Adaptive shift of active electroreception in weakly electric fish for troglobitic life

Daphne Soares[1]*, Kathryn Gallman[1], Maria Elina Bichuette[2] and Eric S. Fortune[1]

[1]Biological Sciences, New Jersey Institute of Technology, Newark, NJ, United States, [2]Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, São Carlos, Brazil

The adaptive-shift hypothesis for the evolution of cave-dwelling species posits that ancestor species in surface habitats had exaptations for subterranean life that were exploited when individuals invaded caves. Weakly electric Gymnotiform fishes, nocturnal South American teleost fishes, have features that appear to be likely exaptations for troglobitic life. These fishes have active electrosensory systems in which fish generate weak electric fields that are detected by specialized electroreceptors. Gymnotiform fishes use their electric fields for navigation, prey capture (scene analysis), and social communication. Although active electrosensory systems appear to be exaptations for troglobitic life, as fish use these systems to "see in the dark", producing electric fields is energetically costly. Cave habitats, which often are low in resources, may not be able to support such high energetic demands. *Eigenmannia vicentespelaea*, a species of weakly electric fish that is endemic to the São Vicente II cave in central Brazil, surprisingly generates stronger electric fields than their surface relatives. The increase in strength of electric fields may result simply from differences in size between cave and surface populations, but may also be due to lack of predation pressure in the cave or increases in "sensory volumes" and acuity that improve prey localization and capture. *Eigenmannia vicentespelaea* exhibits the classical phenotypes of any troglobitic fish: these fish have small to nonexistent eyes and loss of pigmentation. The closest living surface relative, *Eigenmannia trilineata*, inhabits streams nearby and has eyes and pigmentation. The electrosensory and locomotor behavior of both species of fish were measured in their natural habitats using a grid recording system. Surface *Eigenmannia* exhibited dramatic circadian changes in social behavior, such as hiding under rocks during the day and foraging in groups at night, while cave *Eigenmannia* displayed territorial behavior with no apparent circadian modulations. The territorial behavior involved electrical and movement-based interactions that may be a form of boundary patrolling. Electrosocial behavior and scene analysis are mechanistically interlinked because both stem from active sensing tactics.

Introduction

Darwin was once befuddled by the unusual phenotypes of cave organisms. He labeled them "*wrecks of ancient life*" and remarked "*As it is difficult to imagine that eyes, though useless, could in any way be injurious to animals living in darkness, I attribute their loss solely to disuse*" (Darwin, 1859). *Absit omen*, we disagree with Darwin – we would like to contend that cave animals are not a wreck, but simply elegant phenotypes that evolved to retain the most important aspects of life. Troglobites feature unusual and idiosyncratic morphologies that arise from a life history adapted to perpetually dark habitats. They brandish regressive features, such as the loss of eyes and pigmentation, as well as compensatory traits, such as a lower threshold for mechanosensation (Culver et al., 1995; Culver and Pipan, 2009; Haspel et al., 2012; Soares and Niemiller, 2013; Niemiller and Soares, 2015; Soares and Niemiller, 2020).

Cave organisms are recognized as unique model systems for testing evolutionary, ecological, and biogeographic hypotheses (Poulson and White, 1969; Jeffery, 2009; Juan and Emerson, 2010; Juan et al., 2010) and are promising systems to increase our understanding of evolutionary and historical processes that promote or constrain biodiversity (Juan et al., 2010). Despite increased interest and study of troglobites in recent years, subterranean biodiversity remains one of the most poorly understood faunas on the planet. Fishes are routinely prominent members of aquatic cave communities, and currently, over 300 species in 10 orders and 22 families (Proudlove, 2010: Soares and Niemiller, 2013) have been identified. Here we review intriguing electrosocial features of a species of weakly electric fish, *Eigenmannia vicentespelaea*, which evolved in a single cave system in central Brazil (Figure 1) and that is yet to be thoroughly studied (Bichuette and Trajano, 2006; Bichuette and Trajano, 2017; Fortune et al., 2020).

