernald 1977; Fernald and Hirata 1977). In contrast, subordinate (also called non-territorial) males make up the majority of the adult male population (~70–90 %), are more dull in coloration and similar to females (lacking eye-bar and humeral patch), do not hold territories or typically reproduce, school with females and other subordinate males, and flee from the aggressive attacks of dominant males.

Astatotilapia burtoni lives in a lek-like social system where dominant males defend clustered territories to guard food, shelter, and spawning substrates from rival males (Fernald 1977). Dominant males establish a spawning area by digging a pit in their territory, engage in agonistic threat displays and border disputes with neighboring dominant males, chase subordinate males away from their territory, and perform courtship quivers toward passing females in an attempt to lead them into their territory to spawn. Since defendable territories for spawning and feeding are often limited, and females are less likely to mate outside the protection of a spawning shelter, there is fierce competition for this resource. As a result, only a minority of males at any one time will defend a territory and successfully mate with females. Typical territory tenure lasts about 4–6 weeks (Fernald and Hirata 1977; Hofmann et al. 1999), and if a dominant male is either challenged by a subordinate male, or disappears from the population, a subordinate male will rise in social rank, and within minutes, display dominance and reproductive behaviors (Burmeister et al. 2005; Maruska and Fernald 2010a). Once a receptive (gravid, "ripe with eggs") female follows a dominant male into his territory and is appropriately stimulated, she will deposit eggs on the substrate and then immediately turn around and collect them into her mouth. The male then displays the egg-spots on his anal fin in front of her, and while she attempts to collect these egg-spots, the male releases sperm near her mouth to fertilize the eggs inside. There are typically several bouts of egg-laying and fertilization that may be briefly interrupted as the dominant male chases away intruders or interacts with neighboring males. During these spawning bouts, subordinate males will also attempt to interrupt the pair and "sneak" fertilization attempts; although these subordinate males do not defend territories, they do maintain sperm in their testes during social suppression (Maruska and Fernald 2011b; Kustan et al. 2012). When spawning and fertilization are complete, the dominant male resumes his territorial defense and continues to court other receptive females, while the female leaves the territory to brood the young in her mouth (mouth-brooding) for ~2 weeks until releasing them as fully-developed fry. Following brood release, females will resume feeding and immediately begin ovarian recrudescence to prepare for subsequent spawning. In contrast to the seasonally breeding midshipman fish described above, *A. burtoni* is a non-seasonal breeder, and while individual females cycle between spawning and brooding every ~28 days (Kidd et al. 2013), dominant males maintain territories and are continuously available for receptive females year-round.

7.3.2.2 Acoustic Communication in *A. burtoni*

As in many cichlids, social communication in *A. burtoni* relies heavily on visual signals (Fernald 1977; Fernald and Hirata 1977; Fernald 1984; Clement et al. 2005), but several studies have now demonstrated the importance of multimodal signaling, including chemosensory and acoustic communication (Crapon de Caprona 1974, 1980; Nelissen 1977; Robison et al. 1998; Maruska and Fernald 2010b, c, 2012; Maruska et al. 2012). Dominant male *A. burtoni* produce pulsed (range, 2–19 pulses; mean, 8.5 pulses per sound) relatively broadband (peak frequency range, 129–904 Hz; mean, 500 Hz) sounds during body quivers associated with courtship behaviors (Maruska et al. 2012) (Fig. 7.5a, b). These sounds are similar to courtship sounds described in other cichlid species (Amorim et al. 2003, 2008; Verzijden et al. 2010), and are intentional (not merely a by-product of body movements), because while sounds are only produced during quivers, not all quiver behaviors are associated with sound production (Fig. 7.5c). Dominant males typically swim out rapidly from their territory shelter toward a receptive female, perform a visual-acoustic quiver display in close proximity to the female (Fig. 7.5a), and then turn around and swim back toward the territory with an exaggerated tail waggle in an attempt to lead the female into the shelter for spawning. The close-proximity of signaling individuals to receivers, as well as the low intensity and rapid attenuation of these courtship sounds, suggests they are used primarily for close-range communication. Larger males produce courtship sounds with lower peak frequencies compared to smaller males, potentially providing females, subordinate males, and neighboring dominant males with an honest indicator of signaler body size (Maruska et al. 2012). Larger dominant males also show a greater percentage of visual quiver displays that are associated with sound production compared to smaller males, suggesting that male experience or age may play a role in acoustic signaling during reproduction. Whether or not female *A. burtoni* also produce sounds, or whether sounds are produced during male–male agonistic interactions or other specific behaviors requires further testing.

Auditory evoked potential (AEP) recordings in *A. burtoni* show that both males and females are most sensitive to low frequency sounds (~200–600 Hz; best frequency, 200–300 Hz), which overlaps the spectral content of the courtship sounds produced by dominant males (Maruska et al. 2012) (Fig. 7.6a, b). Playback experiments also demonstrate that gravid females prefer males associated with courtship sound production over males without sounds or males associated with noise control sounds, suggesting that they gain some valuable information on male

