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SYMPOSIUM

Reproductive- and Social-State Plasticity of Multiple Sensory Systems in a Cichlid Fish

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Synopsis Intra- and inter-sexual communications are vital to the survival and reproductive success of animals. In species that cycle in and out of breeding or other physiological condition, sensory function can be modulated to optimize communication at crucial times. Little is known, however, about how widespread this sensory plasticity is across taxa, whether it occurs in multiple senses or both sexes within a species, and what potential modulatory substances and substrates are involved. Thus, studying modulation of sensory communication in a single species can provide valuable insights for understanding how sensory abilities can be altered to optimize detection of salient signals in different sensory channels and social contexts. The African cichlid fish *Astatotilapia burtoni* uses multimodal communication in social contexts such as courtship, territoriality, and parental care and shows plasticity in sensory abilities. In this review, we synthesize what is known about how visual, acoustic, and chemosensory communication is used in *A. burtoni* in inter- and intra-specific social contexts, how sensory funtion is modulated by an individual's reproductive, metabolic, and social state, and discuss evidence for plasticity in potential modulators that may contribute to changes in sensory abilities and behaviors. Sensory plasticity in females is primarily associated with the natural reproductive cycle and functions to improve detection of courtship signals (visual, auditory, chemosensory, and likely mechanosensory) from high-quality males for reproduction. Plasticity in male sensory abilities seems to function in altering their ability to detect the status of other males in the service of territory ownership and future reproductive opportunities. Changes in different classes of potential modulators or their receptors (steroids, neuropeptides, and biogenic amines) occur at both peripheral sensory organs (eye, inner ear, and olfactory epithelium) and central visual, olfactory, and auditory processing regions, suggesting complex mechanisms contributing to plasticity of sensory function. This type of sensory plasticity revealed in males and females of *A. burtoni* is likely more widespread among diverse animals than currently realized, and future studies should take an integrative and comparative approach to better understand the proximate and ultimate mechanisms modulating communication abilities across taxa.

Introduction

Communication is vital for survival and reproductive success in all animals. To optimize information transfer, individuals must be able to detect and interpret signals sent from conspecifics in different social contexts like territorial, reproductive, and parental care interactions. Reproductive and endocrine states are also known to influence the function of many senses (e.g., vision, audition, and olfaction), both at peripheral sensory organs and centrally in the brain, across a range of vertebrate taxa (Mousley et al. 2006; Lynch and Wilczynski 2008; Maney et al. 2008; Maney and Pinaud 2011; Maruska and Sisneros 2015; Butler et al. 2019). This reproductive-state plasticity often allows receptive individuals to better detect signals like mating calls, visual displays, and pheromones from the opposite sex at times when these decisions are critical (Sisneros and Bass 2003; Lynch et al. 2006; Mousley et al. 2006; Miranda and Wilczynski 2009a; Forlano

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et al. 2016; Butler et al. 2019). In addition to reproductive cycles, many animals also progress through different metabolic conditions and social states (e.g., dominant [DOM] and subordinate [SUB]) in their lifetimes. As individuals cycle in and out of breeding or other condition, there are also associated physiological changes in the brain and body. These include variations in circulating hormones and changes in expression of different modulatory substances (e.g., steroids, peptides, biogenic amines, and others) and their receptors in many tissues, all of which have the potential to modulate peripheral and central sensory processing. Thus, there is a plethora of potential mechanisms for modulating sensory function, and examining this in a comparative context is important to understand how sensory abilities change to optimize communication for adaptive social behaviors.

Studying modulation of sensory communication in a single species provides valuable information for understanding the complexities of this phenomenon from sender and receiver perspectives, in different sensory channels and social contexts, and for exploring the potential modulators and mechanisms that mediate changes in sensory abilities. We have examined many of these aspects of sensory plasticity in the African cichlid fish *Astatotilapia burtoni* and present it here to highlight some of the different approaches used to examine plasticity in sensory function related to an individual's reproductive, metabolic, and social state. In the sections below, we first introduce the *A. burtoni* system for studying sensory plasticity, then synthesize and review what is known about how visual, acoustic, and chemosensory communication is used in *A. burtoni* in inter- and intraspecific social contexts, how it is modulated by an individual's reproductive, metabolic, and social state, and discuss associated changes in potential modulators that could contribute to changes in sensory abilities and behaviors. Lastly, we discuss some general conclusions and perspectives from this work.

African cichlid fish *A. burtoni* as a model for studying sensory plasticity

The cichlid *A. burtoni* is an ideal model to better understand how reproductive, social, metabolic, and endocrine state might impact sending and receiving signals during social communication. This species lives in shallow shore pools and river systems of Lake Tanganyika, East Africa, and has been an important neuroethological subject for decades with a rich literature on many aspects of its general biology, ecology, and behaviors that are crucial for interpretation of sensory studies (for reviews, see Fernald and Maruska (2012) and Maruska and Fernald (2014, 2018)). Furthermore, genomic resources are available to facilitate probing the cellular and molecular mechanisms of endocrine modulation of sensory abilities (Brawand et al. 2014). Both males and females cycle between reproductive and nonreproductive states, with corresponding changes in hormones and other physiological measures (Fig. 1). Males exist in a dominance hierarchy in which a small number of DOM males maintain and defend territories that serve as a resource for spawning activities. The majority of males are SUB, do not hold territories, shoal with females, lack the bright body coloration of the DOM males, have small testes and low circulating steroid levels, and have few to no reproductive opportunities. DOM males are brightly colored and perform courtship behaviors (body quivers, tail waggles, leads, and chases) that provide females with information in visual, chemosensory, auditory, and mechanosensory channels, and females visit the clustered lek of male territories as they approach spawning condition. DOM males also have large testes, high levels of circulating sex-steroids, and upregulation of the hypothalamic–pituitary–gonadal axis (Maruska and Fernald 2014). Male social status is also reversible and associated with dramatic changes in behavior and physiology at many levels (Maruska and Fernald 2010a; Fernald and Maruska 2012; Maruska and Fernald 2014), which are adapted to their distinct needs based on their social position in the hierarchy.

Females develop large yolky eggs as they approach spawning, and these gravid females (ripe with eggs) show extended abdomens. Gravid females then ovulate (eggs released from follicular ovarian membrane) and need to choose a male or males for spawning within hours. Once a choice is made, receptive ovulated females will follow a male (or multiple males) into his territory and deposit eggs on the substrate. Females will immediately turn around and pick the eggs up into their mouths and the DOM male will release sperm to fertilize the eggs in her mouth as she nips at the egg spots on his anal fin. Females then brood the developing young in their mouths for ∼2 weeks and do not feed during this time (i.e., mouthbrooding). Following mouthbrooding, females release their fry and perform maternal behaviors for several days as they allow fry to re-enter their mouth for protection. After the maternal phase, females go through a recovering period while they begin feeding and allocate resources toward egg growth in preparation for the next spawning cycle (∼28 days). Because females cycle between different reproductive and parental states, their behaviors, physiology, and