Speciation in cavefishes

There are two contrasting hypotheses for the speciation of subterranean fishes: the *climate-relict* hypothesis (Holsinger, 1988; Peck and Finston, 1993; Holsinger, 2000) and the *adaptive-shift* hypothesis (Howarth, 1973; Howarth, 1981; Holsinger, 2000; Niemiller and Soares, 2015). The climate-relict hypothesis suggests that surface ancestors retreated into subterranean habitats in response to climate fluctuations. As surface conditions became more inhospitable, extirpation of surface populations promoted allopatric speciation. In contrast, the adaptive-shift hypothesis suggests that surface ancestors with exaptations to subterranean life (e.g., a nocturnal lifestyle) exploited new subterranean niches that offer reduced competition and quickly evolved in parapatry or sympatry with related surface populations (Juan et al., 2010; Niemiller and Soares, 2015). A key distinction between the climate relict and the adaptive shift hypotheses is whether divergence occurs in the absence (allopatric) or presence (parapatric or sympatric) of gene flow (Niemiller et al., 2008). In both hypotheses, cavefish species are derived from ancestral populations from the surface, whether the original population is extinct or not.

Weakly electric fishes and the adaptive shift hypothesis

Weakly electric fishes have a suite of features that appear to be obvious exaptations for troglobitic life. Most species of weakly electric fishes are nocturnal, and many live in turbid waters. While in the absence of visual cues, weakly electric fishes use electrosensory feedback from self-generated electric fields in social communication, navigation, predator avoidance, and prey capture (Heiligenberg, 1991; Caputi and Budelli, 2006; Skeels et al., 2023). Such active electrosensory systems are considered to be adaptations for nocturnal lifestyles, and thus may be an exaptation for troglobitic habitats.

Specifically, weakly electric fishes have evolved specialized electric organs for the generation of electric fields in the water and have evolved corresponding electrosensory receptors that detect these fields (Hopkins, 1988; Heiligenberg, 1991; Caputi and

FIGURE 1
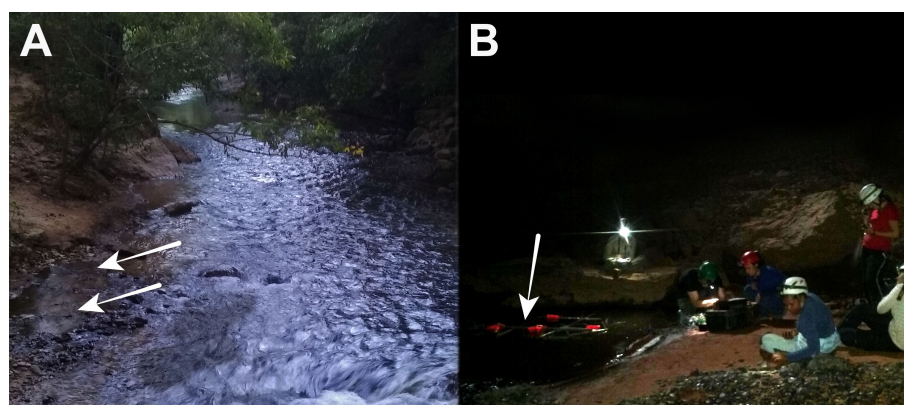Habitats are composed of faster-moving rivers with quiet eddies and pools. **(A)** Surface habitat outside cave Rio de Lapa. Arrows point at the location where *Eigenmannia triliniata* were found and recorded in Fortune et al. (2020). **(B)** Cave Sao Vicente II where *Eigenmannia vicentespelaea* are endemic. Arrows show the recording rig: red floating inflatables maintained the position of the grid in the pool.

Budelli, 2006; Crampton, 2019). In most species, the electric organ is composed of modified epaxial muscle cells, but some species rely on modified spinal axons for the generation of electric fields (Caputi and Budelli, 2006; Shifman et al., 2015; Crampton, 2019; LaPotin et al., 2022). These organs produce transient potential differences between the outside and inside of the fish (Babineau et al., 2006). These potential differences are detected by specialized electroreceptors that have lower resistances than the surrounding skin (Zakon, 1988; Gallant, 2019). Most of the electric current flows across these receptors, which are densely packed in the head of the fish (Heiligenberg and Bastian, 1984; Hopkins, 1988; Zakon, 1988; Nelson and Maciver, 1999). Two categories of signals modulate the flow of current across an individual's electroreceptors: differences in the local resistance near the fish and the electric fields produced by nearby conspecifics and other organisms (Yu et al., 2012).

