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Sensory modalities in cichlid fish behavior

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Abstract

Among teleosts, cichlids are a great model for studies of evolution, behavior, diversity and speciation. Studies of cichlid sensory systems have revealed diverse sensory capabilities that vary among species. Hence, sensory systems are important for understanding cichlid behavior from proximate and ultimate points of view. Cichlids primarily rely on five sensory channels: hearing, mechanosensation, taste, vision, and olfaction, to receive information from the environment and respond accordingly. Within these sensory channels, cichlid species exhibit different adaptations to their surrounding environment, which differ in abiotic and biotic stimuli. Research on cichlid sensory capabilities and behaviors incorporates integrative approaches and relies on diverse scientific disciplines from physics to chemistry to neurobiology to understand the evolution of the cichlid sensory systems.

Graphical Abstract

Introduction

Cichlidae is one of the largest families of teleost fishes with more than 2000 species. It is widely distributed across ecosystems from Africa and South Asia, to Central and South America. Cichlid species are diverse, varying in ecology, and behavior. They have evolved to forage on a variety of foods (e.g. zooplankton, plants, invertebrates, scales, and fish). They also vary in mating systems (monogamy, harem or polygyny) and parental care (paternal, maternal, or biparental, and mouth brooding or substrate spawning). Cichlids have been studied for many years to examine their ecology, morphology, sensory biology, and behavior [1–3]. Their diverse mating signals based on different sensory modalities make them an ideal model for studying how sensory systems shape behavioral ecology.

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Nothing declared.

Cichlid behaviors are mediated by sensory capabilities that enable them to survive and reproduce. Cichlids are often sexually dimorphic with mating preferences shaped by both natural and sexual selection. These preferences are stimulated by cues during courtship (acoustic, morphological, olfactory, visual, tactile and behavioral) produced by the signaler [4]. Cues modified by selection for communication purposes are a special type of cue called a signal. Signals can consist of one or more cues that are evaluated together as a single signal. If its components belong to different sensory modalities, the signal is considered multimodal [4]. Candolin (2003) detailed different hypotheses of why multimodal signals exist. Multiple cues might be adaptive, may no longer be adaptive but be a remnant of past selection, or may be maladaptive as the result of intersexual conflict. The adaptive advantages of multiple cues might include: providing information on different aspects of mate quality; serving as back-up signals to allow a better assessment of mate quality; promoting behavioral isolation for species recognition; eliciting a greater response than that of a single component signal; or gaining more conspicuousness in a changing environment where the ability to assess signals varies under different conditions [4]. In this latter context, multimodal signals are thought to compensate for environmental fluctuations in signal strength or noise that result from complex ecological and social environments that make cue assessment difficult [5]. Thus, multimodal signals may facilitate mate preferences in variable conditions and may reduce mating costs [4]. Furthermore, the origin of female preference based on multimodal signals may arise by sensory exploitation implying pre-existing biases [6,7]. Such biases might be harmful and exploited by signalers or might still involve signals that are helpful to the receiver. With their diversity of signals and complex behaviors, cichlids are a useful system for exploring adaptation, evolution, and sexual selection of these types of signals, where signalers and receivers interact through a multimodal pathway.

In this review, we will discuss how signals in the cichlid model are generated, transmitted, and detected. Signal detection relies on sensory systems, which receive information through mechanosensation, through chemicals, or by the detection of light. To understand the evolutionary mechanisms shaping these behavioral inputs requires an integrative approach incorporating the perspective of physics (to measure how the environment alters signal transmission), genetics and physiology (to decipher the molecular and cellular transduction of signals), and neuroethology (to determine the neural comparisons and how they impact cichlid decisions). Here, we describe what has been learned about how mechanosensation (lateral line and hearing), chemosensation (smell and taste), and photodetection (vision), operate in the cichlid model and how multimodal signals relate to mate preference, foraging, and survival. Although there are other sensory inputs that fish gather, such as detecting touch or temperature, these are much less well studied. They are also less important for communication between individuals.

Mechanosensation

Hearing

The fish inner ear consists of three semicircular canals, each with an otolithic organ: the utricle, the saccule and the lagena (Figure 1a). Each otolithic organ contains a single calcium

carbonate stone about three times denser than the surrounding tissue. These otoliths are in contact with hair cells of the sensory epithelium through an otolithic membrane [8]. Within the sensory epithelium, polarized hair cells are arranged in groups called ciliary bundles that vary in orientation [8]. Differences in the orientation of ciliary bundles have been suggested to be involved in the localization of the sound source [9*].

