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Sound Production during the Spawning Season in Cavity-Nesting Darters of the Subgenus *Catonotus* (Percidae: *Etheostoma*)

CAROL E. JOHNSTON AND DAWN L. JOHNSON

The cavity-nesting darters *Etheostoma nigripinne*, *Etheostoma crossopterum*, and their hybrid (*E. nigripinne* × *E. crossopterum*) were found to produce sounds associated with reproduction. Males produced sounds during aggressive encounters and courtship activities. All three taxa produced nonpulsed sounds categorized as drums and shorter, usually pulsed, sounds categorized as knocks. In addition, *E. nigripinne* produced pulsed sounds referred to as purrs that differ from knocks in having a higher pulse number and rate. All sound types were made under both aggressive and courtship contexts by males of all three taxa. The dominant frequency and duration of sounds differed by sound type (drums, knocks, purrs) for all taxa. In addition, within the drum sound type, the dominant frequency differed between contexts (aggression vs courtship) and among taxa. Although sound production has been documented for numerous fish species, this is the first time sounds have been described for percids. The mechanism and role of sound production in darters has yet to be determined.

NUMEROUS fishes are known to produce sounds (Myrberg, 1981). However, in relation to their diversity, this aspect of behavior and ecology has been poorly investigated among North American freshwater fishes. Exceptions are studies on the minnow genus *Cyprinella* (Delco, 1960; Winn and Stout, 1960; Stout, 1975), species of topminnows (*Fundulus*; Drewry, 1962), ictalurid catfishes (Rigley and Muir, 1979; Fine et al., 1997), and sunfishes (*Lepomis*; Gerald, 1971; Ballantyne and Colgan, 1978). The context of sound production in all of these groups is aggression and courtship associated with spawning, which is typical among fishes that produce sounds (Fine et al., 1977; Lobel, 1992). Other contexts associated with sound production in fishes include disturbance, social aggregation, and aggression not associated with spawning (Hawkins, 1993).

This paper investigates sound production during the spawning season in *Etheostoma nigripinne*, *E. crossopterum*, and a hybrid/intergrade population (*E. nigripinne* × *E. crossopterum*). The breeding ecology of these three taxa is typical of other species in the darter subgenus *Catonotus*, which are egg-clusterers (Page, 1985). Males establish nesting territories in cavities, typically made by flat rocks, which they clean. During spawning, a female enters the cavity, the pair invert, and the female lays eggs in a single layer on the ceiling of the cavity. After the eggs are fertilized, the male guards the eggs. In typical egg-clusterers, more than one clutch of eggs is laid in a cavity (Constantz, 1979). Males, which are larger than females, compete for nest cavities and females, and aggression is common.

The objectives of this study were to describe the contexts under which sound production occurs, describe sound parameters, and compare selected sound characteristics (dominant frequency and duration) between contexts and among species.

MATERIALS AND METHODS

To control for ambient noise levels, and to allow for detailed behavioral observations, fishes in breeding condition (males with breeding coloration and females with abdomens distended with eggs) were brought into the laboratory. Trials were conducted 5–15 May 1996, 1 April to 10 May 1997, and 7 April to 10 May 1998. Water temperatures at collection sites ranged from 18 to 20 C.

Fishes were collected with seines or dip nets during their breeding season (April to May). *Etheostoma nigripinne* were collected from Johnson Creek (Tennessee River drainage), Decatur County, Tennessee, 4 April 1998. Mean standard length (mm) of males was 53.7 ± 4.5, range 45.5–60.7, n = 11; and females was 39.2 ± 3.0, range 33.0–46.0, n = 17. *Etheostoma crossopterum* were collected from a tributary of Dry Fork (Stones River drainage), Rutherford County, Tennessee, and Bradley Creek (Stones River drainage), Rutherford County, Tennessee, on 29 March 1997, 1 May 1997, and 4 April 1998. Mean SL (mm) of males was 66.3 ± 10.2, range 43.0–82.0, n = 33; and females was 43.7 ± 4.6, range 37.5–52.2, n = 47. Hybrid/intergrade *E. nigripinne* × *E. crossopterum* were collected from Jack's Branch (Buffalo River drainage), Lewis

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TABLE 1. CONTEXTS AND NUMBERS OF SOUNDS PRODUCED BY MALE *Etheostoma Nigripinne*, *Etheostoma Crossopterum*, AND HYBRIDS (*E. Nigripinne* × *E. Crossopterum*).