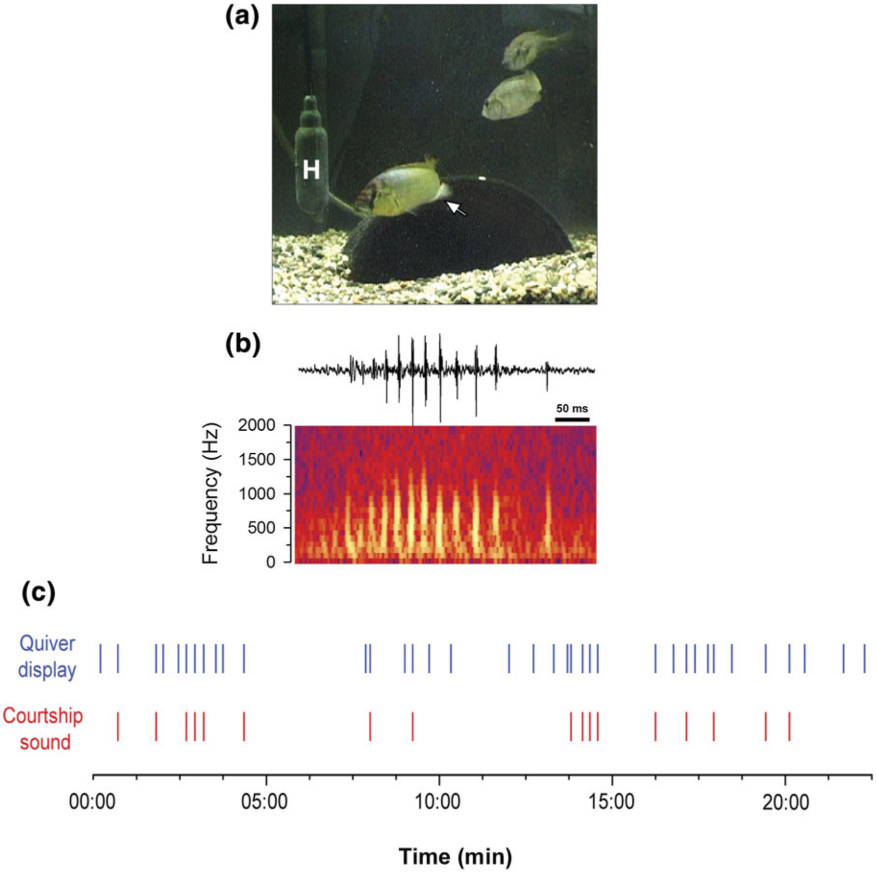


Fig. 7.5 *Brightly-colored* dominant male cichlids, *Astatotilapia burtoni*, produce pulsed sounds during body quiver behavior as part of visual-acoustic courtship displays. **a** Photograph of a *yellow* dominant male in front of his territory shelter performing a quiver and courtship sound while presenting his anal fin egg spots (*arrow*) toward attentive reproductively-receptive females. H, hydrophone. **b** Representative waveform and spectrogram of a pulsed broadband courtship sound produced by a dominant male. **c** Temporal sequence of courtship sounds (*red lines*) and visual quiver displays (*blue lines*) produced by an individual dominant male shows that not all quivers are associated with sound production. The percentage of visual quivers associated with sound production is also positively correlated with male body size in *A. burtoni*. (Modified from Maruska et al. 2012)

quality, status, or motivation from his sounds (Maruska et al. 2012) (Fig. 7.7). Thus, *A. burtoni* dominant males use sound production as part of their multimodal courtship repertoire, and females are attending to these sounds. What type of information these sounds provide to females and how it is integrated with other sensory channels in the brain to control mating decisions requires further study.

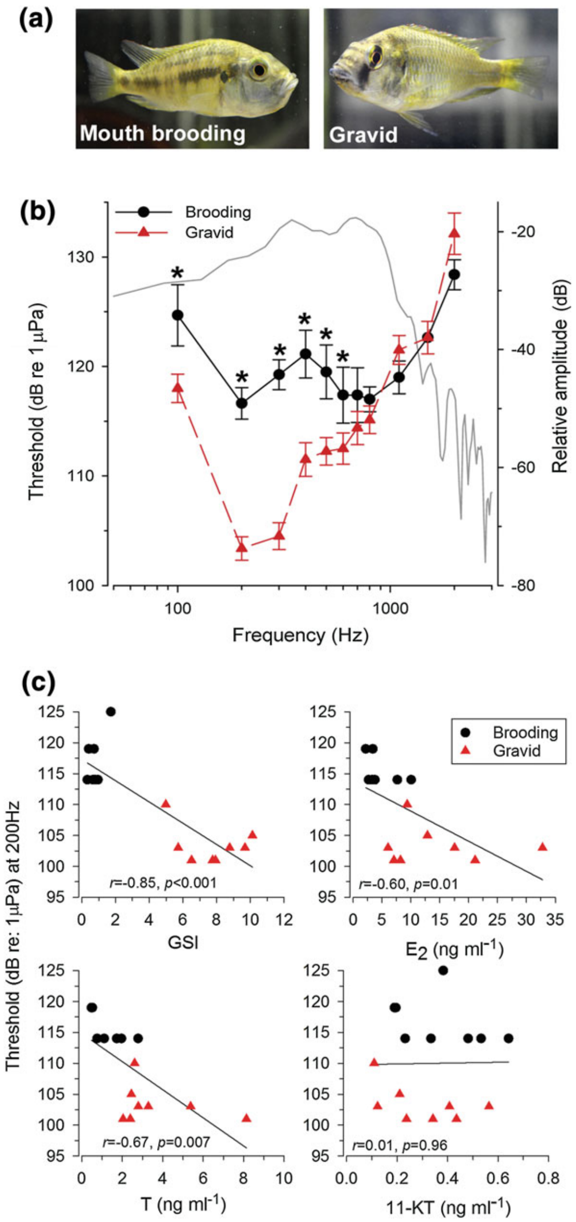


Fig. 7.6 Hearing thresholds in *A. burtoni* differ with female reproductive state and circulating sex-steroid levels. **a** Photographs of a reproductively-receptive gravid female and a parental care phase mouth-brooding female cichlid. **b** Hearing thresholds measured via auditory evoked potentials (AEP) show that gravid females have lower thresholds at low frequencies from 100 to 600 Hz compared to mouth-brooding females, which overlaps the spectral content found in male courtship sounds. Data are plotted as mean ± SE (*left axis*) and *asterisks* indicate statistical differences between female reproductive states within a frequency. *Gray line* represents the power spectra of a representative male courtship sound for comparison. **c** Auditory thresholds at best frequency (200 Hz) are also negatively correlated with gonadosomatic index (GSI), and plasma levels of T and E_2, but not 11KT, suggesting that receptive females with higher steroid titers have improved hearing sensitivity. (Modified from Maruska et al. 2012)

7.3.2.3 Steroid Cycling and Sex-Steroid Receptors in *A. burtoni*

In contrast to the seasonally-breeding midshipman fish, *A. burtoni* breeds year-round, but both males and females still undergo cyclical changes in circulating sex-steroid levels related to social status and gonadal state (Parikh et al. 2006; Maruska and