There are two pathways by which fish detect sound. First, all teleosts can hear through particle motion where the sound source causes a delayed movement of the otolith that results in a shearing movement of the hair cells [10]. Hence, the sound source stimulates the inner ear directly [8]. The second pathway involves indirect stimulation and involves the swim bladder. The gas of the swim bladder is less dense than the fish body. When in a sound field, the swim bladder vibrates, transmitting the energy to the inner ear endolymph, consequently causing the otolith to move relative to the sensory epithelium [11**]. Many teleosts have accessory structures like intracranial gas cavities, anterior extensions of the swim bladder, or connections of the swim bladder to the inner ear via ossicles and ligaments, that increase indirect stimulation and hearing sensitivities [11**].

Cichlids show great diversity in the indirect pathway because of variations in swim bladder morphology. Swim bladders can be small or large, and some even possess anterior extensions that make contact with the inner ear, as found for Malagasy-South Asian cichlids (Figure 1a) [12]. This anterior extension is connected to the lagena, a trait that is not observed in other teleosts [11**]. Schulz-Mirbach et al. (2014) showed that *Etroplus maculatus*, which has a swim-bladder-inner ear connection, has improved audition, detecting frequencies up to 3 kHz versus 0.7 kHz for the African cichlid *Steatocranus tinanti*, which has a ‘vestigial’ swim bladder without extensions [9*]. Additionally, Ladich and Schulz-Mirbach (2013) showed that auditory sensitivities of *E. maculatus* were masked by white noise, whereas *Steatocranus tinanti* was less affected. Thus, sound detection and localization varies within Cichlidae [13]. However, modifications of the anterior portion of the swim bladder may not be the only reason for hearing differences. Differences in the inner ear morphology and orientation patterns of ciliary bundles may also influence hearing capabilities [9*].

Cichlids are known to produce acoustic signals. Sound production has been documented in approximately 30 species and for some species, both sexes produce sounds [14**]. Generally, cichlids produce more than one type of sound and use them for agonistic interactions and courtship (Figure 2d). Agonistic experiments with the haplochromine cichlid *Metriaclima zebra* showed that larger males produce longer pulse duration and greater amplitude modulation suggesting that acoustic signals convey information about the emitter [15]. Indeed, acoustic signals in *M. zebra* may be used by territorial males for detecting rivals in their vicinity [16]. In the Nile tilapia (*Oreochromis niloticus*), acoustic signals occur between both sexes and are only for territorial defense [14**].

Acoustic signals are also important for cichlid mate choice. Assays with the Lake Tanganyikan cichlid, *Astatotilapia burtoni*, showed that acoustic communication is used for reproduction as females favored males using vocal and visual cues over males with only visual displays [17]. Furthermore, Danley et al. (2011) analyzed courtship sound from six

sympatric rock dwelling species of Lake Malawi. Analyses of trill duration, pulse duration, pulse period, and number of pulses per trill showed that all species were easily differentiated according to these parameters, and that geographically isolated intraspecific populations exhibited dialects [18]. Similar patterns have been found in other species of *Metriaclima* [19]. The difference in acoustic signals between closely related species could mean that sounds may be important for generating or maintaining species boundaries. However, sounds are only one part of a multimodal signaling pathway [17,20]. In *Pundamilia nyererei* from Lake Victoria, females do not respond to acoustic signals in the absence of males, which suggest visual displays are key for courtship interactions [21].

Lateral line system

The lateral line system is an ancient sensory system found in fish and aquatic adult amphibians that mediate behaviors such as predator avoidance, communication, prey detection, obstacle avoidance, rheotaxis, and schooling [22,23^{**},24]. The functional units of the lateral line are neuromasts. Neuromasts are sensory structures formed by a group of sensory hair cells that are covered by a gelatinous cupula (Figure 1b) [25]. Sensory cells are stimulated by unidirectional or oscillatory fluid flow that causes the cupula to move, stimulating the hair cells [24]. Therefore, when an aquatic animal moves, water movements, and pressure fluctuations trigger a neural response from neuromasts providing information to the receiver [26].