The electric fields generated by these fishes are affected by local differences in resistance in the surrounding water (Von der Emde, 1999). vzsavcwbcvSuch local differences can be caused by, for example, the presence of rocks (higher resistance) or other organisms (generally lower resistance) (Fotowat et al., 2013). These differences in resistance affect the flow of current through and voltages occurring at an individual's electroreceptors, which are encoded by changes in neurophysiological activity (Assad, 1997; Rose, 2004; Fukutomi and Carlson, 2020). In this way, this active electric sense provides a sensory channel for the control of a wide range of behaviors in which the organism interacts with its surroundings (von der Emde, 2006). Indeed, an elegant set of experiments demonstrated how a species of weakly electric fish, Apteronotus albifrons, uses its electrosensory system to capture prey in the absence of visual cues (Bastian, 1981; Nelson and Maciver, 1999; MacIver et al., 2001).

Although these fishes use electric fields to detect nearby objects, evidence from catfish are nevertheless consistent with the hypothesis that the generation of weak electric fields evolved in the context of social signaling (Baron et al, 1994; Orlov et al, 2021). Weakly electric fishes detect the electric fields of nearby conspecifics (Heiligenberg, 1991) and the active electric sense is an important channel for social communication between conspecifics (Henninger, 2015; Caputi, 2017; Crampton, 2019). The ancestors of weakly electric fishes had a category of electroreceptors known as ampullary receptors, which detect low-frequency electric signals in the water. Ampullary receptors can detect, for example, the currents released by muscles that move the operculum (Bodznick and Montgomery, 2005; Grewe et al., 2011), or by the movements of prey items (MacIver et al., 2001).

Variations in muscle cell size (Zakon, 2012), morphology (Mills et al., 1992; Zakon, 1995; Gallant, 2011), and ion channels (Zakon et al., 2006; Gallant et al., 2014; Swapna et al., 2018) in the ancestors of weakly electric fishes may have resulted in increased leakage of current into the water. This increase in current leakage may have made those individuals easier to detect by electroreceptive conspecifics in dark or muddy water, therefore potentially leading to increased reproductive success. Findings from Clarias gariepinus catfish, which generate rudimentary electric fields during social encounters (Baron et al, 1994; Orlov et al, 2021), are consistent with this hypothesis.

The costs of producing electric fields

This ability to "see in the dark" using self-generated electric fields, however, comes at a cost. The generation of electric fields in water is energetically expensive, consuming up to 30% of an individual's energy budget (Salazar et al., 2013; Markham et al., 2016). This budget includes the cost of producing the electric field, which involves the cycling of sodium and potassium across cell membranes of electrolytes that comprise the electric organ and the activity of brain areas that both detect the electric fields and control behavioral responses to them.

Another potential cost of generating electric fields is the increased risk of predation by electroreceptive predators. Ampullary electroreceptors are found on many species of fishes that may be predators of weakly electric fishes, including catfish and electric eels. When weakly electric fish produce signals with power at low frequencies, e.g., below about 100 Hz, they may reveal themselves to fish with ampullary electroreceptors. Indeed, electric signals containing low-frequency components that are preferentially detected by ampullary receptors were shown to be more salient to an electric eel than electric signals without these low-frequency components (Electrophorus electricus; Stoddard, 1999; Stoddard, 2002).

Electroreceptive predators of weakly electric fishes appear to be overrepresented in the catfish group (Stoddard, 1999). Pimelodidae, a family of piscivorous catfishes, regularly prey upon weakly electric gymnotiform fishes (Reid, 1983; Duque and Winemiller, 2003; Petrere et al., 2004) in South America and the African sharptooth catfish, Clarias gariepinus has been described as a predator of mormyrid weakly electric fishes (Merron, 1993).