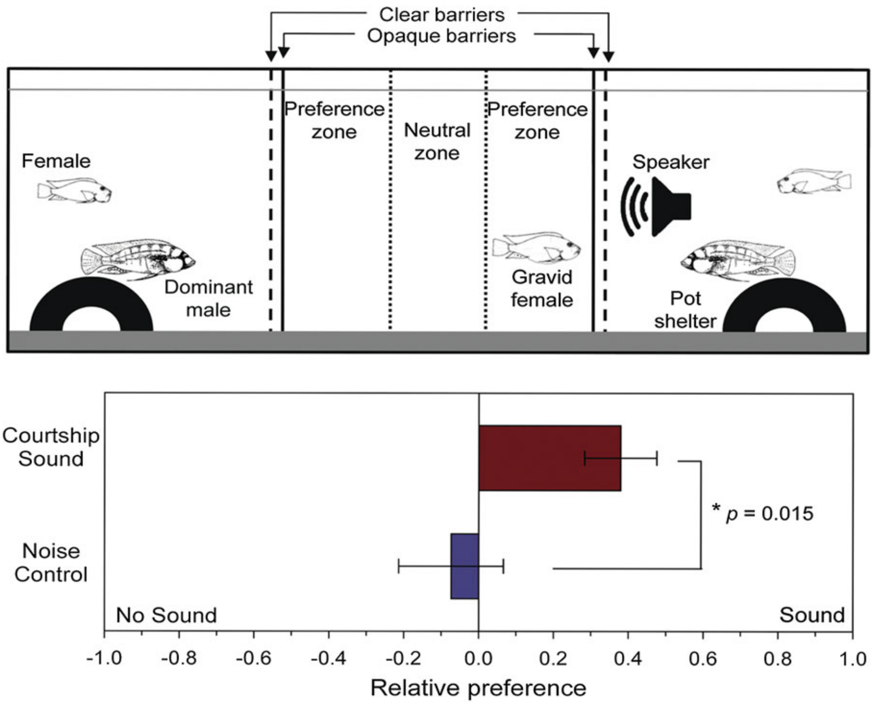


Fig. 7.7 Gravid receptive female cichlids prefer to affiliate with males associated with playbacks of courtship sounds compared to no sounds and noise controls. *Top* shows the experimental tank setup used for female preference trials. *Bottom* shows the relative preference (mean ± SE, $N = 10$ females per sound condition) of gravid females for males associated with playback of courtship sounds compared to playbacks of control noise sounds. (Modified from Maruska et al. 2012)

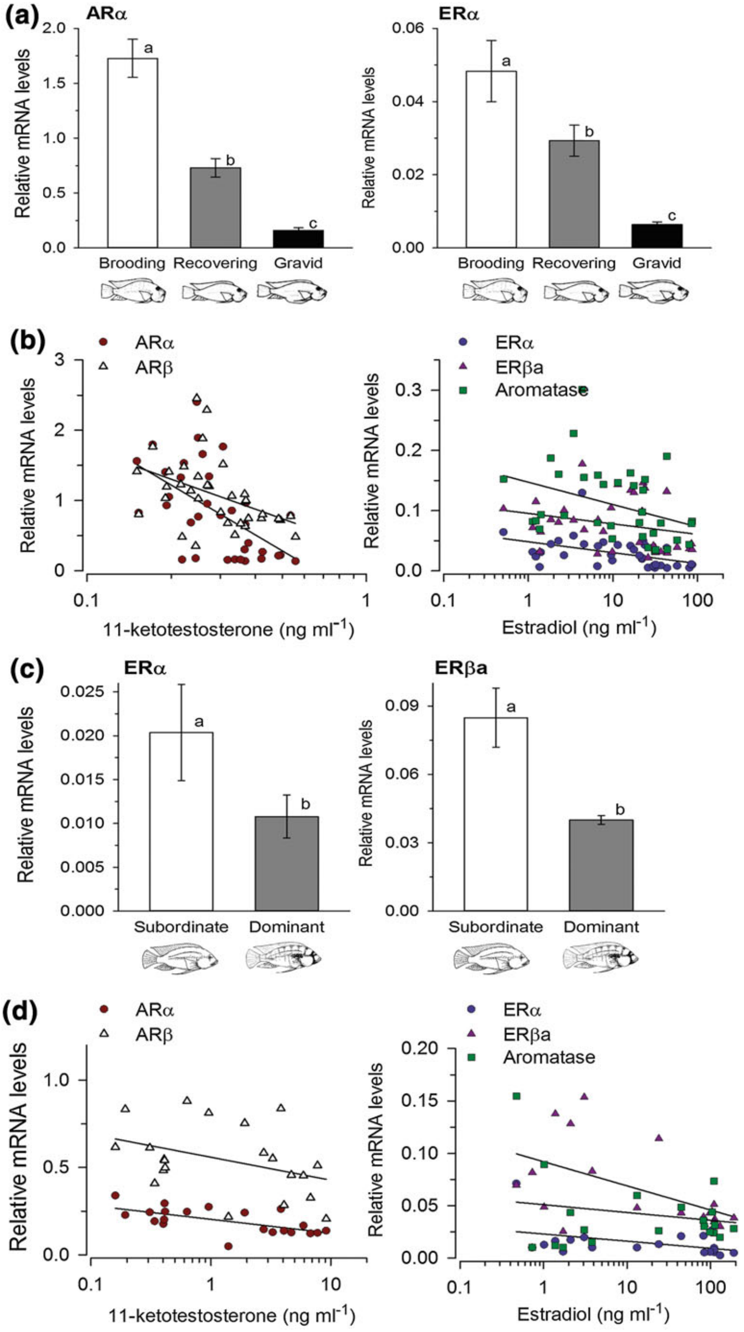
Fernald 2010c; Grone et al. 2012; O'Connell and Hofmann 2012; Renn et al. 2012; Maruska et al. 2013). For example, dominant reproductively-active males have higher plasma levels of testosterone (T), 11-ketotestosterone (11-KT; a potent fish-specific androgen), 17β-estradiol (E_2), and progesterone compared to subordinate males. Similarly, gravid females have higher circulating levels of androgens (T and 11-KT) and E_2 than recovering females (midway between brooding and gravid states), which in turn, have higher steroid levels than mouth-brooding females. Further, relative steroid sensitivity, measured by changes in sex-steroid receptor mRNA levels, also varies with reproductive state in both the saccule of the inner ear and within specific nuclei in the brain (although auditory processing regions have not yet specifically been examined) (Fig. 7.8a, b) (Maruska and Fernald 2010c; Maruska et al. 2013). In the saccule of males, for example, mRNA levels of the estrogen receptors (ER), ERα and ERßa, are higher in subordinate compared to dominant individuals (Fig. 7.8c), while there are no social status differences in androgen receptor (AR) subtypes, ERßb, or aromatase. Females also have higher relative mRNA levels of aromatase, ARα, ARß, and ERα, but not ERßa or ERßb, in the saccule compared to males (Maruska and