There are two receptor classes within the lateral line system: canal neuromasts and superficial neuromasts. Canal neuromasts are located under the skin in pored canals contained in the dermal bones of the head, trunk and caudal peduncle (Figure 1b). Superficial neuromasts are freely distributed over the surface of the head, trunk and tail [27]. Canal neuromasts are important for detecting high frequency motion such as from prey, whereas superficial neuromasts assist in responding to more slowly changing flows such as for rheotaxis [28].

Neuromast function and development have been studied in cichlids. Mogdans and Nauroth (2011) tested lateral line function in the South American cichlid *Astronotus ocellatus*. Trained individuals were able to discriminate 100 Hz stimuli from 70 Hz and lower frequencies in calm and turbid waters [29]. Furthermore, neuromasts are also believed to be stimulated in females during male quivering displays in some species (Figure 2c and f) [30]. Lateral line canals can vary in morphology across cichlid species according to their feeding strategies. The Lake Malawi cichlid *Aulonacara stuartgranti* swims close to the sandy sediment hunting buried invertebrates. This species exhibits enlarged pores on the lower part of the head, and these widened canals enhance sensitivity to hydrodynamic flow changes enabling detection of prey just below the surface [31]. Behavioral experiments have shown that *Aulonacara stuartgranti* can use its canal neuromasts to feed in the dark, giving them an advantage over other cichlids that also forage on benthic prey but hunt visually. This suggests that divergence in sensory biology may contribute to different feeding ecologies of African cichlids [23^{*}].

Tarby and Webb (2003) characterized the development of the canal lateral line system in *Archocentrus nigrofasciatus* (*Amatitlania*) in which canal morphogenesis consists of the

growth of each canal segment from the underlying dermal bone and then subsequent fusing of the bone to form the canal roof [32]. The evolution of the lateral line has been examined in developmental studies comparing Lake Malawi cichlids with widened canals, *Aulonacara baenschi*, and narrow canals in *Metriaclima zebra*, *Labeotropheus fuelleborni* and *Tramitochromis* sp. (Figure 1b). They suggest canal widening is a product of dissociated heterochronic processes where there is an increase in rate of canal and neuromast growth and a delay in the beginning of canal morphogenesis [33^{**},34].

Chemosensation

Olfaction

The fish olfactory system modulates numerous behaviors related to foraging, imprinting, finding sexual or social individuals, and avoiding predators or other dangers. Studies have shown that cichlid olfactory sensitivities enable them to recognize kin [35^{*}], recognize conspecifics [36,37], and identify reproductive status of females [38] and social status in males [39^{*},40]. Chemical communication is also exploited at a young age; fry are able to distinguish their parents' odors and show preferences toward the mother [41]. Furthermore, olfaction can trigger physiological and behavioral responses such as egg maturation in females [42^{*}] and mating displays by males (Figure 2e). Additionally, olfaction is likely involved in cichlid imprinting that may impact mate preferences [43,44]. Although cichlids are sensitive to particular chemical compounds, their specific response is unknown in some cases. Experiments on Mozambique tilapia (*Oreochromis mossambicus*) and Nile tilapia (*Oreochromis niloticus*) showed that both species had similar olfactory sensitivities to urine from either species and suggested that chemical cues have not diverged. However, whether these chemical cues trigger the same physiological and behavioral response in both species remains to be investigated [39^{*}]. In conclusion, olfactory cues are honest signals that convey information about fish identity, reproductive status and social rank, shaping the behavioral response of the receiver toward the signaler [42^{**}].

The olfactory organ in fishes is located in the nasal cavity. This rosette is a multi-lamellar structure lined by an olfactory epithelium, which contains the olfactory sensory neurons (OSNs) (Figure 1c) [45]. The rosette harbors sensory and non-sensory epithelia and there is great diversity within fishes on distributions of these types of epithelia [46]. In the sensory epithelium the OSNs are directly exposed to the aquatic environment. They can be categorized into three types: ciliated, microvillar, and crypt neurons (Figure 1c) [47]. These three types of neurons are distributed along the olfactory epithelium. OSNs contain transmembrane proteins on their surface called olfactory receptors, which are the first component of the olfactory transduction cascade. These olfactory receptors bind to an odorant molecule, inducing a cascade of protein interactions that convert a primary chemical signal into an electrical signal that is later decoded in the brain leading to a response [48^{**}].