	Aggression			Courtship			Male in nest cavity			
	drums	knocks	purrs	drums	knocks	purrs	drums	knocks	purrs	Total
E. nigripinne	91	5	8	50	12	3	0	0	0	169
E. crossopterum	82	17	0	21	8	0	48	17	0	193
Hybrid	7	0	0	51	5	0	0	0	0	63
Total	180	22	8	122	25	3	48	17	0	425

County, Tennessee, 5 May 1996 and 3 April 1998. Mean SL in mm of males was 62.0 ± 8.2, range 47.0–71.2, n = 13; and females was 46.8 ± 5.2, range 39.2–53.2, n = 15. Specimens collected in 1996 and 1997 were vouchered in the Illinois Natural History Survey fish collection; those collected in 1998 were vouchered in the Auburn University fish collection. The Jack's Branch population was determined as hybrid *E. nigripinne* × *E. crossopterum* by morphological examination (L. M. Page, pers. comm.). The possibility that these animals are intergrades cannot be ruled out at this time.

Fishes were held in 84-liter aquaria and provided with two to three rock nest cavities. No more than two males were kept together in a given aquarium. Fishes were fed previously frozen blood worms daily, and maintained at a water temperature of 21 C. The photoperiod ranged from 10 to 12 h of light during the study period.

Observation periods during the breeding season ranged from 30 min to 1 h, and from 0700–1800 h. Prior to observation, a single male was added to the test aquarium, which had two nesting cavities. The test aquarium was isolated from the lab table with layers of foam. After at least 30 min of acclimation, either an additional male, a female, or a male and a female from different holding tanks than the first male were added to the tank. Behavioral contexts and sounds produced were recorded during the observation periods. All fishes collected were not used for trials due to poor health, mortality, or lack of reaction to other stimulus fishes. Male *E. crossopterum* often produced sounds while alone in the nest cavity; this context was treated separately. Several spawning episodes and representative aggressive encounters were video taped using an 8 mm video cassette recorder. These same individuals were observed after the breeding season. Trials were run using both male and female fishes (males alone, and with one additional male; females alone, with one male and with one additional female), which did not interact, and no sounds were detected. During observation periods, all filtration and aeration devices were turned off. Sounds contaminated by fishes making contact with each other, the nest cavity, or the aquarium were not used for analysis.

Sounds were recorded using a Brüel and Kjaer 8103 hydrophone, Brüel and Kjaer 2635 charge amplifier, and Sony model TC-D5 ProII stereo cassette recorder. Calibration of the recording system was conducted using a Brüel and Kjaer 4223 hydrophone calibrator. Calls were digitized and then analyzed using MATLAB (Mathworks, Inc., 1997, Natick, MA, unpubl.). Duration was measured from the waveform, and dominant frequency was measured from the power spectrum. Statistical analyses (repeated measures analysis of variance, one-way analysis of variance, Duncan's multiple range test, Student's *t*-test, Levene's test for equality of variances) were conducted in SPSS (SPSS Inc., 1995, Chicago, IL, unpubl.). Within individual variation in sound parameters was not significant (results of repeated measures analysis); therefore data from each fish were treated as independent for analyses of the effect of context on call parameters, and one-way analysis of variance was used. Sounds were filtered below 65 Hz and above 1 kHz and down sampled to 2756.3. Spectrograms were generated using a hanning window of 112. Power spectra were generated using a hanning window of 256.