Fernald 2010c). These receptor expression levels in females are also negatively correlated with circulating androgen and estradiol levels, suggesting down-regulation of ARs and ERs by elevated sex-steroids produced by the developing ovaries as females approach spawning (Fig. 7.8b). Similarly, the same receptor expression levels are also negatively correlated with circulating androgen and estradiol levels in males (Fig. 7.8d). Saccular levels of some steroid receptors (ARα, ARß, ERα, ERßa, aromatase), but not others (ERßb), differ among reproductive states in female *A. burtoni*, with mouth-brooding individuals always having higher receptor expression compared to gravid individuals (Fig. 7.8a). These reproductive and social state changes in hormone cycling and relative steroid sensitivity provide the substrate for steroid-induced plasticity of acoustic communication in this species.

7.3.2.4 Sex Steroids and Hearing in *A. burtoni*

Gravid sexually-receptive female *A. burtoni* have lower hearing thresholds (~5–15 dB SPL re: 1 μPa lower) at low frequencies (100–600 Hz) compared to mouth-brooding females in the parental care phase of the reproductive cycle, while thresholds at higher frequencies (>600 Hz) do not differ between female states (Maruska et al. 2012) (Fig. 7.6a, b). This improved hearing in the spectral range of male courtship sounds may allow females to detect courting males at greater distances, or to better discriminate individual male qualities within the lek, both of which can lead to more informed mating decisions and increased reproductive fitness. Hearing thresholds are similar between dominant and subordinate males, but subordinate males have slightly lower thresholds (~3–6 dB) at high frequencies between 600 and 800 Hz. The biological significance of this difference is unclear, but one hypothesis is that improved hearing near the upper spectral range of male courtship sounds could allow subordinate males to better locate territories of smaller dominant males (e.g., individuals that produce higher frequency sounds) where they might have a better chance for sneak fertilization attempts, or of winning a challenge with a smaller resident male to then acquire his territory.

Hearing thresholds in *A. burtoni* are also correlated with circulating sex-steroid levels in both females and males, but in different directions (Maruska et al. 2012). In females, higher hearing thresholds at best frequency (200 Hz) are negatively correlated with gonadosomatic index and plasma levels of T and E_2, but not 11-KT (Fig. 7.6c). This suggests that high circulating T and E_2 produced by the developing ovaries as females approach spawning could contribute to the twofold to fivefold improved hearing sensitivity observed in gravid females compared to brooding females. As mentioned above, gravid females also have lower mRNA levels of several ER subtypes and ARs in the saccule compared to brooding females (Fig. 7.8a). Thus, as females approach spawning readiness, circulating sex-steroid levels increase, relative steroid sensitivity of the saccule decreases (e.g. lower mRNA levels of steroid receptors), but overall hearing sensitivity is improved (Fig. 7.9). Interestingly, relative sex-steroid sensitivity of the whole brain is higher


(a)
ARα
Relative mRNA levels
2.0
1.5
1.0
0.5
0.0
a
b
c
Brooding
Recovering
Gravid
ERα
Relative mRNA levels
0.06
0.04
0.02
0.00
a
b
c
Brooding
Recovering
Gravid
(b)
ARα
ARβ
Relative mRNA levels
3
2
1
0
0.1
1
11-ketotestosterone (ng ml^{-1})
ERα
ERβa
Aromatase
Relative mRNA levels
0.3
0.2
0.1
0.0
0.1
1
10
100
Estradiol (ng ml^{-1})
(c)
ERα
Relative mRNA levels
0.025
0.020
0.015
0.010
0.005
0.000
a
b
Subordinate
Dominant
ERβa
Relative mRNA levels
0.09
0.06
0.03
0.00
a
b
Subordinate
Dominant
(d)
ARα
ARβ
Relative mRNA levels
1.0
0.5
0.0
0.1
1
10
11-ketotestosterone (ng ml^{-1})
ERα
ERβa
Aromatase
Relative mRNA levels
0.20
0.15
0.10
0.05
0.00
0.1
1
10
100
Estradiol (ng ml^{-1})

◀**Fig. 7.8** Sex-steroid receptor expression in the saccule of the *A. burtoni* inner ear differs with reproductive state in females and social status in males. **a** mRNA levels of several steroid receptor subtypes differ in the saccule of gravid, recovering, and mouth-brooding female cichlids. mRNA levels of ARα and ERα are shown, measured via quantitative PCR and referenced to the geometric mean of the reference genes 18s and g^3pdh. **b** Correlations between circulating steroid levels (11-ketotestosterone, estradiol) and steroid receptor mRNA levels in the saccule of female cichlids. **c** mRNA levels of estrogen receptor subtypes (ERα, ERβa) that differ between reproductively-active dominant and reproductively-suppressed subordinate male *A. burtoni*. **d** Correlations between circulating steroid levels (11-ketotestosterone, estradiol) and receptor mRNA levels in the saccule of male cichlids. ARα, androgen receptor α; ARβ, androgen receptor β; ERα, estrogen receptor α; ERβa, estrogen receptor βa. Different *letters* above *bars* in (**a**) and (**c**) indicate statistical differences at $p < 0.05$, and $N = 11$–12 fish per group. (Modified from Maruska and Fernald 2010a, b, c)