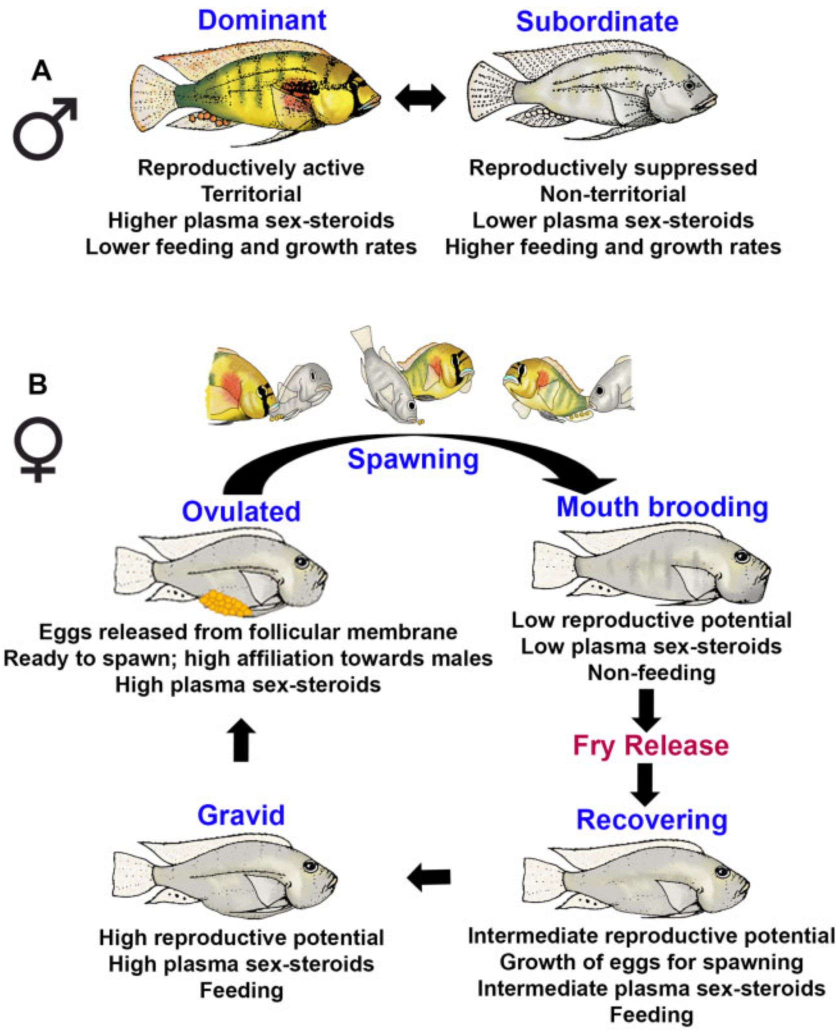

Fig. 1. Characteristics associated with male social status and female reproductive states. Males reversibly switch between DOM reproductively active territory-holding and SUB nonterritorial individuals with suppressed reproductive potential. Females become gravid (ripe with eggs), ovulate (eggs released from follicular/ovarian membrane prior to spawning), and then choose males for spawning. After deposition on the substrate and picking them up in the mouth, eggs are fertilized within the female's mouth and she becomes a mouthbrooding female as she cares for the developing young in her mouth for ~2 weeks and does not feed. After the brood period, she releases free-swimming fry, performs maternal care for several days as she permits fry to re-enter her mouth for protection, and then becomes a recovering female as she begins to feed again, grow oocytes, and prepare for the next spawning cycle.

status-dependent needs are quite different (Renn et al. 2009, 2012; Maruska and Fernald 2018; Butler et al. 2020). Circulating sex-steroid levels (testosterone, estradiol, and 11-ketotestoserone, a potent fish specific androgen) are highest in gravid and ovulated females, intermediate in recovering females, and lowest in mouthbrooding females (Maruska and Fernald 2010c). Further, female hormone profiles measured non-invasively via collected water samples show that estradiol peaks ~6 days prior to spawning, testosterone and progestins ~4 days before spawning, and prostaglandin-F2α [PGF2α; has paracrine function to stimulate/modulate follicular rupture at ovulation, and actions in the brain to elicit female sexual behaviors (Sorensen and Goetz 1993; Juntti et al. 2016) ~3 days prior to spawning (Kidd et al. 2013). In addition to using multiple sensory channels for courtship, intra-specific social interactions in both sexes also involve multimodal communication. Thus, the natural cycling through different reproductive conditions and social states in males and females of this cichlid make it an excellent system to study changes in sensory and communication abilities.

Plasticity in the visual system

Vision is arguably one of the most important senses used for reproductive communication across a wide range of species. Cichlids in particular are well known for their diverse body and fin coloration patterns and distinctive behavioral displays, which play an important role in their courtship repertoires (Fernald and Hirata 1977b; Maruska and Fernald 2018). For example, DOM male *A. burtoni* produce flashy multicomponent visual courtship displays that include changes in body coloration and behaviors (Fig. 2A). In the presence of receptive females, males intensify the coloration of their yellow or blue bodies, black markings on the lower jaw and pelvic fins, and red/orange coloration in the humeral patch and on the fins. Male courtship behaviors include chasing of females, courtship body quivers, tail waggles, leads to the spawning area, and male–female circling. These visual signals can be used by females as they approach spawning to make decisions about which males to spawn with, and to coordinate the consummatory act of egg deposition and fertilization once the choice is made. In fact, visual displays from males alone are sufficient to cause egg deposition in females as long as they have ovulated. Similarly, seeing a receptive gravid female is also sufficient to induce courtship behaviors from DOM males (Field et al. 2018). The visual signals given off by receptive females and received by males are less understood but may include perception of the female's enlarged egg-filled abdomen, protruding genital papilla at ovulation, or other affiliative gestures. Nevertheless, males appear able to distinguish female reproductive state based on visual signals alone because they increase urination rates and courtship behaviors toward gravid/ovulated females but not toward mouthbrooding females (Maruska and Fernald 2012; Field 2018).

Once female *A. burtoni* ovulate (follicular release of eggs), they need to choose a male (or multiple males) for spawning within a few hours (K.P. Maruska, unpublished observations). Males court ovulated females more intensely than gravid nonovulated females, and ovulated females are more responsive to male courtship behaviors than nonovulated gravid females (Butler et al. 2019). While detection of female ovulation status is likely conveyed via chemosensory signals, the importance of visual signals from courting males to ovulated females suggests that improved visual capabilities at ovulation could facilitate female mate choice. In fact, electroretinography recordings revealed that gravid, reproductively-ready females have increased visual sensitivity at wavelengths associated with male courtship coloration compared to nongravid recovering females (Butler et al. 2019; Fig. 2B). In teleosts, prostaglandin-F2α levels in circulation peak around the time of ovulation, and injections of PGF2α are commonly used to induce ovulation and spawning in fishes (Takahashi et al. 2018). After hormonally inducing ovulation in gravid *A. burtoni* females by injection of PGF2α, spectral sensitivity measured via electroretinograms (ERGs) further increases compared to pre-injection measurements (Fig. 2C). This increased sensitivity after hormone injection is absent in nongravid recovering females, suggesting an ovulation-triggered increase in visual sensitivity. Ovulated females also show greater activation in ganglion cell and inner nuclear layers of the retina after viewing courting males compared to nonovulated gravid females (revealed by staining of phospho-S6 ribosomal protein marker), suggesting retinal cells are more sensitive to male visual signals at this time (Butler et al. 2019). What might mediate these changes in retinal sensitivity? One possibility is the action of neuromodulators within the eye that might differ among females of different reproductive states. To investigate this, we examined mRNA levels of several neuromodulatory receptors (sex-steroids; gonadotropins) in the eye and show that ovulated females have higher mRNA expression levels of many modulatory receptors compared to nonovulated gravid and mouthbrooding females (Fig. 2D; Butler et al. 2019). In addition, female mate choice-like behaviors positively correlate with expression of gonadotropin system receptors (e.g., luteinizing hormone receptor and gonadotropin releasing hormone [GnRH] receptor 2) in the eye, suggesting that changes in gonadotropin signaling in the eye may contribute to visual plasticity.

Hormonal and reproductive state-dependent plasticity also exists in the peripheral visual system of other teleosts and other vertebrates. For example, many neuromodulators and their receptors are found in the retina of other fishes such as goldfish and various reef fishes (Callard et al. 1993; Maruska and Tricas 2007; Mangiamele et al. 2017). Injections of human chorionic gonadotropin (induces ovulation and mating behaviors) in female tungara frogs also increase visual sensitivity measured by ERGs under scotopic conditions (Leslie et al. 2019). Further, in mammals, estrogens are essential for healthy ocular function (Affinito et al. 2003), decreased estrogen signaling after menopause is linked to decreased tear production (Mathers et al. 1998), estrogen signaling may help protect against age-related eye diseases like glaucoma (Zhou et al. 2007; Vajaranant et al. 2010), and estrogens may even be produced in the eye (Cascio et al. 2007). Thus, modulation of visual function by hormones at the level of the retina may be common across vertebrate taxa.

Expression of short wavelength sensitive opsins (*sws1*, *sws2a*, and *sws2b*) in *A. burtoni* is also