Weakly electric cavefish

Eigenmannia vicentespelaea from central Brazil is the only known species of gymnotiform weakly electric fish that show complete troglomorphy. The closest epigean species, Eigenmannia trilineata, is found in the same watershed (Bichuette and Trajano, 2006). The cavefish show regression of eyes and loss of pigmentation (Bichuette and Trajano, 2006), while surface fish are pigmented and have functioning eyes (Figure 2). Nevertheless, the surface fish Eigenmannia trilineata and other species of Eigenmannia have been observed to be nocturnal (Tan et al., 2005). Eigenmannia hide in roots, rocks, and leaf litter during the day and actively forage at night (Hopkins, 1974; Hopkins, 1981; Deng and Tseng, 2000; Tan et al., 2005; Stamper et al., 2010; Fortune et al., 2020; Gouveia et al., 2022)

We traveled to the São Vicente II cave and measured the electrosensory and locomotor behavior of both surface Eigenmannia trilineata and cave Eigenmannia vicentespelaea (Fortune et al., 2020). We used a custom array of amplified electrodes, 50cm spacing, that both captured the electric behavior of nearby fish, and allowed us to calculate the positions of these fish (Madhav et al., 2018). These grid recording systems have allowed unprecedented insights into the behaviors of weakly electric fishes in their natural habitats (Raab et al., 2019; Henninger et al., 2020).
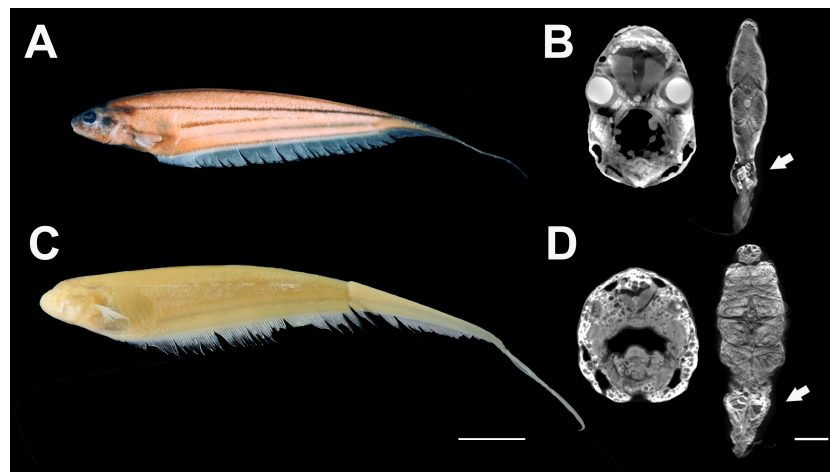
FIGURE 2
Anatomical differences between ancestral surface and derived cave *Eigenmannia*. **(A)** *Eigenmannia trilineata* collected in Rio da Lapa. **(B)** DICEuCT scan through the head and mid-body of *Eigenmannia trilineata*. Note the larger eyes of the surface fish. The arrow points to the electric organ. **(C)** *Eigenmannia vicentespelaea* specimen collected in the cave of Sao Vicente II. **(D)** DICEuCT scan through the head and mid-body of *Eigenmannia vicentespelaea*. Note small and vestigial eyes and larger electric organs (arrows). Scale bars 10 mm and 2 mm.

Effects of troglobitic conditions on the amplitudes of cavefish electric fields

Generating electric fields is energetically costly, consuming up to 30% of an individual weakly electric fish's energy budget (Salazar et al., 2013; Markham et al., 2016). Therefore, if a cave environment is poor in resources, one might expect that weakly electric cavefish might produce lower-amplitude electric fields. Indeed, non-electric species of cavefish have adaptations related to the scarcity of resources (Fišer, 2019). On the other hand, active electrosensation permits weakly electric fishes to image their environment (von der Emde, 2004) and capture prey in darkness (MacIver et al., 2001) and therefore might serve as an exaptation for increasing access to food in cave habitats.