in gravid females compared to mouth-brooders, but the exact neuroanatomical locations of these changes in mRNA receptor levels are unknown (Maruska and Fernald 2010b). It is possible, therefore, that the improved hearing in gravid females is due to plasticity in central processing regions, or in peripheral auditory structures (inner ear), or both. In males, however, increased hearing thresholds at best frequency are positively correlated with plasma levels of androgens (11-KT and T), but not E_2, suggesting that individuals with lower circulating androgens have better hearing. In *A. burtoni*, subordinate males have smaller testes with lower plasma levels of all sex-steroids compared to dominant males, raising the possibility that low androgens (or removal of an androgen-dependent inhibition in the auditory system) contribute to improved hearing at the high frequencies observed in the AEP experiments. In contrast to estrogens (Al-Mana et al. 2008; Sisneros 2009a; Maney and Pinaud 2011; Caras 2013), however, relatively little is known about how androgens influence auditory processing and hearing thresholds in vertebrates (McFadden 2009; Forlano et al. 2010; Snihur and Hampson 2012). As mentioned above, *A. burtoni* does express androgen receptors in the saccule of the inner ear, and in several auditory processing nuclei of the brain (Maruska and Fernald 2010c; Munchrath and Hofmann 2010; Maruska et al. 2012), which may serve as neural substrates for changes in androgen-related hearing ability associated with social status. Nevertheless, these sex differences also suggest there may be different mechanisms controlling steroid-induced plasticity in the auditory system of males versus females that requires further study.

While direct manipulations are needed to determine causation between steroids and auditory processing in *A. burtoni*, the studies thus far suggest that circulating sex-steroids may regulate cyclical changes in auditory perception such that females show enhanced sensitivity to male courtship signals when they approach spawning readiness. This hypothesis is supported by the fact that there are similar examples of changes in hearing ability associated with variations in reproductive state and circulating steroids, particularly estrogens, in females of every major vertebrate group (Sisneros et al. 2004a; Al-Mana et al. 2008; Maney et al. 2008; Arch and Narins 2009; Sisneros 2009b; Caras 2013). Future work examining where improved

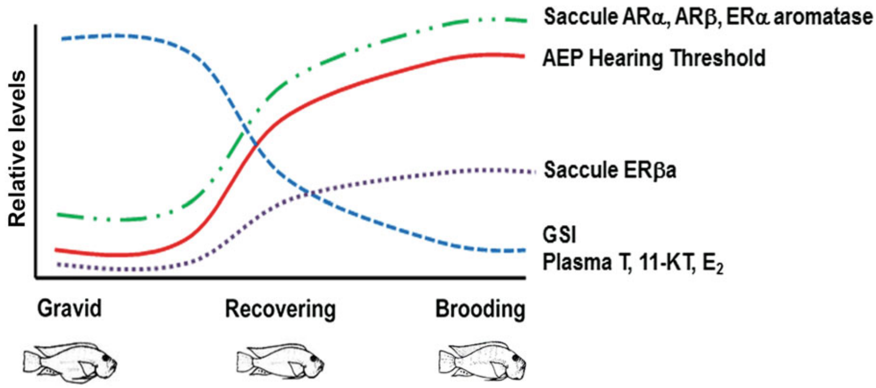


Fig. 7.9 Schematic summary of relationships between hearing thresholds, circulating steroids, and steroid receptor levels in the saccule across the female *A. burtoni* reproductive cycle. In gravid receptive females, plasma steroid levels are high, hearing sensitivity to low frequencies is improved (lower thresholds), and mRNA levels of some steroid receptors in the saccule are low. In parental mouth-brooding females, these relationships are primarily opposite in relative value. Data is compiled from Maruska and Fernald (2010a, b, c) and Maruska et al. (2012)

hearing sensitivity occurs along the auditory pathway, and what cellular and molecular mechanisms are involved, will shed light on the biological significance of steroid-induced auditory plasticity in this important model cichlid species.

7.4 Summary, Conclusions, and Future Directions

Acoustic communication is widespread in fishes, and recent interest in this topic has revealed that internal hormonal state can profoundly influence the ability of individuals to produce and perceive sounds in the aquatic environment. While steroid-mediated plasticity in vocal-acoustic processing exists in many taxa, we have only just begun to explore the importance, mechanisms, and diversity of this plasticity in fishes, the largest group of vertebrates. Here we reviewed the current knowledge on how sex-steroid hormones can influence auditory capabilities and vocal-motor patterning using examples from two incipient model teleosts, the plainfin midshipman fish *P. notatus* and the African cichlid *A. burtoni*.

One common emerging theme from this review is that steroid-mediated improvements in vocal-acoustic processing are typically associated with reproductive readiness. This holds true for species that rely heavily on acoustic signaling during seasonal breeding such as the midshipman fish, as well as non-seasonally breeding species like cichlids that appear to use sound production as one component of a more complex multimodal courtship repertoire. This reproductive-associated plasticity is supported by changes in gonadal state, circulating sex-steroids, and steroid receptor expression in peripheral and central auditory structures. In addition to cichlids and midshipman fish, studies in other species such as the round goby

Neogobius melanostomus also demonstrate sex-steroid associated changes in auditory processing (Zeyl et al. 2013). Thus, the continued examination of diverse fish species should reveal conserved and divergent cellular and molecular mechanisms mediating steroid-auditory plasticity. Further, while this review has concentrated on the influence of sex-steroids on vocal-acoustic processing, there is also evidence for biologically-relevant roles for stress hormones such as cortisol (Remage-Healey and Bass 2005; Arterbery et al. 2010; Maruska and Fernald 2010b; Genova et al. 2012) and neuropeptides such as gonadotropin-releasing hormone (Maruska and Tricas 2011) modulating acoustic communication in fishes that requires further attention. Importantly, this review has highlighted how little is known about steroid-mediated auditory plasticity in the >30,000 species of fishes and future work should focus on exploring both the phylogenetic extent of this phenomenon, as well as the molecular and cellular mechanisms mediating changes at different locations along the auditory pathway. The widespread presence of steroid-dependent auditory plasticity in all vertebrate groups suggests it is an evolutionary labile solution, but future work on diverse fish species are needed to fully appreciate how this solution may have contributed to sexual selection and evolution of the mechanisms to support hormone-mediated vocal-acoustic plasticity across taxa.