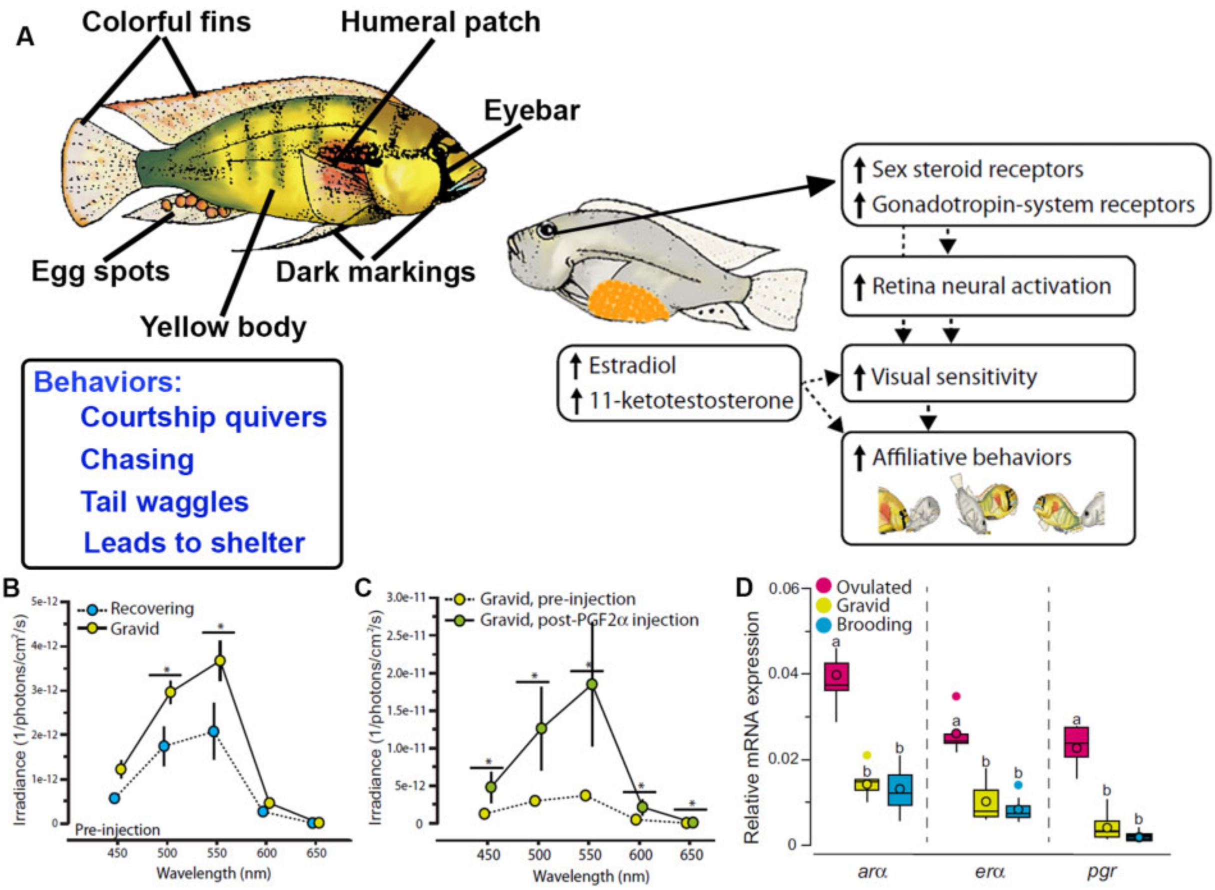

Fig. 2. Reproductive-state plasticity in the visual system of *A. burtoni* females. (**A**) DOM males provide visual courtship signals to females in the form of coloration patterns and behavioral displays. Ovulated females show increased visual sensitivity, retinal activation, higher levels of steroid and gonadotropin receptors in the eye, higher circulating levels of sex-steroids, and greater affiliation behaviors toward males compared to non-ovulated gravid females. (**B**) Gravid females approaching spawning have greater retinal spectral sensitivity measured by ERGs compared to recovering females at wavelengths associated with male courtship coloration (asterisks). (**C**) Gravid females induced to ovulate by injection with PGF2α show an increase in retinal sensitivity at all wavelengths compared to their pre-injection sensitivity (asterisks). Gravid plot in (**B**) is identical to the gravid pre-injection plot in (**C**), but plots are on different y-axis scales. (**D**) Levels of several sex-steroid (androgen receptor α, *arα*; estrogen receptor α, *erα*; progesterone receptor, *pgr*) and gonadotropin (data not shown) receptors are higher in the eyes of ovulated compared to gravid nonovulated and brooding females. Different letters indicate statistical differences at $P < 0.05$. Modified from Butler et al. (2019).

dependent on a female's reproductive state, with ovulated females having higher expression than mouthbrooding females, and gravid nonovulated females as an intermediate (Butler and Maruska 2021). Further, *sws2a* expression, the dominant opsin expressed in the *A. burtoni* eye, positively correlates with circulating levels of estradiol and 11-ketotestosterone (a potent fish-specific androgen) in females. In mosquitofish, exogenous estrogens also influence opsin expression in the eye (Friesen et al. 2017). Thus, changes in both opsins and neuromodulatory systems in the eye suggest potential regulation at multiple retinal layers, from photoreceptors to ganglion cells. Collectively, these data provide evidence linking endocrine modulation of visual plasticity to mate choice behaviors in females and demonstrate the potential importance of this type of phenomenon for reproductive fitness across taxa.

While there are clear reproductive-state changes in visual function at the level of the eye in female *A. burtoni*, males do not appear to show this same plasticity. Males (not separated into DOM and SUB phenotypes) have similar spectral sensitivities measured via ERGs to recovering and non-ovulated gravid females, and injection with PGF2α does not change male retinal sensitivity as it does in females (Butler et al. 2019). Further, DOM and SUB males show no differences in mRNA levels of modulatory receptors in the eye (Butler et al. 2019). While seeing a female is necessary for males to perform courtship behaviors, in contrast to male coloration, females lack obvious coloration changes associated with reproductive state (at least to human perception). Thus, changes in retinal sensitivity at specific wavelengths in males may not be needed for detection of females during courtship and spawning, especially since females visit male territories as they approach spawning. In male goldfish, injections of both testosterone and estradiol rapidly (30–45 min) increase approach responses toward visual signals from females (Lord et al. 2009). Authors suggest that surges of testosterone induced by sexual stimuli (including pheromones released by females) can rapidly prime males to mate by increasing sensitivity within visual pathways that guide approach responses toward females and/or by influencing the motivation to approach mates through actions in limbic neural circuits. Thus it is also possible that more rapid modulation occurs in the visual system of DOM male cichlids to facilitate courtship and spawning, but this requires further examination.

In addition to reproductive-state plasticity in the eye, visual processing may also be modulated at central levels in the brain. For example, aromatase b (*aromb*; enzyme that converts testosterone to estradiol; teleosts contain two different aromatase forms, *aroma* [*cyp19a*] primarily expressed in gonads, and *aromb* [*cyp19b*] primarily expressed in brain and sensory tissues) mRNA levels are greater in the tectum (receives primary visual projections from retina via the optic nerve) of gravid female *A. burtoni* compared to recovering and mouthbrooding states, with no reproductive-state differences in estrogen receptors (Maruska et al. 2020). This suggests greater local estradiol production in tectal regions that process visual and multisensory information as females approach spawning, which could modify both ascending and descending visual circuitry depending on the visual needs of females in different reproductive stages. Similar to *A. burtoni*, other species also express aromatase and estrogen receptors in central visual processing regions like the tectum, as well as in the retina, and aromatase levels vary seasonally with the reproductive state in some species, suggesting estradiol-mediated visual modulation may be common in fishes (Pasmanik and Callard 1988; Gelinas and Callard 1997; Goto-Kazeto et al. 2004; Mangiamele et al. 2017; Shaw 2018). There is also evidence in mammals for central estradiol modulation of visual function, primarily in the visual cortex. For example, the primary visual cortex of mice is a site of production and sensitivity to estrogens which may shape visual cortical processing (Jeong et al. 2011), and perceptual processing of visual cues like faces and performance in visual memory tasks is positively correlated with estradiol levels through the menstrual cycle in women (Phillips and Sherwin 1992; Peters et al. 2009).

GnRH1 neurons of the preoptic area/hypothalamus regulate the hypothalamic–pituitary–gonadal axis in all vertebrates, leading to gamete production and sex-steroid production. Thus, GnRH1 may influence sensory function by altering levels of circulating sex-steroids, which then influence processing at either peripheral structures or centrally in the brain. However, fishes also contain GnRH2 (midbrain tegmentum) and GnRH3 (terminal nerve ganglia) cell populations that have widespread projections throughout the brain and function as neuromodulators (Yamamoto et al. 1995; Oka 1997; Karigo and Oka 2013). GnRH is also demonstrated to modulate visual function of some fishes (Kinoshita et al. 2007; Okuyama et al. 2014; Umatani et al. 2015). For example, GnRH3 neurons in medaka function as a gate for activating mating preferences based on visual familiarity (Okuyama et al. 2014). In *A. burtoni*, GnRH may have effects in both the eye and visual centers of the brain based on distribution of varicose GnRH-immunoreactive axons and GnRH receptors in these regions (Grens et al. 2005; Chen and Fernald 2006a; Butler et al. 2019). *Astatotilapia burtoni* contains two functionally distinct GnRH receptors, *gnrhr1* and *gnrhr2* (Chen and Fernald 2006b; Flanagan et al. 2007). In the retina, GnRH-immunoreactive axons originating from the GnRH3 cells are found primarily in the interplexiform layer (synaptic contacts among bipolar, amacrine, horizontal, and ganglion cells), *gnrhr1* is expressed in amacrine cells and *gnrhr2* in ganglion cells (Grens et al. 2005), and both *gnrhr1* and *gnrhr2* mRNA levels in the eye change with female reproductive state (Butler et al. 2019). Further, mRNA levels of *gnrhr2* are also positively correlated with female *A. burtoni* affiliative behaviors toward males (Butler et al. 2019). Thus, GnRH3 input to the retina has potential to influence visually-guided behaviors related to reproduction in the cichlid, but requires further electrophysiological and behavioral experiments.