OSNs express specific olfactory receptor proteins from different gene families which include odorant receptors (ORs), vomeronasal receptors type 1 (V1Rs) and type 2 (V2Rs), and trace amine-associated receptors (TAARs) [49]. ORs and TAARs are expressed in ciliated neurons, V2R in microvillar neurons and V1R in crypt neurons [47,50]. Cichlids have large sets of genes that encode for receptor proteins; 88–158 for ORs, 61 for V2Rs, and

six for V1R genes [47,48^{**},51]. Most ORs and V2Rs are involved in eliciting feeding behavior [48^{**},51]. However, less is known about V1R gene function. Comparisons of the V1Rs genes suggest they are variable, and show evidence of positive selection [52^{*}]. This suggests that V1Rs might have an important behavioral role, perhaps as pheromone receptors, and could play a role in speciation [47,52^{*}].

Taste

In fish, taste is important for the capture and selection of food and for the rejection of unwanted items. Taste is mediated by taste buds (TBs) which are clusters of gustatory cells located in the oral cavity, the pharyngeal cavity, the gills, fins, skin and appendages, and over the entire body in some fish species [53,54]. TBs have an ovoid shape and incorporate three types of cells: sensory, supporting, and basal [53]. Sensory cells are elongated and connected to the environment by microvilli, which contain the taste receptors. Adult taste buds cells are renewed from epithelial cells that surround the taste bud base [53,55]. Teleosts and mammals share the same signaling pathway for umami, sweetness and bitter. However, teleosts do not differentiate umami and sweetness, showing a preference for both [54].

In fish, three main types of taste buds have been described. Types I and II protrude above the epithelium situated on a dome (papillae) of the epidermis whereas type III remains at the epithelium level (Figure 1e). Type I TBs are more elevated than type II. They are also surrounded by a depression and are innervated by cholinergic nerves whereas type II and III are innervated by both aminergic and cholinergic nerves [56]. Type I and II TBs are believed to operate as mechanoreceptors and as chemoreceptors while type III may be only chemoreceptive [56,57].

Cichlids have all three types of TBs. Aspects of the taste sensory neurons vary with ecology. The Central American cichlid, *Cichlasoma cyanoguttatum* and the mouth brooding cichlid from Israel, *Astatotilapia flavijosephi*, have a coincident maturation of taste buds, the gustatory tracts, and brain centers, though, it happens earlier in the substrate brooding *C. cyanoguttatum*, than in the mouth brooding *A. flavijosephi* [55]. Early maturation has been observed in the South American cichlid *Astronotus ocellatus*, which is also a substrate brooder [58]. Hence, the early development of TBs might be an adaptation for survival in substrate brooding species where fry forage at an earlier stage. Brain morphology can also be affected by foraging habit as the gustatory sensory lobe increases in size from rocky to sandy substrate species in African cichlids [59]. Taste buds types differ in their distribution. Elsheikh et al. (2012) found that in the buccal cavity of the Nile tilapia, *Oreochromis niloticus*, type I TBs are located in the proximal part, type II in the middle region, and type III in the masticating apparatus epithelium within the metabranchial buccal cavity [57]. Similar patterns were found on *C. cyanoguttatum* and *A. flavijosephi* [55].

Photodetection

Cichlids are highly colorful fishes and visual communication is critical for cichlid behaviors [60]. Males use color patterns to determine whether to attack and defend their territories, directing more aggressive acts at conspecifics relative to heterospecifics [61,62]. Females

also use color patterns to choose mates. In laboratory studies where males and females are physically separated, females will correctly choose males, laying eggs in front of conspecifics, using only visual cues [63]. If the lighting is altered so that females cannot distinguish different male hues, they will make random mating choices both in the lab and in the wild [64,65,66]. Visual cues may sometimes be supplemented with other cues such as olfactory ones [35]. However, in low quality environments, these cues may not be sufficient, resulting in, hybridization [65].

Vision begins when light is collected by the eye. Fish focus light onto the retina using a large spherical lens with high focusing power. Light is then detected by rod and cone photoreceptors. Rods work in dim light conditions, while cones are for bright diurnal light detection and color vision [67]. Photoreceptor visual pigments are composed of an opsin protein bound to a light sensitive chromophore, such as 11-cis retinal. Typically there are multiple cone types containing different visual pigments, which absorb light maximally in different parts of the spectrum [68]. Fish typically have shorter wavelength sensitive single cones and longer wavelength sensitive double cones (where two cones are joined along their inner segments, but remain neurally independent (Figure 1d)). Neural comparisons of cone outputs produce the perception of color. Behavioral experiments have shown that fish can be trained to recognize certain colors and therefore have color discrimination [69,70].