We measured the amplitudes of the electric fields (technical details for these measurements are described in Madhav et al., 2018) produced by the weakly electric cavefish in the São Vicente II cave and of surface fish in the nearby Terra Ronca stream (Figure 1). We were surprised to find that the cavefish produced significantly higher amplitude electric fields (Fortune et al., 2020) compared to their closest living surface ancestors (Figure 3). These more powerful electric fields are likely to be energetically costly, but likely provide benefits to the fish. Stronger electric fields may increase the volume of water around the fish in which it can detect objects including prey – known as the "sensing volume" (MacIver et al., 2001; Snyder et al., 2007). A larger sensing volume increases the likelihood of detecting and capturing nearby prey items. Further, stronger electric fields could potentially result in greater spatial acuity and sensitivity.

We currently do not know the mechanism for the increase in amplitudes seen in the cavefish. The increase in amplitudes may simply result from size differences between the cave and surface populations of *Eigenmannia*: larger fish have larger electric organs, resulting in stronger electric fields. Our impression is that the population of adult cavefish we observed was generally larger than the population of adult surface fish. Other mechanisms that might contribute to increased electric field amplitudes of cave *Eigenmannia* include adaptations of the electric organ, including increases in the relative size of the electric organ in relation to body size, changes in the density or structure of electrocyte ion channels, and/or changes in other structural or resistive features in the skin.

Interestingly, pressure from potentially electroreceptive predators may limit the sizes of surface fish and may also lead to a reduction in the strength of their electric fields. We observed evidence of predation in the surface *Eigenmannia* population, with several adults having obvious morphological signs of regrowth of their tails (Figure 4). Loss of the tail and its regrowth has been considered evidence of predatory attacks (Dunlap et al., 2016). Our conclusion is that surface
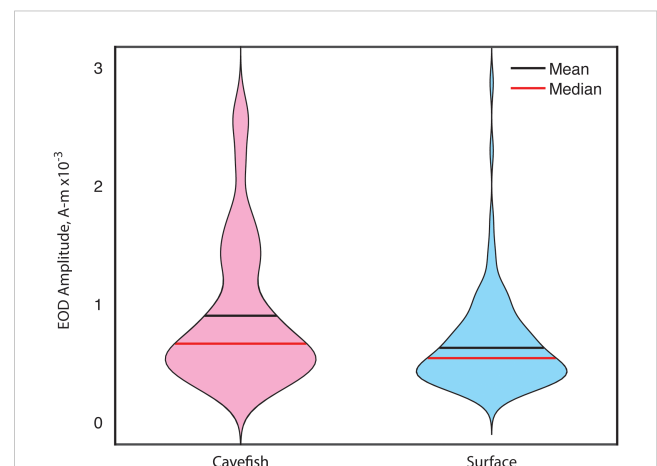

FIGURE 3
A comparison of *Eigenmannia* EOD amplitudes from both habitats shows an increase in the median and mean amplitude in the cavefish (RED line). Also note greater numbers of the strongest EODs in cavefish.

FIGURE 4
Surface *Eigenmannia* showing predation and regrowth of tail. Notice the lack of black stripe and thickness change starting at the outlining box. Image was taken from a video recording in the field (Fortune et al., 2020).

Eigenmannia may face significant predation pressure, supporting the adaptive-shift hypothesis for the emergence of cave populations. If so, the relative increase in the electric field amplitudes of the cavefish might result from a release from predation pressure.

Finally, the area in which Sao Vicente II cave is located has been classified as rupestrian grassland (Barbosa and Fernandes, 2016). This region was not frozen during the last glacial maximum (~21,000 years ago) and in the middle Holocene (~6,000 years ago), making the climate-relict hypothesis an unlikely explanation of the emergence of cave *Eigenmannia*.

Effects of troglobitic conditions on circadian patterns of social behavior

Surface *Eigenmannia* exhibit overt diurnal behavioral cycles. During daylight hours, fish exhibit refuge-seeking behavior, hiding in crevices between rocks and root systems. While hiding during the day, surface *Eigenmannia* are most commonly found in aggregates of several fish (Tan et al., 2005; Fortune et al., 2020). During night

hours, surface *Eigenmannia* emerge from their refugia to forage and perform other behaviors. Videos recorded at night of surface *Eigenmannia* in the streams outside the Terra Ronca cave show the fish foraging in groups (Supplemental material, Fortune et al., 2020). These video data corroborate the grid tracking data, which shows groups of several fish swimming near each other at night (Fortune et al., 2020). Most surface *Eigenmannia* were found in groups, and do not appear to maintain territories at any time during 24-hour diurnal cycles (Tan et al., 2005; Fortune et al., 2020).