Deep layers of the tectum receive primary visual inputs from the retina, as well as information from other senses, such as audition, mechanosensation, and touch. In *A. burtoni* and other fishes, this region contains abundant GnRH innervation (from both midbrain GnRH2 and terminal nerve GnRH3 cell populations) (Yamamoto et al. 1995; Oka 1997; Maruska and Tricas 2007) and expresses GnRH receptors (Chen and Fernald 2006b). In microdissected tectum samples of *A. burtoni*, *gnrhr2* shows reproductive-state plasticity such that levels are higher in mouthbrooding females compared to recovering and gravid females but GnRH varicosity density (putative release sites) does not change across reproductive states (Maier 2020). The effects of GnRH on visual neuron response properties in the tectum of fishes, however, vary across species. For example, GnRH has inhibitory effects on visual processing neurons in the gourami tectum (Umatani et al. 2015), but excitatory effects in the tectum of rainbow trout (Kinoshita et al. 2007). Thus, GnRH in the midbrain may play a role in fine-tuning sensory processing related to multisensory integration and behavioral outputs, possibly via excitatory–inhibitory balance. This would allow females to make adaptive behavioral decisions that reflect the sensory needs relevant to each stage of their reproductive cycle. For example, modulation may tune down both visual–spatial and auditory processing during the brooding stage but tune up this same information in gravid females paying attention to visual–acoustic courtship signals from males.

In *A. burtoni*, there is potential for modulation of visual processing at both peripheral (eye) and central (tectum) levels in females that is associated with the reproductive cycle. This same visual plasticity does not occur in males, although central mechanisms have not yet been examined. Once females become gravid and ovulate, the sensitivity of their visual system improves possibly to increase the salience of visual sensory information relayed to decision circuits at a time when these inputs are crucial to mate choice decisions based on visual courtship signals from males. Because females invest heavily in post-spawning maternal care, choosing high-quality mates is important, and modulation of sensory function with ovulation would ensure that females have enhanced detection when it is needed most. Future studies are needed, however, to uncover the cellular and molecular mechanisms acting peripherally and centrally to modulate vision in this species.

Plasticity in the auditory system

In addition to flashy visual signals, DOM male *A. burtoni* also produce broadband, low-intensity pulsed sounds during courtship quiver behaviors toward females as part of a combined visual–acoustic signal (Fig. 3A; Maruska et al. 2012). These sounds are only produced during the body quiver (male bends body into a C-shape, displays anal fin with egg spots, and vibrates body) but are intentional because not all quivers are associated with sound production (Fig. 3A). The courtship sounds also appear to provide females with some additional information (i.e., are nonredundant) about the male signaler that may not be apparent solely from the visual displays. In experiments where gravid females are exposed to visual only, auditory only, or visual and auditory signals from courting males across different barriers (which control which sensory information reaches females), gravid females show reduced affiliation toward males when they can only hear a male compared to when they can only see a male (K.P. Maruska, unpublished observations). The visual system is likely dominant, however, because affiliation is similar when females can see and hear a male compared to when they only see a male. Peak frequency of courtship sounds and the percentage of quivers associated with sound production are also related to male body size, suggesting that females could use this information as honest indicators of male quality, size, experience, and condition (Maruska et al. 2012). Playback experiments also demonstrate that gravid females prefer to affiliate with males that have courtship sounds coming from their territories compared to males only providing visual displays. This female preference is not present when noise control sounds are played through the speaker, demonstrating the affiliation is likely due to male courtship sounds specifically (Maruska et al. 2012). There is also evidence that mouthbrooding females do not show this same affiliation response to male courtship sounds (K.P. Maruska, unpublished observations). Thus, in *A. burtoni*, males produce specific courtship sounds that provide females with close range honest non-redundant information used for mating decisions, making acoustic communication a crucial component to their reproductive success.

The importance of inter-sexual acoustic communication in *A. burtoni* is further emphasized by the observation that females show reproductive-state plasticity in their hearing abilities. Auditory evoked potential (AEP; electrodes positioned beneath the skin over the brain to record brain waves induced in body tissues from presentation of sounds via an underwater speaker) recordings demonstrate that gravid females approaching spawning have two- to five-fold better hearing (lower thresholds) than mouthbrooding females in the parental care phase (Fig. 3B; Maruska et al. 2012). This difference in hearing thresholds occurs at low frequencies from ∼100 to 600 Hz, which corresponds to the frequencies with the greatest energy in male courtship sounds. There is also a correlation between hearing abilities and circulating estradiol levels such that gravid females with high estradiol levels have the lowest hearing thresholds (Fig. 3C; Maruska et al.

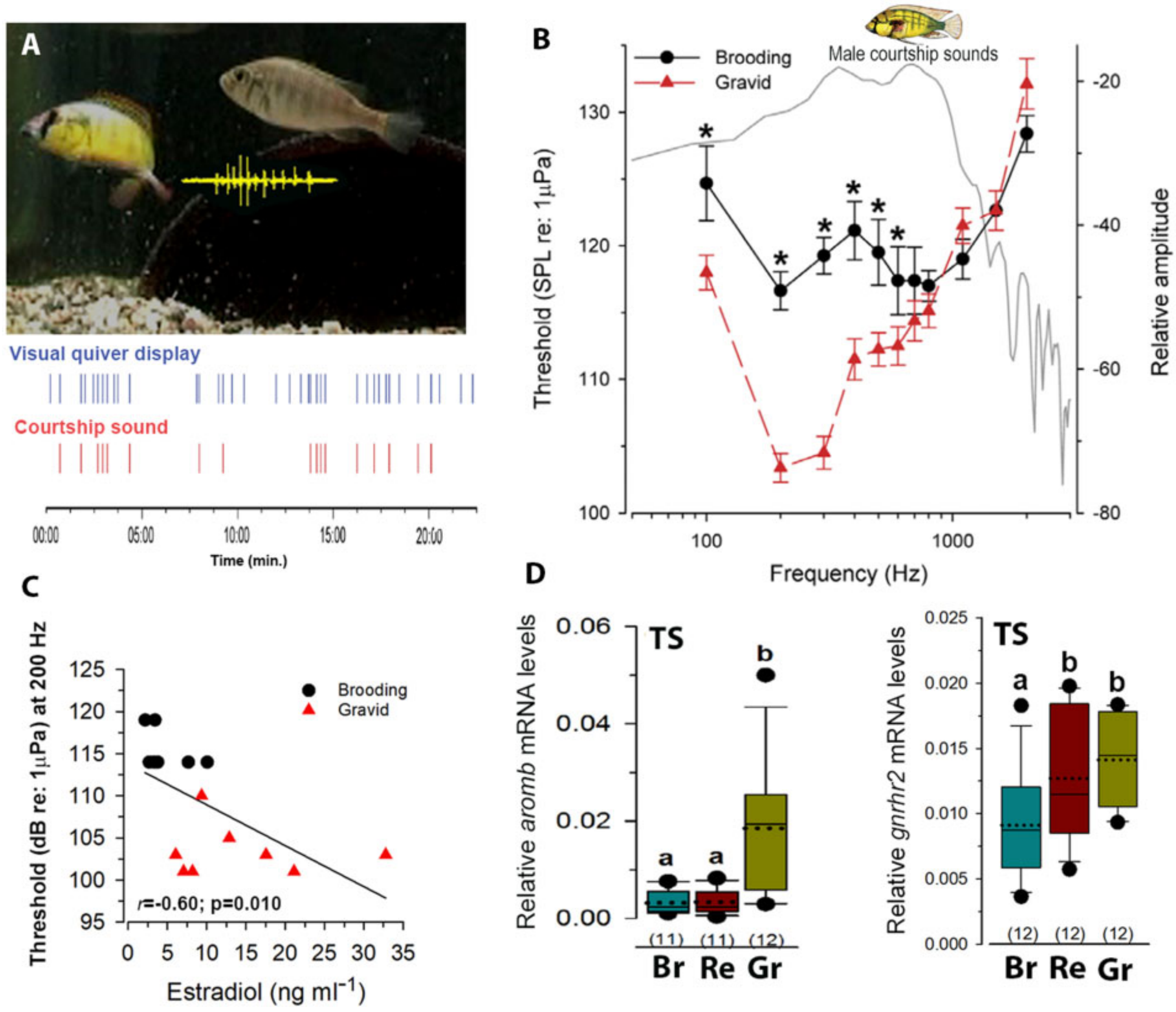

Fig. 3. Reproductive-state plasticity in the auditory system of female *A. burtoni*. (**A**) A DOM male producing a low-intensity broadband courtship sound (waveform inset) during a visual body quiver toward a receptive gravid female. Time series below photo shows a single trial to illustrate that not all visual quivers (blue lines) are associated with courtship sound production (red lines). Modified from Maruska et al. (2012). (**B**) AEP recordings show that gravid females have lower hearing thresholds at frequencies from 100 to 600 Hz compared to brooding females (asterisks), which overlaps the greatest energy found in male courtship sounds (line labeled male courtship sounds). Modified from Maruska et al. (2012). (**C**) Female hearing thresholds are negatively correlated with circulating levels of estradiol. Modified from Maruska et al. (2012). (**D**) Gravid females approaching spawning condition have higher mRNA levels of *aromb* and *gnrhr2* in microdissected samples of the auditory TS (Br, brooding; Re, recovering; Gr, gravid). Modified from Maier (2020) and Maruska et al. (2020).