References

Al-Mana D, Ceranic B, Djahanbakhch O, Luxon LM (2008) Hormones and the auditory system: a review of physiology and pathophysiology. Neuroscience 153:881–900

Alderks PW, Sisneros JA (2013) Development of the acoustically evoked behavioral response in larval plainfin midshipman fish *Porichthys notatus*. PLoS ONE 8:e82182

Amorim M (2006) Diversity of sound production. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes. Science Publishers, Enfield, pp 71–105

Amorim MCP, Fonseca PJ, Almada VC (2003) Sound production during courtship and spawning of *Oreochromis mossambicus*: male-female and male-male interactions. J Fish Biol 62:658–672

Amorim MCP, Knight ME, Stratoudakis Y, Turner GF (2004) Differences in sounds made by courting males of three closely related Lake Malawi cichlid species. J Fish Biol 65:1358–1371

Amorim MCP, Simoes JM, Fonseca PJ, Turner GF (2008) Species differences in courtship acoustic signals among five Lake Malawi cichlid species (*Pseudotropheus* spp.). J Fish Biol 72:1355–1368

Arch VS, Narins PM (2009) Sexual hearing: the influence of sex hormones on acoustic communication in frogs. Hear Res 252:15–20

Arterbery AS, Deitcher DL, Bass AH (2010) Corticosteroid receptor expression in a teleost fish that displays alternative male reproductive tactics. Gen Comp Endocrinol 165:83–90

Bass AH (1990) Sounds from the intertidal zone: vocalizing fish. Bioscience 40:249–258

Bass AH (1996) Shaping brain sexuality. Am Sci 84:352–363

Bass AH, Baker R (1991) Evolution of homologous vocal control traits. Brain Behav Evol 38:240–254

Bass AH, Clark CW (2003) The physical acoustics of underwater sound communication. In: Simmons AM, Fay RR, Popper A (eds) acoustic communication, springer handbook of auditory research, vol 16. Springer, New York, pp 1–64

Bass AH, Ladich F (2008) Vocal-acoustic communication: from neurons to behavior. In: Webb JF, Popper AN, Fay RR (eds) Fish bioacoustics, springer handbook of auditory research, vol 32. Springer, New York, pp 253–278

Bass AH, McKibben JR (2003) Neural mechanisms and behaviors for acoustic communication in teleost fish. Prog Neurobiol 69:1–26

Bass AH, Bodnar DA, Marchaterre MA (1999) Complementary explanations for existing phenotypes in an acoustic communication system. In: Hauser MD, Konishi M (eds) The design of animal communication. MIT, Cambridge, pp 493–514

Bertucci F, Beauchaud M, Attia J, Mathevon N (2010) Sounds modulate males' aggressiveness in a cichlid fish. Ethology 116:1179–1188

Bertucci F, Attia J, Beauchaud M, Mathevon N (2012a) Sounds produced by the cichlid fish *Metriaclima zebra* allow reliable estimation of size and provide information on individual identity. J Fish Biol 80:752–766

Bertucci F, Scaion D, Beauchaud M, Attia J, Mathevon N (2012b) Ontogenesis of agonistic vocalizations in the cichlid fish *Metriaclima zebra*. CR Biol 335:529–534

Blais J, Plenderleith M, Rico C, Taylor MI, Seehausen O, van Oosterhout C, Turner GF (2009) Assortative mating among Lake Malawi cichlid fish populations is not simply predictable from male nuptial colour. BMC Evol Biol 9:53

Brantley RK, Bass AH (1994) Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish, *Porichthys notatus* (Teleostei, Batrachoididae). Ethology 96:213–232

Brantley RK, Wiingfield JC, Bass AH (1993) Sex steroid levels in *Porichthys notatus*, a fish with alternative reproductive tactics, and a review of the hormonal bases for male dimorphism among teleost fishes. Horm Behav 27:332–347

Burmeister SS, Jarvis ED, Fernald RD (2005) Rapid behavioral and genomic responses to social opportunity. PLoS Biol 3:e363

Caras ML (2013) Estrogenic modulation of auditory processing: a vertebrate comparison. Front Neuroendocrinol 34:285–299

Clement TS, Parikh V, Schrumpf M, Fernald RD (2005) Behavioral coping strategies in a cichlid fish: the role of social status and acute stress response in direct and displaced aggression. Horm Behav 47:336–342

Coffin AB, Mohr RA, Sisneros JA (2012) Saccular-specific hair cell addition correlates with reproductive state-dependent changes in the auditory saccular sensitivity of a vocal fish. J Neurosci 32:1366–1376

Crapon de Caprona MD (1974) The effect of chemical stimuli from conspecifics on the behavior of *Haplochromis burtoni* (Cichlidae, Pisces). Experientia 30:1394–1395

Crapon de Caprona MD (1980) Olfactory communication in a cichlid fish, *Haplochromis burtoni*. Z Tierpsychol 52:113–134

DeMartini EE (1988) Spawning success of the male plainfin midshipman. I. Influences of male body size and are of spawning. J Exp Mar Biol Ecol 121:177–192

Estramil N, Bouton N, Verzijden MN, Hofker K, Riebel K, Slabbekoorn H (2013) Cichlids respond to conspecific sounds but females exhibit no phonotaxis without the presence of live males. Ecol Freshw Fish 23:305−312

Fergus DJ, Bass AH (2013) Localization and divergent profiles of estrogen receptors and aromatase in the vocal and auditory networks of a fish with alternative mating tactics. J Comp Neurol 521:2850–2869

Fernald RD (1977) Quantitative behavioral observations of *Haplochromis burtoni* under semi-natural conditions. Anim Behav 25:643–653

Fernald RD (1984) Vision and behavior in an African cichlid fish. Am Sci 72:58–65

Fernald RD (2009) Social regulation of reproduction: what changes and why? Horm Brain Behav 1:683–691

Fernald RD, Hirata NR (1977) Field study of *Haplochromis burtoni*: quantitative behavioral observations. Anim Behav 25:964–975

Fernald RD, Maruska KP (2012) Social information changes the brain. Proc Natl Acad Sci USA 109(Suppl 2):17194–17199

Fettiplace R, Fuchs PA (1999) Mechanisms of hair cell tuning. Annu Rev Physiol 61:809–834

Fine ML, Lenhardt ML (1983) Shallow-water propagation of the toadfish mating call. Comp Biochem Physiol A 76:225–231