Cichlid visual sensitivities have been measured by micro-spectrophotometry which quantifies the absorption properties and peak sensitivities of visual pigments (reviewed in [71]) Cichlid species differ significantly in visual sensitivities, sometimes between closely related species. These differences result from variation in both opsin sequence and opsin gene expression. Cichlids, of the clear Lakes Tanganyika and Malawi, that inhabit deeper waters where the light spectrum is blue-shifted, alter the rod opsin sequence to shift their sensitivities 10 nm or more to shorter wavelengths [72]. Cone sensitivities also vary drastically between species. This is a result of cichlids having seven different cone opsin genes, but varying the subset of genes which are expressed [73]. The expressed gene set can vary through development, and it is likely that heterochronic changes in this developmental program have led to alternate gene sets being expressed in different species [74]. Recent studies have shown that differential opsin expression is genetically controlled [75]. At least one transcription factor has been identified where a deletion in its promoter changes its expression to modify opsin expression [76]. However, gene expression is also moderated through changes to the fish's light environment with subtle shifts on developmental time scales [77] or more significant shifts through evolutionary time as cichlids adapted to the light transmitted in different lakes [73].

Changes in cichlid visual sensitivity can play important roles in cichlid behavior and even drive speciation. In Lake Victoria cichlids, where waters are murky, the long wavelength sensitive cone opsin gene differs between two sympatric species that occupy shallow versus deeper habitats. This sequence variation causes 5–15 nm spectral shifts and is under selection [78]. It contributes to cichlid speciation in both rock and sand dwellers in Lake Victoria [79,80]. This is the result of a red shifting of the down welling light that favors the longer wavelength LWS allele at depth. Females with this longer wavelength sensitivity prefer to mate with redder males at depth. Conversely, shallower females with the shorter

wavelength allele prefer to mate with blue males closer to the surface [79]. So the gradient in light environment leads to visual sensitivity differences that select for alternate male signals leading to species divergence.

The lens of the cichlid eye can also moderate visual sensitivities by limiting which wavelengths of light reach the retina. Studies have found that cichlid lenses can absorb or transmit UV light. Species that have UV sensitive cones maintain a UV transparent lens, while species that have lost UV sensitivity often have a UV blocking lens [77]. Cichlids are also well known for their multifocal length lenses that ensure that light across the spectrum is carefully focused on to the retina [81**]. These spectral properties depend on the light-rearing environment [82].

Cichlids also show variation in non-visual light sensitivity. Recent work suggests that cones can produce a strong input to the circadian rhythm of cichlids [83]. Cone opponency is therefore proposed to be important not only for color discrimination, but for telling the time of day. This intriguing idea needs further study across a diversity of species.

Multimodality

Multimodal communication is important because receivers benefit from assessing multiple sensory inputs versus just a single modality. In cichlids, it is unclear how different sensory modalities are integrated and processed. Visual cues may be the most important component of multimodal signals. Behavioral experiments have demonstrated that visual cues are sometimes sufficient for mate choice. However, it has also been shown that olfaction and vocalizations are useful and may even be required for correct mate choice [21,66**]. This suggests that there is a hierarchy among sensory modalities, and that cues may occur at different times or in particular orders. As shown in the ethogram (Figure 2), females first view the lek from a distance, where visual cues will be the most informative for recognizing conspecific males exhibiting nuptial coloration. Later, as males move closer, chemical and sound cues may assist female mate choice [21,84]. However, only some species are known to produce vocalizations and not all sound producing cichlids use vocalizations for courtship. In contrast, chemical cues are informative signals of individual rank and reproductive status; and chemical communication is known to be widespread in cichlid groups [41]. Thus, olfaction may be the next most important sensory modality and key for close-range encounters already initiated on the basis of visual signals. In summary, visual cues are primary for female mate recognition and preference, while other cues may provide complimentary information.