2012). In contrast, female hearing thresholds are not correlated with circulating levels of the androgen 11-ketotestosterone. Intraperitoneal injections of the aromatase inhibitor fadrozole, which blocks estradiol synthesis, results in a ∼5 dB increase in hearing thresholds at 200–400 Hz in gravid females 1 h after injection (K.P. Maruska, unpublished observations). This is the same frequency range contained in the male courtship sounds. While this fadrozole-induced increase in threshold does not mimic the large differences in hearing thresholds seen in this same frequency range between gravid and mouthbrooding females, it is consistent with estradiol signaling playing at least some role in this female auditory plasticity. However, because there are many physiological differences between gravid and mouthbrooding females, other hormones or modulators may also play a role in auditory plasticity.

This type of auditory plasticity associated with the female reproductive cycle or hormones is also present in other diverse species where males produce sounds/vocalizations during courtship and mating. For example, female midshipman fish show improvements in auditory sensitivity at the primary auditory endorgan (saccule) during the breeding season so they are better tuned to the male's advertisement "hum" vocalizations, and this hearing improvement can also be induced with estrogen implants in nonreproductive females (Sisneros and Bass 2003; Sisneros 2009). In many calling frog species, auditory sensitivity in females varies with reproductive state, season, breeding condition, and hormone manipulations (Wilczynski et al. 2005; Arch and Narins 2009; Baugh et al. 2019; Gall et al. 2019). Female songbirds show changes in auditory perception associated with breeding condition, and neuroestrogens mediate improved auditory sensitivity (London et al. 2009; Remage-Healey et al. 2010, 2012; Brenowitz and Remage-Healey 2016). Hormones also modulate auditory function in mammals, including humans (Al-Mana et al. 2008; Caras 2013). Endocrine-mediated plasticity in the auditory system is clearly widespread across taxa, particularly in those species that cycle in and out of breeding condition.

The AEP recording technique in fishes is thought to primarily represent evoked activity in the otolithic endorgans, primary afferents of the auditory nerve, and hindbrain (but there is also evidence that lateral line inputs contribute to the AEP response at low frequencies [Higgs and Radford 2013]). This suggests that reproductive-state hearing changes in *A. burtoni* may result from modulation at the peripheral auditory structures of the inner ear. Studies in the midshipman fish, for example, show that reproductive summer females have better hearing than nonreproductive winter females that is in part due to modulation by estradiol and dopamine at the level of the saccule (largest otolithic endorgan in teleosts; Sisneros 2009; Perelmuter et al. 2019). Furthermore, these reproductive female midshipman fish have more hair cells and higher levels of BK potassium channels compared to nonreproductive fish, providing physiological mechanisms for the differences in hearing (Coffin et al. 2012; Rohmann et al. 2013). While the mechanisms responsible for hearing changes in *A. burtoni* are not yet known, several studies provide some insights. First, mRNA levels of potential modulators such as sex-steroid receptors and components of the corticotropin-releasing factor signaling pathway differ in the saccule of *A. burtoni* with sex and among different reproductive states (Maruska and Fernald 2010c; Butler 2019). For example, gravid females have lower mRNA levels of many sex steroid receptors in the saccule compared to mouthbrooding females, and these levels are negatively correlated with circulating sex-steroid levels (Maruska and Fernald 2010c). Thus, while plasma levels of estradiol and androgens are high in gravid females, the mRNA levels of their receptors in the saccule are low. If steroid action at the inner ear is important for mediating the reproductive-state plasticity in hearing abilities, then one might predict that receptor levels would also be higher in the saccule when females are gravid. There are several scenarios that might account for the fact that this is not the case. First, it is possible that females approaching spawning have a higher turnover of mRNA into functional protein receptors so that mRNA levels are low. Second, high circulating sex-steroids may downregulate mRNA production of receptors as part of a negative feedback system to maintain some threshold level of steroid action in the ear as a protective or homeostatic mechanism. Third, sex-steroid effects at the inner ear may play a minimal role in changing hearing sensitivity or may be only one aspect of a more complicated mechanism involving other modulators or changes in hair cell density. While these studies provide potential substrates for neuromodulatory action at the saccule, the exact mechanisms require further examination,

It is also possible that auditory processing in *A. burtoni* is modulated at higher centers in the brain, especially in the context of perceiving salient reproductive signals or integrating auditory signals with other sensory information. In fishes, auditory information is received by the hair cell-based otolithic endorgans of the inner ear (saccule, lagena, and utricle), transferred via primary afferents of the auditory nerve to hindbrain octaval nuclei, and then sent to the midbrain torus semicircularis (TS). The TS is homologous to the inferior colliculus of mammals and is an important gateway for sending contextual salient auditory information to forebrain decision centers (Bass et al. 2005). In *A. burtoni*, preliminary single neuron recordings in the TS show improved sensitivity to both pure tones and playbacks of complex male courtship sounds in females with higher gonadosomatic index (GSI = [gonad mass/body mass]*100, used as a measure of reproductive investment) that are approaching spawning compared to those with lower GSI (K.P. Maruska, unpublished observations), raising the possibility that the TS also serves as a substrate for modulation of auditory processing.

The midbrain TS of *A. burtoni* contains many different classes of modulators that could influence auditory circuitry including neuropeptides, steroids, and biogenic amines. For example, the TS receives varicose projections from modulatory neurons with putative release sites for dopamine, serotonin, GnRH, neuropeptide Y, and many others, as well as expresses receptors for these same modulators (O'Connell et al. 2011; Loveland et al. 2014; Porter et al. 2017). This brain region also contains cells expressing many modulatory substances (e.g., corticotropin-releasing hormone [*crh*], neuronal nitric oxide synthase, and others) and neurotransmitters (e.g., gamma-aminobutyric acid, GABA and glutamate) that could provide local release to influence auditory circuits (Maruska et al. 2017; Grone et al. 2021). In mammals, for example, serotonin is a well-known modulator of auditory processing in the homologous inferior colliculus (Hurley et al. 2002; Hurley and Pollak 2005). If the TS serves as a substrate for modulation of reproductive-state auditory plasticity in female *A. burtoni*, then there should be some evidence of changes in the synthesis, release, or action of modulators across the reproductive cycle. Previous studies do in fact demonstrate this plasticity in modulatory potential within the TS of *A. burtoni* females. For example, mRNA levels of *aromb* are higher in the TS of gravid compared to brooding and recovering females, but the mRNA levels of estrogen receptors do not differ with reproductive state (Fig. 3D; Maruska et al. 2020). Thus, the production of estradiol in the TS is likely greater as females approach spawning, which may influence the processing of auditory signals from courting males in the service of mate decisions. Modulation of auditory processing in the brain by estradiol is also present in other taxa including songbirds (Maney and Pinaud 2011; Tremere and Pinaud 2011; Remage-Healey 2012; Krentzel and Remage-Healey 2015) and mammals (Pinaud and Tremere 2012; Moreno et al. 2018), and may be a key regulator of auditory function in the vertebrate brain.

Another example is the decapeptide GnRH that is a known neuromodulator in the teleost brain, and was shown to influence auditory processing in the TS of the damselfish (Maruska and Tricas 2011). While the density of GnRH-immunoreactive varicosities (putative peptide release sites) does not differ in the *A. burtoni* TS across female reproductive states, mRNA levels of the *gnrhr2* receptor are greater in gravid compared to brooding females (Fig. 3D; Maier 2020). Binding of GnRH to *gnrhr2* is known to inhibit potassium M-currents, making cells more likely to generate action potentials (Millar 2003). Because the TS contains so many different potential modulators, it is likely a shift in the balance of excitatory and inhibitory signaling associated with changing reproductive condition that ultimately leads to modified auditory processing in different contexts that is then transmitted to forebrain decision centers leading to appropriate behaviors. Modulation of auditory processing in the TS also occurs in other species. For example, recordings in the TS of frogs show that responses vary with reproductive state and are modified by androgens (Miranda and Wilczynski 2009a, 2009b), and auditory processing in the TS homolog (inferior colliculus) of mammals changes with season, reproductive state, and steroids and monoamines (Hurley and Pollak 2005; Charitidi et al. 2012; Miller et al. 2016). The auditory midbrain is likely a substrate for modulation of auditory processing across taxa, integrating salience of contextual sounds with internal physiological state.