RESULTS

Sounds were produced by 11 *E. nigripinne* (mean SL, mm = 56.1 ± 3.8, range 50.0–60.7), 11 *E. crossopterum* (mean = 75.8 ± 5.8, range 66.0–82.0), and three hybrids (mean = 60.3 ± 9.0, range 50.0–64.0) males. Contexts of sound production included aggressive encounters and courtship. Aggressive encounters included male:male chases, lateral displays, circle swims and fights. Courtship activities included displays to females and spawning. All three taxa produced sounds under both aggressive and courtship contexts (Table 1, Figs. 1–2). In addition,

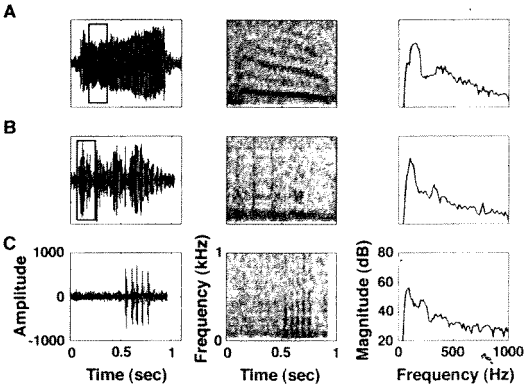

Fig 1. Waveform, spectrogram, and power spectra (from left to right) of a drum (A), knocks (B), and purr (C) from *Etheostoma nigripinne*. Areas outlined are expanded in Figure 2.

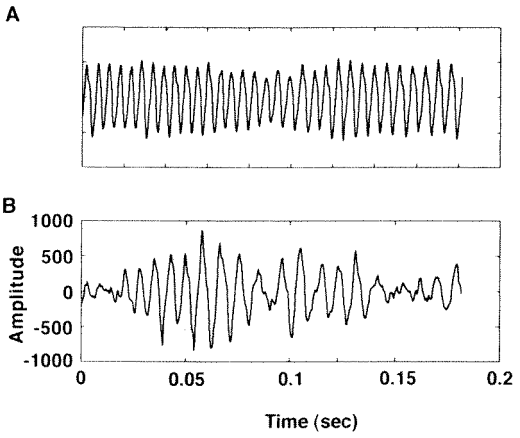

Fig 2. Expanded waveforms of the drum and a knock from Figure 1.

male *E. crossopterum* often made sounds while alone in the nest cavity.

Sounds produced by all taxa occurred both outside and inside the nest cavity, and fishes appeared relatively stationary during sound production (i.e., the sounds were not a mechanical artifact of fishes hitting a structure with their bodies). Sounds were produced during, or immediately prior to (while the pair was in the nest cavity), the spawning act in all three taxa. Although sounds were produced during most encounters between fish, some chases, which were the most common encounter, did not result in sounds. Sounds were not observed when the fishes were reproductively inactive (i.e., outside of the breeding season) or when not interacting (i.e., no aggressive encounters or courtship). Although observations of females suggested that they do not produce sounds, this does not rule out the possibility that both sexes produce sounds during spawning or aggressive encounters. For the purposes of this descriptive paper, we assume that males produced the sounds observed and that the dominant male produced sounds during interactions with other males.

Sounds were placed into three categories on the basis of duration and pulse characteristics: drums, knocks, and purrs (Tables 1–2, Figs. 1–2). Drums were the most common sound type (82% of total sounds) under both aggressive and courtship contexts for all three taxa and were made by all males (100%). Drums were the only sound type with harmonic structure. Knocks were less common (15% of total sounds), produced under all contexts, and produced by 70% of the males. Knocks were produced singly or in combination before or after drums and purrs. Purrs were only produced by *E. nigripinne* (27% of males, 3% of total sounds; Tables 1–2, Fig. 1) and were produced during both aggressive and courtship contexts.

In *E. nigripinne*, drums, which were nonpulsed, ranged from 63.0–203.0 Hz (138.7 ± 31.5 Hz) in dominant frequency (also the fundamental frequency) and lasted from 170–2400 ms (640 ± 340 ms; Table 2). Drums were harmonic; the range of the first harmonic was 86–516 Hz (267.3 ± 81.2) and the second, weaker band was 212–687 Hz (365.5 ± 95.9). Knocks produced by *E. nigripinne* were pulsed (76%) or single (24%). Knocks consisted of a rapid series of 1–5 (1.9 ± 1.3) pulses (mean pulse rate = 5.7 ± 1.0 pulses/sec) that lasted 40–360 ms (230 ± 100 ms; Table 3). Series of knocks ranged from 42.0–215.0 Hz (103.7 ± 32.3 Hz) in dominant frequency and lasted from 130–1280 ms (380 ± 310 ms). Purrs ranged from 43.0–238.0 (89.3 ± 62.3) in dominant frequency and from 170–930 ms (350 ± 220 ms) in duration. Purrs consisted of a rapid series of 3–13 (6.4 ± 3.1) pulses (mean pulse rate = 19.1 ± 5.1 pulses/sec) that lasted from 40–120 ms (60 ± 20 ms; Table 3). Analysis of variance indicated significant differences in dominant frequency and duration of sound types in *E. nigripinne* (Table 2). The results of Duncan's multiple range test indicate that drums differ from knocks and purrs in both metrics; drums have a higher dominant frequency and are longer than both other sound types. There are no statistically significant differences in dominant frequency or duration for knocks and purrs produced by *E. nigripinne*, but they differ in both pulse number ($t = 4.5$, $P < 0.0001$) and rate ($t = 5.8$, $P < 0.0001$).