Forlano PM, Deitcher DL, Bass AH (2005) Distribution of estrogen receptor alpha mRNA in the brain and inner ear of a vocal fish with comparisons to sites of aromatase expression. J Comp Neurol 483:91–113

Forlano PM, Marchaterre M, Deitcher DL, Bass AH (2010) Distribution of androgen receptor mRNA expression in vocal, auditory and neuroendocrine circuits in a teleost fish. J Comp Neurol 518:493–512

Forlano PM, Kim SD, Krzyminska ZM, Sisneros JA (2014) Catecholaminergic connectivity to the inner ear, central auditory, and vocal motor circuitry in the plainfin midshipman fish, *Porichthys notatus*. J Comp Neurol 522:2887–2927

Furukawa T, Matsura S (1978) Adaptive rundown of excitatory postsynaptic potentials at synapses between hair cells and eighth nerve fibers in goldfish. J Physiol (London) 276:193–209

Genova RM, Marchaterre MA, Knapp R, Fergus D, Bass AH (2012) Glucocorticoid and androgen signaling pathways diverge between advertisement calling and non-calling fish. Horm Behav 62:426–432

Grone BP, Carpenter RE, Lee M, Maruska KP, Fernald RD (2012) Food deprivation explains effects of mouthbrooding on ovaries and steroid hormones, but not brain neuropeptide and receptor mRNAs, in an African cichlid fish. Horm Behav 62:18–26

Hau M, Perfito N, Moore IT (2008) Timing of breeding in tropical birds: mechanisms and evolutionary implications. Ornithol Neotrop 19:39–59

Hofmann HA, Benson ME, Fernald RD (1999) Social status regulates growth rate: consequences for life-history strategies. Proc Natl Acad Sci USA 96:14171–14176

Ibara RM, Penny LT, Ebeling AW, van Dykhuizen G, Cailliet G (1983) The mating call of the plainfin midshipman fish, *Porichthys notatus*. In: Noakes DGL, Lindquist DG, Helfman GS, Ward JA (eds) Predators and prey in fishes. The Hague, Netherlands, pp 205–212

Kidd MR, O'Connell LA, Kidd CE, Chen CW, Fontenot MR, Williams SJ, Hofmann HA (2013) Female preference for males depends on reproductive physiology in the African cichlid fish *Astatotilapia burtoni*. Gen Comp Endocrinol 180:56–63

Knapp R, Wingfield JC, Bass AH (1999) Steroid hormones and paternal care in the plainfin midshipman fish (*Porichthys notatus*). Horm Behav 35:81–89

Kustan JM, Maruska KP, Fernald RD (2012) Subordinate male cichlids retain reproductive competence during social suppression. Proc R Soc B 279:434–443

Lin JW, Faber DS (1988) An efferent inhibition of auditory afferents mediated by the goldfish Mauthner cell. Neuroscience 24:829–836

Longrie N, Poncin P, Denoel M, Gennotte V, Delcourt J, Parmentier E (2013) Behaviours associated with acoustic communication in Nile tilapia (*Oreochromis niloticus*). PLoS ONE 8: e61467

Maney DL, Pinaud R (2011) Estradiol-dependent modulation of auditory processing and selectivity in songbirds. Front Neuroendocrinol 32:287–302

Maney DL, Goode CT, Lange HS, Sanford SE, Solomon BL (2008) Estradiol modulates neural responses to song in a seasonal songbird. J Comp Neurol 511:173–186

Maruska KP, Fernald RD (2010a) Behavioral and physiological plasticity: rapid changes during social ascent in an African cichlid fish. Horm Behav 58:230–240

Maruska KP, Fernald RD (2010b) Steroid receptor expression in the fish inner ear varies with sex, social status, and reproductive state. BMC Neurosci 11:58

Maruska KP, Fernald RD (2010c) Reproductive status regulates expression of sex steroid and GnRH receptors in the olfactory bulb. Behav Brain Res 213:208–217

Maruska KP, Fernald RD (2011a) Social regulation of gene expression in the hypothalamic-pituitary-gonadal axis. Physiology 26:412–423

Maruska KP, Fernald RD (2011b) Plasticity of the reproductive axis caused by social status change in an African cichlid fish: II. testicular gene expression and spermatogenesis. Endocrinology 152:291–302

Maruska KP, Fernald RD (2012) Contextual chemosensory urine signaling in an African cichlid fish. J Exp Biol 215:68–74

Maruska KP, Fernald RD (2013) Social regulation of male reproductive plasticity in an African Cichlid Fish. Integr Comp Biol 53:938–950

Maruska KP, Tricas TC (2011) Gonadotropin-releasing hormone (GnRH) modulates auditory processing in the fish brain. Horm Behav 59:451–464

Maruska KP, Ung US, Fernald RD (2012) The African cichlid fish *Astatotilapia burtoni* uses acoustic communication for reproduction: sound production, hearing, and behavioral significance. PLoS ONE 7:e37612

Maruska KP, Zhang A, Neboori A, Fernald RD (2013) Social opportunity causes rapid transcriptional changes in the social behaviour network of the brain in an african cichlid fish. J Neuroendocrinol 25:145–157

McFadden D (2009) Masculinization of the mammalian cochlea. Hear Res 252:37–48

McKibben JR, Bass AH (1998) Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish. J Acoust Soc Am 104:3520–3533

McKibben JR, Bass AH (1999) Peripheral encoding of behaviorally relevant acoustic signals in a vocal fish: single tones. J Comp Physiol A 184:563–576

McKibben JR, Bass AH (2001a) Peripheral encoding of behaviorally relevant acoustic signals in a vocal fish: harmonic and beat stimuli. J Comp Physiol A 187:271–285

McKibben JR, Bass AH (2001b) Effects of temporal envelope modulation on acoustic signal recognition in a vocal fish, the plainfin midshipman. J Acoust Soc Am 109:2934–2943

Miller DJ, Lea RN (1972) Guide to the coastal marine fishes of California. Calif Dept Fish Game Bull 157:72–73

Munchrath LA, Hofmann HA (2010) Distribution of sex steroid hormone receptors in the brain of an African cichlid fish, *Astatotilapia burtoni*. J Comp Neurol 518:3302–3326

Nelissen MHJ (1977) Sound production by *Haplochromis burtoni* (Gunther) and *Tropheus moorii Boulenger* (Pisces, Cichlidae). Ann Soc R Zool Belg 106:155–166