Female *A. burtoni* do not appear to produce sounds, nor do males in male–male interactions (K.P. Maruska, personal observations, but remains to be fully experimentally tested), but males do show a social status plasticity in hearing abilities that may be related to obtaining reproductive opportunities (Maruska et al. 2012). SUB males have lower AEP hearing thresholds at frequencies from 600 to 800 Hz compared to DOM males. Improved hearing at these frequencies near the upper spectral range of male courtship sounds may allow SUB males to better locate territories of smaller DOM males (e.g., those that produce higher peak frequency sounds) where they would have a greater chance to win a challenge with the resident and acquire his territory. Improved sensitivity may also allow these SUB males, which typically have minimal spawning opportunities without a territory, to detect when a territorial DOM male is close to spawning so that he can capitalize on the chance to sneak spawn (e.g., interrupt the DOM male and female spawning pair by swimming between them to release sperm and fertilize eggs; Kustan et al. 2012). SUB males also have lower circulating levels of sex-steroids, but have higher mRNA levels of some estrogen and glucocorticoid receptor subtypes in the saccule of the inner ear compared to DOM males, which may play a role in the improved hearing at these higher frequencies, or may simply be a negative feedback or homeostatic mechanism as described above for females (Maruska and Fernald 2010c).

Female *A. burtoni* show greater affiliation toward DOM courting males when they are gravid and especially after ovulation compared to a nonreproductive state, making this period a crucial time for reception of salient male-generated signals (Clement et al. 2005; Butler et al. 2019). Improved sensory perception associated with this time would be advantageous for greater reproductive fitness. It is likely that there are multiple modulatory mechanisms responsible for reproductive-state auditory plasticity in female *A. burtoni*, but similarly to that shown in other species (Sisneros 2009; Remage-Healey et al. 2010), estradiol does appear to play at least some role. Thus, as females approach spawning and grow their eggs, become gravid, and produce more estradiol, their hearing abilities improve specifically in the frequency range of male courtship sounds. This plasticity may allow females to make more informed mate choice decisions based on information they obtain from male acoustic signals, and may allow them to detect courting males at further distances and in conditions that might obscure visual information (e.g., turbidity). Since the visual–acoustic courtship quiver signals by males occur simultaneously, the improvement of both female vision and hearing as they approach spawning condition may facilitate detection of these multimodal signals to fine-tune mate choice decisions. Coincident detection of visual and acoustic courtship signals in specific regions of the female brain, for example, may be important for regulating behavioral decisions and execution of appropriate behaviors. Choosing high-quality males is very important in this species because the females invest heavily in parental care immediately after spawning, which includes a period of starvation as she broods and cares for the developing young in her mouth. Furthermore, the care investment continues after the brood period because the mother allows released fry to re-enter her mouth when threatened. Therefore, modulation of auditory capabilities associated with the reproductive cycle is likely important in this species that uses multimodal communication, and future functional studies are needed to reveal the cellular and molecular mechanisms that lead to changes in audition.

Plasticity in the olfactory system

In addition to visual–acoustic communication, *A. burtoni* males and females use chemosensory signaling for intra- and inter-sexual communications (Fig. 4; Crapon de Caprona 1974, 1980; Maruska and Fernald 2012; Field and Maruska 2017). In reproductive contexts, DOM males release urine sooner and increase their urination frequency in the presence of receptive gravid females, and urine pulses do not occur simultaneously with visual–acoustic quivers, but during pauses between behaviors (Maruska and Fernald 2012). Gravid females also increase their urination in the presence of DOM males (Field and Maruska 2017), and males will change their aggressive and reproductive behaviors and the release of testosterone into the water depending on the reproductive state of females (Kidd et al. 2013). Thus, males and females signal to each other in the chemosensory channel during courtship, and it impacts the behavior and physiology of the opposite sex. Males can distinguish gravid and nonreproductive mouthbrooding females because they increase their urination frequency in the presence of gravid females close to spawning (Maruska and Fernald 2012). Furthermore, males can also distinguish gravid nonovulated females from ovulated females because they increase their reproductive effort and intensify their body coloration toward ovulated females (Fig. 4B; Butler et al. 2019). Ovulation status is likely conveyed via chemosensory signals because male courtship behaviors are increased when he can see and smell a female compared to only receiving visual signals alone (K.P. Maruska, unpublished observations; Field et al. 2018). The functional significance of male-released chemosensory signals on female behavior and physiology is less understood, but it may function to stimulate ovulation or affiliative behaviors similar to that seen in other fishes (Sorensen et al. 1988; Stacey and Sorensen 2005), or indicate male dominance status (Barata et al. 2008). While the identity of the released putative pheromones in *A. burtoni* are not yet known, and it is likely a combination of compounds, there is some evidence that a PGF2α metabolite released from females may be involved in the reproductive context (Kidd et al. 2013; O'Connell et al. 2013; Juntti et al. 2016). In intra-sexual contexts, DOM males also increase their urination frequency and aggressive displays in the presence of rival DOM males (Maruska and Fernald 2012), suggesting they may convey dominance status to other males via chemosensory signaling as shown in tilapia (Barata et al. 2007). Gravid *A. burtoni* females also increase their urination frequency and aggression toward mouthbrooding females (Field and Maruska 2017). The reasoning behind this is unclear, but it may be related to female dominance hierarchies. Collectively, these studies show that urine is used as a potent social signal in both reproductive and aggressive contexts and in both males and females of this species, suggesting that chemosensory communication is also an important component of a multimodal social repertoire.

If chemosensory communication is important for intra- and inter-sexual interactions in *A. burtoni*, then do olfactory capabilities also change with reproductive and social state? There is physiological evidence that the olfactory epithelium (OE) does in fact differ among males and females of different states, which may be related to reproductive, social, and metabolic conditions (Nikonov et al. 2017).