Conclusion

In this review we have described the diversity of cichlid sensory systems and their roles in cichlid behavior. Cichlids use five main channels to receive information that then trigger behavioral responses: hearing, lateral line system, olfaction, taste, and vision. There is variation within cichlid species for each of these senses, both in their sensitivities and in the behavioral ways in which they are stimulated. Examples include the extensions of the swim bladder to the inner ear, specialized lateral line modification in the canal neuromast system,

specific sex pheromones and taste buds types, and, differential gene expression of opsins, among others. Thus, different cichlid species exhibit specialized features of their sensory organs that are important for adaptation, survival, reproduction, and communication. Furthermore, sensory capabilities are important for decision-making in social behaviors including shoaling decisions, courtship, and dominant-subordinate interactions and selecting a mate. Since sensory signals are important for reproductive behavior, they may be subject to sexual selective pressures that could play roles in species divergence. Sounds used in cichlid courtship are diverse and species specific and likely the same is true for chemical cues. Visual sensitivities also differ between species and can cause speciation through sensory drive. Therefore, sound, chemical, and visual cues should be under constant selection that can maintain species boundaries, promote speciation or both. More research is needed to evaluate the potential of different sensory cues to promote speciation, and to quantify their importance in multimodal courtship. Furthermore, studies are needed to determine how other sensory channels, such as the lateral line system and taste, influence mate preference and determine where they fall in the hierarchy of mating cues. Finally, it is clear that integrative biology is necessary for understanding the role of the senses in cichlid behavior since many fields and perspectives are needed to characterize the role of the environment, as well as behavior's genetic, cellular, and neural basis. We are encouraged that much progress has been made regarding cichlid sensory biology and cichlid behavior. However, much remains unknown with regards sensory diversity between closely related species, the role of particular senses in particular behaviors, and the relative hierarchy of sensory systems in providing input to cichlid behaviors. Therefore, we hope more integrative research is still to come.

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Highlights

- Developmental stress impairs song in species with complex songs.
- Evidence for this hypothesis is mixed in domesticated songbirds.
- Experimental stressors vary in ecological validity and experimental control.
- It is unclear if song reflects early environment or developmental resilience.
- Song appears to reflect developmental trade-offs rather than phenotypic programming.

Figure 1.

Schematic representation of cichlid sensory biology. **(a)** The cichlid ear. Left: There are two types of swim bladder morphology, the vestigial and the more specialized one with extensions; Middle: the inner ear and its otolithic organs: the utricle (ult), the saccule (sac), and the lagena (lag); Right: the otolithic organ including the otolith, the otolithic membrane and the hair cells. **(b)** The cichlid lateral line. Left: a juvenile cichlid and its Supraorbital (So), Preopercular (Po), and Infraorbital (Io) neuromast canals; Middle: a neuromast unit showing sensory (brown), supporting (yellow) and mantle (blue) cells; Right: the dentary

bone morphology of *Aulonocara* sp. and *Tramitichromis* sp. showing differences in canal diameter. Dentary bone illustrations were reproduced from photographs in Schwalbe and Webb, 2014 [22]. **(c)** The cichlid nose. Left: The nares connecting to the environment; Middle: the Rosette; Right: the olfactory epithelium with the three types of olfactory sensory neurons: ciliated (ci), microvillar (mv), and crypt (cr) neurons. **(d)** The cichlid eye. Left: Light would enter from the left and pass through the cornea, pupil, large spherical lens (ls), vitreous humour and be detected by the retina (re) which is backed by the retinal pigment epithelium; Middle: retina organization from the side showing single cones (purple), double cones (green), and rods (blue); Right: retinal mosaic of cones. **(e)** Cichlid taste buds. Three types of taste buds (TBs) with sensory (yellow), supporting (orange) and basal (violet) cells.

Figure 2.

Behaviors associated with multimodal courtship in cichlids. We show an ethogram for the Malawi species *Metriacrima zebra*. (a) Females swim freely above the lek and view males on their territories. Females may first use visual cues to detect conspecifics or dominant individuals looking for their pigmentation color patterns. (b) Males approach the females to attract them to their territory. Males may also use visual cues to select which females to approach. (c) Males extend their fins and display in front of the females, quivering their fins and body. (d) Males produce vocalizations toward the female which may be coincident with (c). (e) Males extend their fins and display in front of the females, quivering their fins and body. (f) Males produce vocalizations toward the female which may be coincident with (e).

their quivering. **(e)** Males exhibit several urine pulses in the presence of females for stimulate eggs maturation and for indicating his social reproductive status. **(f)** Males quiver close to the female potentially stimulating superficial neuromasts of the lateral line. Courtship behavior may vary among cichlids being present in some species and absent in others. In some cichlid species quivering, vocalization and urine pulses from the males may occur simultaneously.

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