In *E. crossopterm*, drums, which were nonpulsed, ranged from 65.0–129.0 Hz (89.1 ± 12.7 Hz) in dominant frequency, which is a funda-

TABLE 2. MEAN DOMINANT FREQUENCY AND DURATION OF VARIOUS SOUNDS PRODUCED BY MALE *Catonotus*. Range in parentheses. *F*-tests from repeated measures ANOVA except where noted.

	Dominant frequency (Hz)		Duration (ms)		
	Sound type	mean	mean	Number	%
E. nigripinne	drum	138.7 ± 31.5 (63.0–203.0)	640 ± 340 (170–2,400)	141	83
	knock	103.7 ± 32.3 (42.0–215.0)	380 ± 310 130–1,380)	17	10
	purr	89.3 ± 62.3 (43.0–238.0)	350 ± 220 (170–930)	11	7
Variation within individuals		$F = 10.35$, $P = 0.003$	$F = 5.78$, $P = 0.03$		
E. crossopterum		$F = 0.35$, $P = 0.84$	$F = 1.48$, $P = 0.23$		
	drum	89.1 ± 12.7 (65.0–129.0)	730 ± 330 (170–2,070)	151	78
	knock	97.5 ± 17.6 (59.0–129.0)	530 ± 350 (110–1640)	42	22
Variation within individuals		$F = 81.0$, $P = 0.0001$	$F = 13.65$, $P = 0.004$		
Hybrid		$F = 0.27$, $P = 0.92$	$F = 0.33$, $P = 0.89$		
	drum	102.3 ± 18.6 (86.0–140.0)	690 ± 470 (140–1,900)	57	92
	knock	105.4 ± 22.0 (86.0–129.0)	480 ± 250 (250–900)	5	8
		$F = 0.12$, $P = 0.7310$[a]	$F = 0.96$, $P = 0.3300$[a]		
		$F = 0.75$, $P = 0.62$	not enough data		

[a] Results of one-way ANOVA.

mental frequency, and lasted from 170–207 ms (730 ± 3300 ms; Table 2). The first harmonic ranged from 64–376 Hz (189.7 ± 61.5) and the second from 54–485 Hz (241.0 ± 71.8). Knocks produced by *E. crossopterum* were pulsed (86%) or single (14%). Most knocks consisted of a rapid series of 1–4 (1.9 ± 0.90) pulses (mean pulse rate = 4.4 ± 1.8 pulses/sec) that lasted 100–570 ms (270 ± 110 ms; Table 3). Series of knocks ranged from 59.0–129.0 Hz (97.5 ± 17.6 Hz) in dominant frequency and lasted from 110–1640 ms (530 ± 350 ms). The drums and knocks produced by *E. crossopterum* differ in both dominant frequency and duration (Table 2). In this species, knocks have a higher dominant frequency and are of shorter duration.

In *E. nigripinne* × *E. crossopterum*, drums, which were nonpulsed, ranged from 86.0–140.0 Hz (102.3 ± 18.6 Hz) in dominant frequency, which is a fundamental frequency, and lasted from 140–1900 ms (690 ± 470 ms; Table 2). The first harmonic ranged from 64–303 Hz (146.8 ± 43.2) and the second from 64–355 Hz (245.8 ± 55.5). Knocks produced by this taxon were pulsed (80%) or single (20%). Most knocks consisted of a rapid series of 1–3 (1.3 ± 0.50) pulses (mean pulse rate = 2.3 ± 0.87 pulses/sec) that lasted 250–450 ms (390 ± 100 ms; Table 3). Series of knocks ranged from 86.0–129.0 Hz (105.4 ± 22.0 Hz) in dominant frequency and lasted from 250–900 ms (480 ± 250 ms). Very few knocks were recorded for hybrids, and no statistically significant differences were found between sound types.