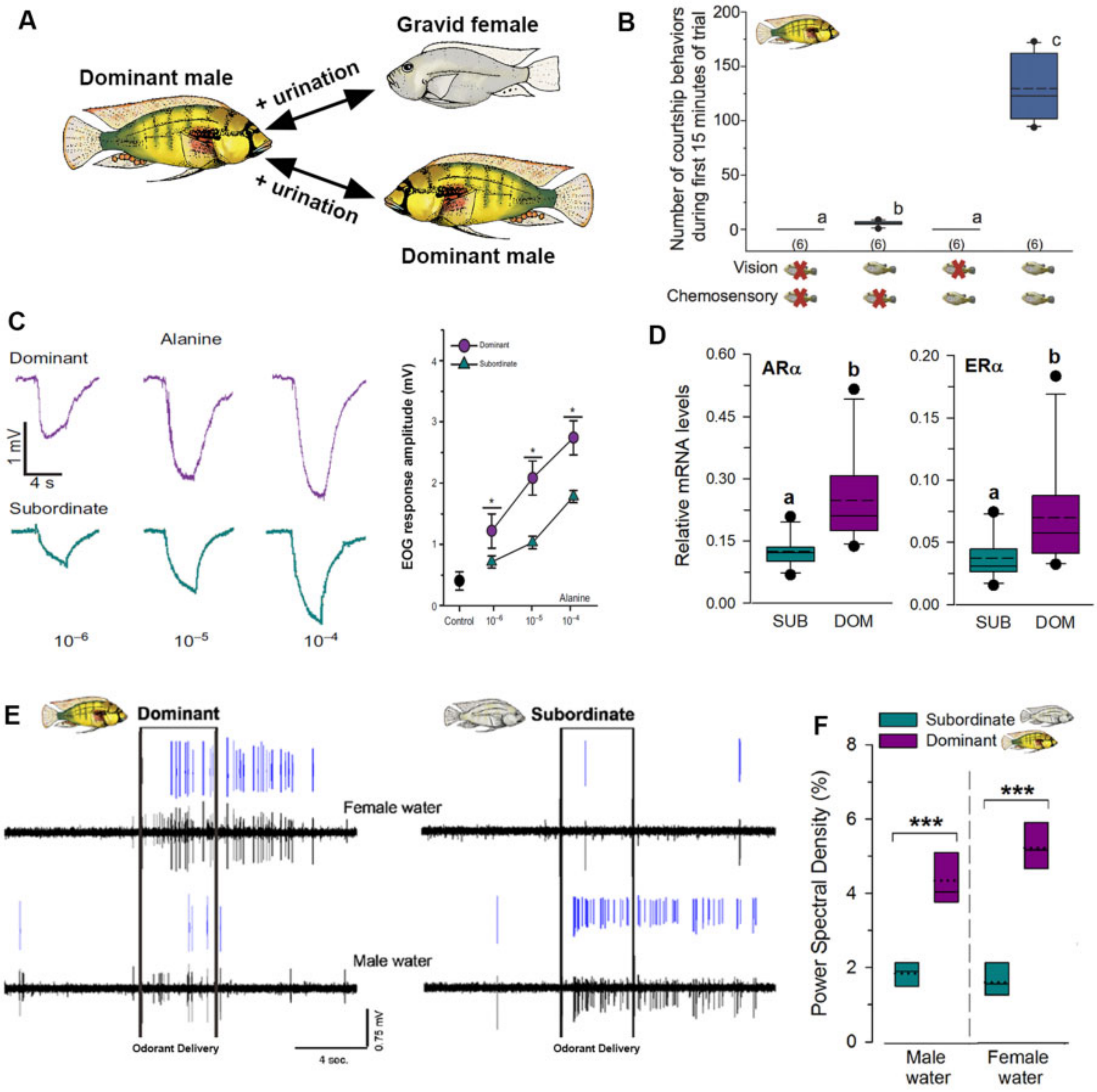

Fig. 4. Social status plasticity in the olfactory system of *A. burtoni* males. (**A**) DOM males increase the release of urine pulses in the presence of receptive gravid females and rival males. Gravid females also increase urination in the presence of courting DOM males. (**B**) Chemosensory signals from gravid females influence male behavior. Visual signals from gravid females alone will increase courtship behaviors in males but combined visual and chemosensory signals dramatically increase male courtship behaviors. Chemosensory signals alone do not induce courtship behaviors in males, but they do increase searching behavior in this context. Modified from Field et al. (2018). (**C**) Responses of the OE measured by EOGs differ between DOM and SUB males. Representative EOG traces in response to different concentrations of alanine are shown for a DOM and SUB male, and mean responses of EOG magnitudes are plotted at right. DOM males have greater EOG response amplitudes in response to the same alanine concentrations compared to SUB males (asterisks). Modified from Nikonov et al. (2017). (**D**) In the olfactory bulbs, mRNA levels of several modulators or their receptors differ with male social status. For example, mRNA levels of ARα and ERα in the olfactory bulb are higher in DOM compared to SUB males. Different letters indicate statistical differences at $P < 0.05$. Modified from Maruska and Fernald (2010b). (**E**) Status-specific differences also exist in olfactory processing regions of the forebrain. Representative single neuron recordings from the Vv for a DOM and a SUB male in response to male- and female-conditioned water passed over the OE (odorant delivery). Black traces show raw neural recordings and blue marks show the discriminated single neuron action potentials from each recording. Vv neurons in DOM males showed robust firing in response to female-conditioned water and only limited response to male-conditioned water. In contrast, neurons in SUB males showed little response to female water and robust firing to male water. Modified from Nikonov and Maruska (2019). (**F**) Odor-evoked power spectral densities of Local Field Potentials (LFPs) in the theta frequency range (4–9 Hz) show that DOM males have spectral densities two to three-fold greater than SUB males in response to both male- and female-conditioned water (asterisks, $P < 0.001$). The transient rhythmicity of LFPs helps link neural activity within and across brain areas, particularly during ongoing and goal-directed behaviors. Greater LFPs in DOM males possibly improves their ability to use olfactory information for rapid decisions related to conflicting behaviors such as fighting, courting, or eating. Modified from Nikonov and Maruska (2019).

Responses of the OE to amino acids measured via electro-olfactograms (EOGs; represents the summated generator potential of the olfactory receptor neurons [ORNs] at OE surface [Silver et al. 1976; Scott and Scott-Johnson 2002]) revealed differences in EOG amplitude and slope between DOM and SUB males, and among brooding, recovering, and gravid females (Nikonov et al. 2017). DOM males (reproductively active and reduced feeding) have greater EOG magnitudes at the same tested amino acid concentrations than SUB males (reproductively suppressed, greater feeding and growth rates; Fig. 4C). Mouth brooding females, which are in a period of starvation while they brood fry in their mouths, have greater EOG magnitudes at the same tested amino acid concentrations than both recovering and gravid females that are feeding. Discriminant function analysis on EOG magnitudes also groups the male (SUB) and female (recovering and gravid) phenotypes with higher food intake together and distinguishes them from brooding females and DOM males with lower food intake (Nikonov et al. 2017). Evidence exists in other vertebrates for the modulation of olfactory epithelial function by metabolic-related signaling molecules. For example, modulators such as NPY, along with several G-protein-coupled receptors that have roles in regulating feeding behavior and energy homeostasis, are found in the OE of many vertebrates, including teleost fishes (Gaikwad et al. 2004; Negroni et al. 2012; Olender et al. 2016). NPY influences olfactory responses at the OE level in rodents and amphibians, particularly in hungry animals (Mousley et al. 2006; Negroni et al. 2012). Thus, there is support for a physiological link between the olfactory periphery and nutritional state. In late-stage *A. burtoni* mouth brooders, greater EOG magnitudes in response to amino acids at the same tested concentration are consistent with a potential function in preparing or priming the starved females (at perceptual and goal-directed neural circuit levels) to rapidly detect, find and consume prey/food once the brood is released. It is also possible that brooding females use amino acids and other olfactory or gustatory cues to facilitate maternal care both during the brood period and after the fry is released. Other mouthbrooding cichlids use chemosensory signals for mother-fry recognition (McKaye and Barlow 1976; Barnett 1977), and amino acids are known to be released from fishes illustrating they can serve as potential social signals (Saglio and Fauconneau 1985). In males, the greater EOG responses in DOM individuals may be related to either metabolic demands or reproductive and social state. DOM males are extremely active and spend considerable time defending and maintaining their territories and courting and spawning with females, which potentially leaves less time for feeding (Fernald and Hirata 1977a; Maruska and Fernald 2010a). This increased energy expenditure and reduced feeding behavior in DOM males suggests that greater olfactory responses may facilitate detection of food within their territorial boundaries to maximize nutrition in support of their active lifestyle during the several-week territory tenure (e.g., increased sensitivity allows better detection to reduce energy expenditure spent searching for food, possibly further from the territory boundaries). The mechanisms responsible for reproductive and metabolic-related changes in EOG response of both male and female *A. burtoni*, however, require further testing.

In fishes, the OE lies beneath the nares openings on each side of the head and contains three main types of ORNs that differ in morphology, receptor expression, and function: microvillus, ciliated, and crypt (other ORNs, kappe and pear-shaped ORNs, were recently discovered but only limited information is available on their distribution and function; Hamdani and Doving 2007; Ahuja et al. 2014; Wakisaka et al. 2017). The OE is the first step of the olfactory pathway, and as shown for the endorgans in the visual (retina) and auditory (saccule) pathways, it may also be a substrate for endocrine or reproductive-state plasticity to facilitate adaptive olfactory-mediated behaviors. For example, the olfactory receptor class-A (ORA)-related receptors are a conserved family of G-protein-coupled receptors hypothesized to play a role in pheromone detection and sexual communication in fishes and are encoded by the *ora* gene family (Saraiva and Korsching 2007; Shi and Zhang 2007; Ota et al. 2012). All six genes of the *ora* family, *ora1-ora6*, are identified in several fish species including cichlids (Ota et al. 2012; Bazaes et al. 2013), and were quantified in the OE of *A. burtoni* (Field 2018). There was no difference in any of the six *ora* transcripts in the OE between DOM and SUB males. Ovulated females, however, have greater mRNA levels of *ora2*, *ora5*, and *ora6* compared to nonovulated gravid and brooding females (Field 2018). While ORAs are hypothesized to detect pheromones, their functions and precise ligands are not known, and only ORA1 is responsive to putative pheromones in zebrafish (Behrens et al. 2014). In addition, the cell type(s) that express *ora* genes has yet to be characterized in fishes, and because the compounds used for chemosensory communication in *A. burtoni* are not yet identified, it is difficult to know the extent of possible reproductive- or social-state plasticity in the OE and the relevance of these observed changes in *ora* expression. Further, there are many other possible pheromone-detecting receptors in fishes that may also be relevant here in cichlids. For example, vomeronasal receptor Type 2 paralogs may mediate species-specific pheromone detection in swordtails (Cui et al. 2017), and trace amine-associated receptors may be involved in pheromone detection in many fishes (Hashiguchi et al. 2008). There are many possible mechanisms at the level of the OE that could alter olfactory processing among males and females of different reproductive states that require further examination.