Nosil P, Harmon LJ (2009) Niche dimensionality and ecological speciation. In: Bridle J, Schluter D (eds) Speciation and patterns of diversity, R Butlin. Cambridge University Press, Cambridge, pp 127–154

Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. Trends Ecol Evol 24:145–156

O'Connell LA, Hofmann HA (2012) Social status predicts how sex steroid receptors regulate complex behavior across levels of biological organization. Endocrinology 153:1341–1351

Parikh VN, Clement TS, Fernald RD (2006) Androgen level and male social status in the African cichlid, *Astatotilapia burtoni*. Behav Brain Res 166:291–295

Popper AN (2011) Auditory System Morphology. In: Farrell AP (ed) Encyclopedia of fish physiology: from genome to environment, vol 1. Academic Press, San Diego, pp 252–261

Remage-Healey L, Bass AH (2005) Rapid elevations in both steroid hormones and vocal signaling during playback challenge: a field experiment in Gulf toadfish. Horm Behav 47:297–305

Renn SC, Fraser EJ, Aubin-Horth N, Trainor BC, Hofmann HA (2012) Females of an African cichlid fish display male-typical social dominance behavior and elevated androgens in the absence of males. Horm Behav 61:496–503

Ripley JL, Lobel PS (2004) Correlation of acoustic and visual signals in the cichlid fish *Tramitichromis intermedius*. Environ Biol Fish 71:389–394

Ripley JL, Lobel PS, Yan HY (2002) Correlation of sound production with hearing sensitivity in the Lake Malawi cichlid *Tramitichromis intermedius*. Bioacoustics 12:238–240

Robison RR, Fernald RD, Stacey NE (1998) The olfactory system of a cichlid fish responds to steroidal compounds. J Fish Biol 53:226–229

Roger PH, Cox M (1988) Underwater sound as a biological stimulus. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer-Verlag, New York, pp 130–149

Rohmann KN, Bass AH (2011) Seasonal plasticity of auditory hair cell frequency sensitivity correlates with plasma steroid levels in vocal fish. J Exp Biol 214:1931–1942

Rohmann KN, Fergus DJ, Bass AH (2013) Plasticity in ion channel expression underlies variation in hearing during reproductive cycles. Cur Biol 23:678–683

Schlinger BA, Remage-Healey L (2012) Neurosteroidogenesis: insights from studies of songbirds. J Neuroendocrinol 24:16–21

Schulz-Mirbach T, Metscher B, Ladich F (2012) Relationship between swim bladder morphology and hearing abilities–a case study on Asian and African cichlids. PLoS ONE 7:e42292

Simoes JM, Duarte IG, Fonseca PJ, Turner GF, Amorim MC (2008) Courtship and agonistic sounds by the cichlid fish *Pseudotropheus zebra*. J Acoust Soc Am 124:1332–1338

Sisneros JA (2007) Saccular potentials of the vocal plainfin midshipman fish, *Porichthys notatus*. J Comp Physiol A 193:413–424

Sisneros JA (2009a) Steroid-dependent auditory plasticity for the enhancement of acoustic communication: recent insights from a vocal teleost fish. Hear Res 252:9–14

Sisneros JA (2009b) Seasonal plasticity of auditory saccular sensitivity in the vocal plainfin midshipman fish, *Porichthys notatus*. J Neurophysiol 102:1121–1131

Sisneros JA (2009c) Adaptive hearing in the vocal plainfin midshipman fish: getting in tune for the breeding season and its implications for acoustic communication. Integr Zool 4:33–42

Sisneros JA, Bass AH (2003) Seasonal plasticity of peripheral auditory frequency sensitivity. J Neurosci 23:1049–1058

Sisneros JA, Bass AH (2005) Ontogenetic changes in the response properties of individual, primary auditory afferents in the vocal plainfin midshipman fish *Porichthys notatus* Girard. J Exp Biol 208:3121–3131

Sisneros JA, Forlano PM, Deitcher DL, Bass AH (2004a) Steroid-dependent auditory plasticity leads to adaptive coupling of sender and receiver. Science 305:404–407

Sisneros JA, Forlano PM, Knapp R, Bass AH (2004b) Seasonal variation of steroid hormone levels in an intertidal-nesting fish, the vocal plainfin midshipman. Gen Comp Endocrinol 136:101–116

Snihur AW, Hampson E (2012) Click-evoked otoacoustic emissions: response amplitude is associated with circulating testosterone levels in men. Behav Neurosci 126:325–331

Sturmbauer C, Husemann M, Danley PD (2011) Explosive speciation and adaptive radiation of East African cichlid fishes. In: Zachos FE, Habel JC (eds) Biodiversity hotspots. Springer-Verlag, Berlin, pp 333–362

Verzijden MN, van Heusden J, Bouton N, Witte F, ten Cate C, Slabbekoorn H (2010) Sounds of Lake Victoria cichlids vary within and between species and affect female mate preferences. Behav Ecol 21:548–555

Yan HY, Popper AN (1992) Auditory sensitivity of the cichlid fish *Astronotus ocellatus* (Cuvier). J Comp Physiol A 171:105–109

Walpurger V, Pietrowsky R, Kirschbaum C, Wolf OT (2004) Effects of the menstrual cycle on auditory event-related potentials. Horm Behav 46:600–606

Xiao Z, Suga N (2002) Modulation of cochlear hair cells by the auditory cortex in the mustached bat. Nat Neurosci 5:57–63

Zeddies DG, Fay RR, Alderks PW, Shaub KS, and JA Sisneros (2010) Sound source localization by the plainfin midshipman fish, *Porichthys notatus*. J Acoust Soc Am 127:3104–3113

Zeddies DG, Fay RR, Gray MD, Alderks PW, Acob A, Sisneros JA (2012) Local acoustic particle motion guides sound source localization behavior in the plainfin midshipman fish, *Porichthys notatus*. J Exp Biol 215:152–160

Zeyl JN, Love OP, Higgs DM (2013) Condition-dependent auditory processing in the round goby (*Neogobius melanostomus*): links to sex, reproductive condition and female estrogen levels. J Exp Biol 216:1075–1084