Unlike surface *Eigenmannia*, the cave *Eigenmannia* appeared to occupy territories 24 hours a day. Cave *Eigenmannia* appeared to perform boundary patrolling behavior on the perimeter of an area of about a square meter (mean = 1.16 sq m, std = 0.76, n = 274). Videos of cave *Eigenmannia* in the São Vicente II karst show the fish engaging in mouth-to-mount conflicts in which both fish swim toward each other (Supplemental material, Fortune et al., 2020), which may be aggressive interactions between individuals defending their territories. We also observed chases between cavefish in the grid recordings in which the retreating fish produced a long frequency rise of its electric frequency (a rise of typically more than 5 Hz over a period on the order of 10s of seconds). In these interactions, the chasing fish did not change its electric frequency, but the retreating fish initiated a long frequency rise seconds before the fish were at their closest during the interaction (Figure 5). The chasing fish followed the retreating fish for about 10 seconds, at which time the retreating fish began to return its electric field to its normal frequency.

Discussion

Eye sizes in *Eigenmannia vicentespelaea*

Eye loss is a trait that is associated with troglomorphy. In all animals studied so far, eyes develop normally in embryonic stages, but eventually the lens undergoes cell death which signals the eyes
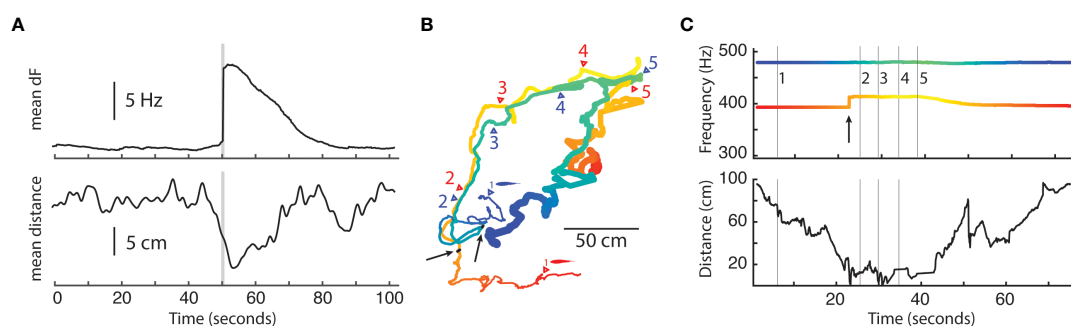

FIGURE 5
Potential boundary patrolling in *Eigenmannia vicentespelaea* (data from Fortune et al., 2020). **(A)** Top panel shows the mean difference (n = 208 events) in electric field frequencies (Hz) between pairs of fish, centered in time on the start of a long-frequency rise produced by one fish in the pair (grey vertical line). Bottom panel shows the average distance between the pairs of fish. Frequency rises were produced as fish approached each other, about 5 seconds before their closest distance. **(B)** Spatial map of the XY positions of two fish during a possible boundary patrolling event (blue fish). Colors of the lines correspond to **(C)**, and the line is thinnest at the start of the epoch and thickest at the end. Numbers correspond to time points shown in **(C)** Black dots with arrows indicate the locations of both fish at the initiation of the frequency rise produced by the red fish. **(C)** Top panel shows the frequencies of both fish over time and bottom panel shows the distance between the fish. In this event, the red fish moved closer to the blue fish. At the moment of the frequency rise produced by the red fish, the blue fish changed direction and rapidly followed the red fish over a distance of well over 2 meters in a period of about 20 seconds. After the event, the blue fish returned to near its original position.

to arrest growth, leading to small eyes sunken into the orbits (Rétaux and Casane, 2013). Interestingly, this mechanism leads to the regression of both eyes. *Eigenmannia vicentespelaea* exhibits a diversity of eye sizes (Bichuette and Trajano, 2006). These include extreme individuals with a full eye on one side and a completely degenerated eye on the other. This suggests that there might be other evolutionary mechanisms at play in eye degeneration in *Eigenmannia vicentespelaea*.