Modulation of olfactory capabilities may also occur at the level of the olfactory bulbs, possibly by sex steroids, neuropeptides, and biogenic amines. In *A. burtoni*, the olfactory bulbs contain cells or receive projections from neurons that express many modulatory neuropeptides including GnRH, NPY, cocaine, and amphetamine-regulated transcript, *crhb*, *urocortin 3*, serotonin, and others (Porter et al. 2017; Grone et al. 2021). mRNA levels of multiple sex-steroid receptors, GnRH receptors, and aromatase in the olfactory bulb also vary with sex, social status in males, and reproductive condition in females (Fig. 4D; Maruska and Fernald 2010b). This suggests potential fine-tuning of the olfactory system may occur at the level of the olfactory bulbs by different classes of modulators depending on fish internal physiological condition. Further, steroid receptor mRNA levels are positively correlated with circulating steroid levels in males, but negatively correlated in females, suggesting different regulatory control between the sexes (Maruska and Fernald 2010b). Olfactory bulbs are also a substrate for modulation in other taxa. For example, in the mammalian olfactory bulb, dopaminergic signaling modulates odor detection and discrimination (Liu 2020), leptin reduces odor discrimination by modulating potassium channels to reduce neural activity in mitral/tufted cells (Sun et al. 2019), and endocannabinoid signaling influences glomerular cell activity with potential effects on olfactory thresholds and behavior (Wang et al. 2019). The presence of many other modulators in the olfactory bulbs suggests alteration of both excitatory and inhibitory circuits to change odor discrimination and other olfactory abilities (Trombley and Shepherd 1993; Harvey and Heinbockel 2018). Collectively, these data support the hypothesis that the first-order olfactory relay station is a putative substrate for modulation by many neurochemicals in *A. burtoni* and other species, and that changes in receptor levels could be an important mechanism for regulating reproductive, social, and metabolic plasticity in olfactory perception.

Olfactory capabilities also differ between DOM territory-holding reproductive *A. burtoni* males and SUB reproductively-suppressed males at the level of forebrain processing centers (Nikonov and Maruska 2019). For example, single and multiunit recordings from an olfactory processing region in the forebrain (Vv, ventral nucleus of the ventral telencephalon) show that DOM males have a greater percentage of neurons that respond to female-conditioned water (water that housed four receptive gravid females interacting with a DOM male across a clear barrier for 4 h) compared to SUB males (Fig. 4E; Nikonov and Maruska 2019). These female-related olfactory inputs are likely important for DOM males who are focused on courting receptive females and need to detect female ovulation status to better direct their courtship efforts. In contrast, SUB males have a greater percentage of neurons that respond to male-conditioned water (water that housed a DOM male interacting with another DOM male across a clear barrier for 4 h) compared to DOM males (Fig. 4E). Studies in tilapia show that male dominance status is conveyed via compounds released in urine to both females and rival males (Barata et al. 2007, 2008), and a similar situation may exist in *A. burtoni*. SUB males may therefore monitor these male-released chemosensory signals to make decisions about which males in the population to challenge for their territory and which males to avoid to minimize physical injury. Quantification of local field potentials (LFPs; indicative of synaptic inputs) in Vv also show that DOM males have two- to three-fold greater power spectral densities in the theta range (4–9 Hz) compared to SUB males (Fig. 4F; Nikonov and Maruska 2019). This further demonstrates status-dependent differences in processing possibly linking olfactory and other neural inputs to goal-directed behaviors, allowing DOM males to better use olfactory information for rapid decisions related to conflicting behaviors such as fighting, courting, or eating. While the mechanisms responsible for this male plasticity in olfactory processing are unknown, neuromodulation of existing circuitry is a possibility. This Vv brain region expresses many modulatory substances and mRNA levels of several sex-steroid receptors are higher in DOM compared to SUB males, suggesting that modulation of olfactory circuits in Vv could play a role in this plasticity (Maruska et al. 2013). Whether females show this same type of reproductive olfactory plasticity in the forebrain for detecting male-released chemicals is not known.

Conclusions and perspectives

Here, we review the studies demonstrating that *A. burtoni* shows reproductive and social status plasticity in its communication abilities and the reception of salient sensory signals during social interactions. In general, changes in sensory abilities in females (vision, auditory, and olfactory) seem to be associated with the natural reproductive cycle and to function primarily in improving detection of courtship signals (visual, auditory, chemosensory, and likely mechanosensory) from high-quality males for reproduction. This would be adaptive in this species where females are the "choosy" sex and will invest heavily in maternal care following successful spawning. In contrast, the plasticity in male sensory abilities (auditory and olfactory) seems to function in altering their ability to detect the status of other males in the service of territory ownership and future reproductive opportunities. This is also adaptive because male reproductive success and overall health are tied to territory ownership where they are visited by receptive females, so improved assessment of other males in the population can increase future benefits. Thus, even within a single species, plasticity in sensory function may be regulated by different mechanisms, serve diverse functions, and be subject to different selective pressures in males and females, highlighting the importance of examining communication in both sexes and across different physiological conditions.

The *A. burtoni* reproductive and social status plasticity is evident in both sexes, is associated with changes in diverse modulators, and can occur at both peripheral sensory organs and in central processing circuits connected with decision centers and motor output centers leading to adaptive behaviors. Importantly, it also highlights an example of sensory plasticity in a species that relies on multimodal communication as part of its natural social behavioral repertoire, with evidence for changes in sensory abilities in all studied senses (e.g., acoustic, chemosensory, and vision) rather than solely the dominant sense (e.g., vision). While vision is necessary and sufficient for both male–female courtship and male–male territorial interactions, *A. burtoni* lives in a dynamic environment with variations in the transmissibility of different sensory signals depending on conditions. Having modulation and flexible circuitry in multiple senses and on different timescales may allow optimization of reproductive and territorial signaling in different situations (e.g., turbidity, water depth, etc.) and may facilitate switching of reliance on one sensory channel to another depending on the conditions. Further, *A. burtoni* is an instance of sensory plasticity occurring in a nonseasonally breeding species, with more rapid effects (minutes to hours) particularly in females associated with ovulation. Thus, it is important to recognize that changes in sensory perception can occur on shorter nonseasonal time scales, with potentially different mechanisms than those observed in seasonal breeders (e.g., genomic versus nongenomic).

While *A. burtoni* sensory abilities do change depending on the state of the animal, what remain less understood are the mechanisms responsible for mediating this plasticity at both peripheral and central levels. For example, what are the endocrine targets in peripheral sensory organs and those in central processing areas, and how is modulation at both the periphery and the brain integrated together? There are many ways that hormones/modulators can influence sensory function including altering the function of ion channels, modulating transcription of relevant genes, influencing structural changes in neural circuits (e.g., dendritic complexity; synaptic organization), and other mechanisms (Pinaud and Tremere 2012). Thus, there may be rapid nongenomic and slower-acting genomic effects, and it is also likely that multiple mechanisms exist for any given sense. Further, how much modulation is linked with natural fluctuations associated with the reproductive cycle, and how much evolved specifically to alter sensory perception possibly related to sexual selection? What is the relative importance of modulation occurring on short (seconds to minutes) versus longer (hours to days) timescales? In addition, the question of why individuals do not just maintain this improved sensory function all the time is unknown. The fact that both males and females undergo state-dependent sensory plasticity suggests there are costs involved that may be linked to metabolism and allocation of nutritional resources, which also differs with reproductive and social status in this species, so this also deserves future attention. With so many potential modulatory substances present in peripheral sensory organs and in central sensory processing areas that change with female reproductive state or male social and reproductive state, these are not easy questions to address. In the case of estradiol, in particular, there is evidence across many teleost fishes that suggests it is involved in modulating many sensory systems (e.g., visual, auditory, olfactory, and electrosensory) possibly at both peripheral and central levels (Shaw 2018). Estrogen modulation of sensory function has received much attention across vertebrates and as more comparative studies on different sensory systems are reported, this avenue of research will likely reveal the mechanisms of action. The rapid development of new technologies in neuroscience, genetics, gene editing, functional genomics, sequencing, machine learning, and other areas that can be applied to the cichlid and a wide range of less well-studied organisms will facilitate discoveries moving forward.

By emphasizing what we have learned about *A. burtoni* sensory plasticity and communication, we hope to inspire others to examine this topic in a wide range of other species from many different perspectives. The *A. burtoni* example represents one of the only species with documented reproductive/endocrine sensory plasticity in multiple senses and using approaches at multiple levels of biological organization from behavior to molecular mechanisms has revealed the complexity of sensory modulation within this species. However, reproductive, social, metabolic, and endocrine state modulation of communication and sensory perception is likely much more widespread than currently realized. Using a comparative and neuroethological approach will allow the field to discover commonalities that may be conserved through evolution, reveal mechanisms for how these changes come about and whether they differ between sexes within a species, uncover novel sensory abilities not previously recognized, and provide insights on evolutionary processes that may be important for understanding how animals will adapt to our changing climate in the future.

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Conflict of interest

The authors have no known or potential conflicts of interest.

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