For *E. nigripinne*, drums made during courtship activities had a lower dominant frequency (mean = 129.5 ± 34.8 Hz) and were longer in duration (mean = 740 ± 420 ms) than those made under aggressive contexts (mean dominant frequency = 145.6 ± 28.0 Hz; mean duration = 580 ± 260 ms; dominant frequency $F = 8.2$, $P = 0.005$; duration $F = 8.8$, $P = 0.004$), although the ranges overlap considerably. There were not enough data for the other sound types to make this comparison.

For *E. crossopterum*, dominant frequency of drums differed among all three contexts ($F = 7.6$, $P = 0.0007$; mean dominant frequency, aggression = 89.6 ± 9.4 Hz; courtship = 76.6 ± 5.1 Hz; male in nest cavity = 93.4 ± 16.2 Hz), but the ranges overlap. Duration of drums was not significantly different ($F = 2.3$, $P = 0.07$; mean, aggression = 660 ± 310 ms; courtship = 960 ± 310 ms; male in nest cavity = 740 ± 340 ms). Dominant frequency and duration of knocks did not differ by context (dominant frequency $F = 0.17$, $P = 0.83$; duration $F = 0.14$, $P = 0.87$; mean dominant frequency, aggression = 95.3 ± 19.6 Hz; courtship = 99.5 ± 20.1 Hz; male in nest cavity = 98.6 ± 14.8 Hz; mean du-

TABLE 3. CHARACTERISTICS OF PULSED SOUNDS PRODUCED BY MALE *Catonotus*. Ranges in parentheses.

	Mean	number of pulses	Mean pulse rate (pulses/sec)	Mean duration (ms)
E. nigripinne	Knock	1.9 ± 1.3 (1–5)	5.6 ± 1.0 (3.3–11.6)	230 ± 100 (40–360)
	Purr	6.4 ± 3.1 (3–13)	19.1 ± 5.1 (8.5–25.6)	60 ± 20 (40–120)
E. crossopterum	Knock	1.9 ± 0.90 (1–4)	4.4 ± 1.8 (1.7–9.4)	270 ± 110 (100–570)
Hybrid	Knock	1.3 ± 0.50 (1–3)	2.3 ± 0.87) (2.2–4.0)	390 ± 100 (250–450)

ration, aggression = 460 ± 160 ms; courtship = 600 ± 510 ms; male in nest cavity = 570 ± 400 ms).

For hybrids, there was no difference in the dominant frequency or duration of drums produced under aggressive or courtship contexts (dominant frequency $F = 0.23$, $P = 0.63$; duration $F = 0.29$, $P = 0.59$; mean dominant frequency, aggression = 105.8 ± 14.12 Hz, courtship = 101.9 ± 19.1 Hz; mean duration, aggression = 780 ± 470 ms, courtship = 670 ± 470 ms). There were not enough data to make this comparison for knocks.

The dominant frequency of aggressive drums produced by *E. nigripinne* is higher than those of the other two taxa ($F = 151.4$, $P < 0.0001$). The duration of aggressive drums does not differ among the taxa, however ($F = 2.3$, $P = 0.10$). Both dominant frequency and duration of courtship drums differ for all three taxa (dominant frequency $F = 34.7$, $P < 0.0001$; duration $F = 3.2$, $P = 0.04$). Knocks (all contexts combined) do not differ for the three taxa in either dominant frequency ($F = 1.9$, $P = 0.15$) or duration ($F = 1.2$, $P = 0.31$). The pulse number for knocks does not differ between *E. nigripinne* and *E. crossopterum* (there was not enough data for this comparison for the hybrid; $F = 0.83$, $P = 0.43$), but pulse rate was significantly different ($F = 3.5$, $P = 0.03$).