Amplitudes of electric fields

The amplitudes of electric fields increase with the size of fish (Hopkins et al., 1990; Curtis and Stoddard, 2003; Gavassa et al., 2012) and can be used as a nonvisual proxy to estimate body size. However, Gavassa et al. (2013) have shown that social interactions can drive significant changes in the amplitude of electric fields. Further, hormones can increase the amplitudes of electric fields (Markham et al., 2009a; Migliaro and Silva, 2016). We already know that on average, the size of the EOD is larger in the cavefish, the next steps will include correlating them to the size of the fish. For example, we predict that the slope of the relationship between size and electric field amplitude will be steeper in the cavefish in comparison to the surface fish. Such differences would indicate active adaptations rather than simply size effects.

Territoriality in caves

Cave *Eigenmannia vicentespelaea* show boundary patrolling, a form of territorial behavior absent in surface *Eigenmannia*. Territoriality can provide insights into how fish integrate social and environmental cues to produce behavioral responses. There is a cost-benefit in territorial defense, whether from breeding or resource defense (Kaufmann, 1983; Adams, 2001; Christensen and Radford, 2018). Territorial defense is usually associated with breeding males seasonally, but year-round territoriality can establish access to foraging areas or protection from predators (Silva et al., 2020).

A good example of weakly electric fish territorial behavior is shown by the *Gymnotus omarorum*. These fish have territory ranges that are independent of sex but are directly correlated to body size (Silva et al., 2020). During the breeding season, however, Silva et al., 2020 showed that *Gymnotus omarorum* establishes territories, which sizes are correlated to with gonadosomatic index in females and 11-ketotestosterone levels in males. We are interested in the roles of hormones in both regions of the body of the *Eigenmannia vicentespelaea* and *trilineata* populations. It will be interesting if expression differences are correlated with a cave habitat and what are the evolutionary forces driving it.

Social behavior and circadian rhythms

Vertebrate circadian behaviors are based on networks of endogenous clocks across tissues throughout the body of the fish that are synchronized to one another by a master circadian clock in the brain (Ripperger and Schibler, 2001). Master clocks guide physiology and behavior via neural and hormonal cues (Ripperger and Schibler, 2001; Patke et al., 2020).

We know that strongly defined cycles caused by inputs such as light, temperature, and other biological influences such as predation, can synchronize the intrinsic internal clock generated by cryptochrome gene expression. Ripperger and Schibler (2001) demonstrated that the endogenous timekeeping system created by the interaction of these genes can be synchronized by diverse types of zeitgebers (time-givers in German) (Takahashi, 1991; Wilsbacher and Takahashi, 1998).

Surface *Eigenmannia* modulates the amplitude of their wave-type electric organ discharges (EOD) in relation to the light/dark cycle, with greater EOD amplitude at night when these nocturnal animals are more active and a lower EOD amplitude during the day when fish are hidden within refugia (Deng and Tseng, 2000; Markham et al., 2009b; Sinnett and Markham, 2015). In *Brachyhypopomus pinnicaudatus*, a pulse-type weakly electric fish, pulse rate, pulse amplitude, and tau_{P2} – the time constant of recovery for the second phase of the pulse waveform, all increased during the subjective night. These circadian rhythms in electric field waveform were even more pronounced under breeding conditions, suggesting a social context (Silva et al., 2007). Similar to the results we report for surface *Eigenmannia*, *B. pinnicaudatus* EOD rhythms were stronger under photo entrained (12 hours of dark:12 hours of light) conditions than under free-running, or constant photic conditions (Stoddard et al., 2007).

Gymnotus omarorum is another pulse-type weakly electric fish with a circadian pattern in electric field pulse rate. These fish live in such dense vegetation in their natural habitat, that they experience no diurnal variation in photic cues, similar to the cave conditions. Because circadian changes in EOD pulse rate persist in *G. omarorum* when measured in the field along with daily fluctuations in temperature it is postulated that daily temperature fluctuations driven by the sun heating the water during the day, act as the primary zeitgeber in these animals (Migliaro et al., 2018). Indeed, temperature variation has been shown to induce changes in the EOD pulse rate in *B. pinnicaudatus* (Silva et al., 2007).

