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Can you hear the dinner bell? Response of cyprinid fishes to environmental acoustic cues

Daniel E. Holt*, Carol E. Johnston

Department of Fisheries and Allied Aquacultures, Auburn University

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Fishes in the superorder Ostariophysi have excellent hearing due to the presence of a synapomorphic hearing specialization called the Weberian apparatus. This structure connects the swim bladder to the inner ear, and increases both sensitivity and upper hearing range. Although numerous experiments have tested the effects of the Weberian apparatus on hearing, few have provided potential evidence for a current adaptive function for the specialization. We conducted a field-based experiment in which a rock shuffling noise and a white noise were played simultaneously from adjacent speakers in a clear, mountain stream in the southern Appalachian Mountains, U.S.A. Our results indicate that species of Cyprinidae, a family within Ostariophysi, were attracted more to rock shuffling noise than to the white noise. This study provides the first evidence that a broadband environmental sound associated with a potential food source is utilized by a potentially large number of species possessing a hearing specialization.

The success or failure of any organism is often closely linked with its ability to detect and interpret signals or cues within its environment. Signals may come in a variety of modalities, and it may benefit an organism to be highly tuned to signals that offer increased survival or reproductive opportunity. Predators, parasites and parasitoids may benefit greatly by eavesdropping on acoustic cues produced by prey items. Female tachinid flies (*Ormia ochracea*), for example, are attracted to the song of the field cricket *Gryllus integer* (Cade 1975). The flies use the cricket as a host and lay their larvae on the body of the cricket. The larvae then burrow through the cricket's exoskeleton and develop inside. Numerous species of blood-sucking flies of the genus *Corethrella* have also been shown to parasitize the túngara frog, *Physalaemus pustulosus*. The flies are able to locate the frogs by the acoustic signals alone, which are produced by males to attract females during the breeding season (Bernal et al. 2006). The flies land on the frogs, move to the nostrils, and obtain a blood meal. Similarly, the fringe-lipped bat, *Trachops cirrhosus*, takes advantage of the acoustic cues produced by calling frogs, including the túngara frog (Tuttle & Ryan 1981). *Trachops cirrhosus* is not only able to locate prey, but can also distinguish between poisonous and palatable species, as well as identify species that are too large for capture, all from the acoustic signals of the frogs.

Despite the ability to echolocate, some bat species passively listen for prey. The rustling sound associated with prey locomotion over a noisy surface is an acoustic cue used for prey detection in several bat species, including the Indian false vampire bat, *Megaderma lyra* (Marimuthu & Neuweiler 1987), African heart-nosed bat, *Cardioderma cor* (Ryan & Tuttle 1987), and the mouse-eared bat, *Myotis myotis* (Arlettaz et al. 2001). A prey item hidden among a cluttered background, such as leaf litter or under a bush, inhibits detection using echolocation. These bats therefore passively listen to prey-generated sounds produced during locomotion in order to locate prey. Similar use of indirect cues produced by prey items have also been documented in other taxa including owls (Payne 1971) and primates (Siemers et al. 2007). Some marine mammals may also use passive listening for prey detection. Barrett-Lennard et al. (1996) reported personal observations of attacks by transient killer whales, *Orcincus orca*, on Dall's porpoises, *Phocoenoides dalli*, without the use of echolocation or visual cues. These authors proposed that the whales were using the surfacing and

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* Correspondence: D. E. Holt, Department of Fisheries and Allied Aquacultures, 203B Swingle Hall, Auburn University, Auburn, AL 36849, U.S.A.
E-mail address: danholt05@gmail.com (D. E. Holt).

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breathing sounds of Dall's porpoises, which were reported to be detectable by onboard recording equipment up to 25 m away.

Members of the second-largest superorder of fishes, Ostariophysi, possess a hearing specialization involving a connection between the gas bladder and the inner ear called the Weberian apparatus. This series of ossicles allows for greater hearing sensitivity and high-frequency range (Popper & Fay 2010). Interestingly, there has been little explanation as to why this widespread hearing specialization evolved in ostariophysians, although several proposals have been put forth. It is unlikely that it evolved to optimize acoustic communication since both vocal and nonvocal ostariophysians have similar hearing abilities, and a clear correlation between hearing sensitivity and sound spectra in vocal species does not exist (Ladich 1999). It is almost certain that high sensitivity evolved in quiet areas, as suggested by Ladich (1999), because masking would probably have negated any benefit of high sensitivity in a noisy environment. However, the question remains, what do these fishes listen to that requires such good hearing? There is evidence that greater hearing sensitivity may increase the chance of escape from predators via Mauthner-mediated escape behaviour (Canfield & Eaton 1990; Canfield & Rose 1996). Furthermore, Markl (1972) observed that piranhas attacked splashing prey more often than silent prey, suggesting that sensitive hearing may also help predators find prey.