DISCUSSION

Although sound production has been described in over 50 families of fishes, this is the first documentation in percids (Myrberg, 1981). Males of two species and their hybrid produced sounds associated with courtship and aggressive encounters during the breeding season. In these species, sounds may be used during breeding and territory defense of a nest cavity for assessment, mate attraction, or spawning synchrony, similar to the functions of sounds produced by cavity-nesting gobies (Lugli et al., 1995, 1997).

The sounds produced by these taxa differed in several parameters: among sound types, contexts, and taxa. Specifically, sounds varied in aspects of temporal patterning (pulse presence, pulse number and rate, and sound duration) and frequency. Differences among call types justified categorization (drums, knocks, and purrs). Both *E. nigripinne* and *E. crossopterum* produced drums that varied in dominant frequency among contexts. *Etheostoma nigripinne* produced sounds, both drums and knocks, during courtship that were longer than the same sound type produced during aggressive encounters. Drums produced during courtship differed in dominant frequency and duration among all three taxa, and the dominant frequency of sounds produced by *E. nigripinne* was higher under aggressive contexts than in the other two taxa. Many fishes are known to use the temporal patterning of sounds for communication (Fine et al., 1977; Myrberg et al., 1978; Bradbury and Vehrencamp, 1998), but the role of frequency coding in fish sounds is poorly understood (Fine et al., 1977). The differences in sounds produced by these darters suggest that they vary sounds according to context, a finding similar to other fishes (Fine et al., 1977). Differences in sounds produced by conspecifics may act as species isolating mechanisms and have been found in other species (sunfishes, Gerald, 1971; damselfishes, Myrberg and Spires, 1980; cichlids, Lobel, 1998).

Generally, the hearing abilities of fishes match the range of sounds they produce (Ladich and Yan, 1998), and fishes are known to discriminate frequency and intensity of sounds (Demski et al., 1973). Hearing sensitivity has not been investigated in these fishes, and it is not known whether they can detect the subtle differences in frequency of the sounds they produce.

The characteristics of the sounds of hybrids/integrades are generally intermediate to both parental species, but this was not true of all sound parameters. Similarly, Ballantyne and Colgan (1978) found both intermediate and non-intermediate characteristics of the breeding behavior of hybrid sunfishes. This population of darters would be useful for investigating the mechanism of signal coding in the sounds produced by *Catonotus*.

The mechanism for sound production in *Catonotus* is unknown. Other fishes are known to produce sounds using the swim bladder or by stridulation of bones (Demski et al., 1973; Hawkins, 1993). The sounds produced by stridulation of bones typically consist of pulses of broadband noise and are not characteristic of the sounds produced by darters (Demski et al., 1973). Sounds are also produced by the contraction of muscles associated with the swim bladder, which is absent in *Etheostoma*. These sounds are typically harmonic with the fundmental frequency being the frequency that the muscles contract (Demski et al., 1973). The swim bladder acts to amplify the sounds produced, without altering the spectral properties of the sound (Demski et al., 1973). The sounds produced by darters are consistent with those produced by fishes using the contraction of muscles as a sonic mechanism. The mechanism used to produce sounds by darters may be similar to that proposed for gobies which also lack a swim bladder (Lugli et al., 1996). Sounds may be generated in fishes that lack swim bladders by the contraction of specialized muscles (Barber and Mowbray, 1956); the difference would be in the intensity of the sounds produced. Generally, fishes that lack a gas bladder perceive only relatively low-frequency sounds (Ladich and Yan, 1998), similar to the range of frequencies reported here for darters.

Sound production undoubtedly plays a role in communication for the species of darters in this study, but the importance of these signals in the mating system of this and other species is yet to be explored. It is unknown whether darters with other types of reproductive strategies also produce sounds or whether this strategy is unique to cavity-nesters. Preliminary work showed that *Etheostoma flabellare*, another species of cavity-nester, produced sounds under similar contexts. Observations of spawning *Percina palmaris* and *Etheostoma luteovinctum*, egg-buriers, and *Etheostoma simoterum* and *Etheostoma duryi*, egg-attachers, did not detect sound production. These observations indicate that work with sound production in darters may uncover some interesting, and unexplored, aspects of their ecology and behavior, as well as patterns of evolution.

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