Study details

The data shown in this review were collected for a previous publication (Fortune et al., 2020). A detailed description of the materials and methods can be found there. In short, the procedures used for these observational studies of Gymnotiform fishes were reviewed and approved by the animal care and use committee of Rutgers University/New Jersey Institute of Technology (Protocol #999900774) and follow guidelines for the use of animals in field research established by the National Research Council. Field research permits in Brazil were granted by the ICMBio and SEMARH/SECIMA.

Study sites

Both species of fish are endemic to the upper Tocantis river basin in the state of Goias, central Brazil (46° 10′–46° 30′ S, 13° 30′–13° 50′ W). The cavefish *Eigenmannia vicentespelaea* population is

located in the cave of São Vicente II (13° 58′37″ S, 46° 40′04″ W), while *Eigenmannia trilineata* population is found in the Rio da Lapa (13° 38′44″ S, 46° 38′ 08″ W) approximately 8 km away. Both habitats have moderate water currents, clear water with a conductivity below 20 µS, and substrate composed of sand, rocks, and boulders (Fortune et al., 2020).

Anatomy

We chose to use Diffusible Iodine-based Contrast-enhanced Computed micro-Tomography (DICEuCT) because it permits visualization of soft tissue details without damage to the specimens. We imaged four previously collected specimens from Dr. Bichuette's laboratory collection at the Universidade Federal de São Carlos, Brazil. Briefly, we submerged 70% ethanol fixed specimens in 11.25 Lugol's iodine (I2KI) solution for up to 36 h before scanning. Stained specimens were washed in water to remove excess stain and sealed in rubber containers to prevent dehydration. Stained and unstained specimens were scanned at the Core Imaging Facility of the American Museum of Natural History (New York, NY), using a 2010 GE Phoenix v|tome|x s240CT high-resolution microfocus computed tomography system (General Electric, Fairfield, CT, USA) in 50 mL polypropylene centrifuge tubes. DScans were made at 125 kV, with an exposure time of 60 seconds. Voxel sizes were 20.0–25.9 µm and volume reconstruction of raw X-ray images was achieved using a GE Phoenix datos|x.

Recordings of electric behavior and movement at field sites

We used a hand-held single-electrode probe attached to a custom amplifier and speaker to find the fish. When the probe was within about 1 meter of an *Eigenmannia*, its electric field was audible to the user. Also, we were also able to see the animals directly due to the clarity of the water. To record the electric behavior and movement of *Eigenmannia*, we deployed a grid (50 cm spacing) of active electrodes (Madhav et al., 2018; Fortune et al., 2020) at sites where we had previously observed fish. The surface fish were recorded along the edges of the Rio da Lapa outside of the Terra Ronca cave after sundown. The cavefish were recorded in eddies and side pools of the primary river within the São Vicente II cave.

We used an algorithm developed by Madhav et al. (2018; code available at doi:10.7281/T1/XTSKOW) to identify each fish via the time-varying fundamental frequency of its electric field. The locations and orientations of each individual were calculated in relation to the distribution of power at each electric field frequency across the electrodes. These recordings were made in shallow water of no more than 40 cm depth: position estimates were restricted to the XY plane. Continuous recording sessions using the grid were made both in the cave (N = 14) and surface (N = 5). Intervals between recording sessions ranged from 5 min to several hours and each recording was from 600 seconds to over 1,200 seconds in duration. The position and electric field frequency data were analyzed in 300 s duration non-overlapping epochs. Other details of the recording procedures and analysis can be found in Fortune et al. (2020).

Perspectives

Our future studies include the identification of the causal evolutionary interactions between categories of behavior: scene analysis and social behavior.

Ethics statement

Written informed consent was obtained from the individuals for the publication of any identifiable images or data included in this article.

Author contributions

MB, DS, and EF contributed to the conception and design of the study. DS, KG, and EF wrote the first draft of the manuscript. All authors contributed to the writing and revision of the manuscript and have read and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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