Our objective was to investigate the potential use of sensitive hearing in fishes for acoustic feeding cues. Using species of Cyprinidae, a large family within Ostariophysi, we investigated whether these fishes are attracted to sounds associated with potential food sources. When a rocky substrate is disturbed, benthic invertebrates are often dislodged or brought to the surface and become readily accessible prey items for many cyprinids. The disruption is also associated with very broadband noises (0.005–22 kHz), whose higher frequencies may be detected by cyprinids at greater distances than fish without a hearing specialization. Sounds below the cutoff frequency, which is defined mainly by water depth and substrate composition, attenuate very rapidly away from the source (Rogers & Cox 1988). Under certain circumstances, using the higher-frequency components of the noise as an early cue for a potential food source may provide cyprinids with an advantage over fishes without hearing specializations. This may be evidence for a contemporary adaptive function of the Weberian apparatus.

METHODS

Rock shuffling noise was recorded onto a Marantz PMD 661 digital recorder (sampling rate = 44 100 Hz) by placing a hydrophone (Hi-Tech HTI-96-MIN; sensitivity: 164.4 re. 1 V/μPa) directly next to a researcher's hand while the researcher disturbed substrate composed predominantly of cobble (64–256 mm) and gravel (2–64 mm), based on a modified Wentworth particle size scale (Allan 1995). White noise (band limited 0.05–11 kHz) was obtained from the example sounds provided by Raven 1.4 (Cornell University, Ithaca, NY, U.S.A.). The root mean square (RMS) amplitude of white noise was matched to that of the shuffling noise. An MP3 file was then generated with shuffling noise and white noise on the left and right channels, respectively, and was saved to a micro SD card. Amplifier gain was then adjusted so that the playback level of shuffling noise was identical to the original recording's level at the same distance. Both sounds were 52 s in duration and were played on a loop during experimental trials.

Two underwater speakers (University Sound UW-30, Oklahoma City, OK, U.S.A.) were mounted on PVC frames, each with an attached underwater camera (Aqua-Vu ZT 60, Nature Vision Inc., Brainerd, MN, U.S.A) that viewed the space in front of the speaker. Sounds were played from a Blackberry curve 8520, and amplified by a Pioneer GM-X372 240W amplifier. Video was recorded onto SD cards in two mini digital video recorders (Super Circuits, MDVR25).

Experimental sites were all located on the Tellico River in Cherokee National Forest (Monroe Co., TN, U.S.A., 35.32147°N, 84.16752°W), and experiments were conducted between 25 September and 3 October 2010. We made an effort to select sites with similar conditions, and we took habitat measurements, including temperature, turbidity, depth, flow and substrate composition, at each site after all experiments had been run. Temperature and turbidity were recorded only once at each site, while five point measurements for the other parameters were taken around each speaker. For each trial, the speaker/camera pods were placed approximately 2 m apart in the river. Because of the disturbance caused by setting the pods up, a 15 min acclimation period was given before each trial began. Each trial lasted a total of 25 min, and the order that different sounds were played to each speaker was randomized. During the first 5 min of each trial, video was recorded in the absence of any playback to obtain a baseline activity level in front of each speaker. During the second 5 min period, shuffling noise was played through one of the speakers and white noise was played through the other (see Fig. 1). After this, a 10 min silent period was given, during which time the speaker channels were switched. During the final 5 min period of the trial, the same shuffling noise and white noise were played again, but through the opposite speaker of the first playback period. This was replicated at six locations, each separated by a minimum of 30 m. Each of these six locations is referred to as a site throughout this study.

Each trial was analysed by first counting the number of fishes in the field of view of each camera at 15 s intervals. We did this by pausing the video every 15 s and counting the total number of fishes in the frame at that second. The most abundant species observed during playbacks included river chub, *Nocomis micropogon*, warpaint shiner, *Luxilus coccogenis*, saffron shiner, *Notropis rubricroceus*, largescale stoneroller, *Campostoma oligolepsis*, and northern hogsucker, *Hypentelium nigricans*. *Hypentelium nigricans* (Catostomidae) is not a cyprinid, but because it possesses a Weberian apparatus, and was seen in all trials, it was counted. For each of the six sites, we averaged all the counts at each speaker, within each period (preplayback, first playback, interval between playbacks, and second playback), giving us a single mean at each speaker, for each period, within each site. These averages were used as the data for every analysis. Analysis was performed using PASW v.18.0 (SPSS Inc., Chicago, IL, U.S.A.). A MANOVA was performed to examine differences in recruitment to the two speakers during each of the four trial periods. We hypothesized that because habitats were similar, the number of fishes present during preplayback and during the interval between playbacks would not differ between speakers. We also hypothesized that more fishes would be recruited to the speaker playing shuffling noise during the playback periods, because shuffling noise is associated with potential food sources. In this MANOVA, average recruitment in each of the four periods for each site was used as the dependent variables, and the two speakers were used as fixed factors (each site was a replicate; $N = 6$ for each speaker). The MANOVA was followed with univariate F tests with Bonferroni correction to determine which periods contributed to the main effect. We used a separate one-way ANOVA to compare recruitment to the speaker playing shuffling noise during the first and second playback periods. This ANOVA was performed to examine whether the fishes would habituate to shuffling noise over time. For this ANOVA, the dependent variable was the average recruitment during the playback period in which shuffling noise was played (for one speaker, it was the first playback period and for the other speaker, it was the second playback period), and the fixed factor was the two speakers.