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Underwater Sound Locating Capability in the American Alligator (*Alligator mississippiensis*)

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?1 Abstract.—**It is known that crocodilians are able to locate the source of air-borne sound. However, locating the source of water-borne sound is difficult for physical reasons. I tested the ability of American Alligators (*Alligator mississippiensis*) to determine the direction toward the source of underwater sound by using their tendency to be attracted to slaps on the water surface. To produce surface slapping sounds with no air-borne component, I slapped the surface of the water inside a submerged diving bell and recorded the direction of alligator movements after the sound. The results show that alligators have a directionally biased response to water-borne sounds, indicating that they are capable of locating the source of a sound signal transmitted through the water. It would be physically difficult for the animal to do so by using the differences in time of sound arrival or in amplitude between left and right sides of the animal's head, so it is likely that alligators use other methods such as a sound pressure gradient system.**

American Alligators *Alligator mississippiensis* (Daudin, 1801) are capable of determining the direction of the source of an air-borne sound (Beach, 1944). Determining the direction of the source of a sound underwater is physically more difficult for two reasons. First, the difference in sound arrival time between left and right sides of the animal's head is smaller because of the higher speed of sound in water. Second, the difference in sound amplitude between left and right sides of the animal's head is also smaller because the shadowing effect of the animal's head is less pronounced. The difference in density between animal tissue and water is smaller than between animal tissue and air, so sound waves can penetrate the animal's head more easily, making it essentially transparent for the sound (Higgs et al., 2002). These complications make localizing the source of sound underwater impossible for humans (Filatova et al., 2006). So far, only species with hearing adapted for underwater conditions, such as cetaceans (Branstetter and Mercado, 2006) and turtles (Christensen-Dalsgaard et al., 2012), have been shown to possess this ability. Crocodilians, however, use both aerial and aquatic sound signals (Dinets, 2011), so their hearing can be expected to be adapted for both mediums. Thus, it is particularly interesting to determine if crocodilians have the ability to localize the source of sound underwater.

One of the signals used by alligators during the mating season is the head-slap, which is usually combined with an infrasound pulse (Garrick and Lang, 1977). Both slaps and infrasound can carry very long distances underwater and, thus, are very effective for long-distance communication in aquatic habitats. For physical reasons, a sharp slapping sound is one of the easiest sounds to locate while infrasound is one of the most difficult. It has been suggested (Dinets, 2011) that head-slaps are used as location beacons for infrasound pulses while the latter serve as honest signals of the animal's size and strength. For this theory to be plausible, it is necessary to demonstrate that alligators are, indeed, capable of locating the source of a slapping sound underwater.

To determine if alligators show a directionally biased response to water-borne sounds, I conducted two series of tests: one in canals and one in large lakes. These experiments used the alligators' natural attraction to slaps made on the water surface.

Materials and Methods

For the experiment, it was crucial to produce slapping sounds underwater while excluding the aerial component of the sound. To produce water-borne sounds with a minimal air-borne component, I used a small diving bell made of a metal bucket weighed down with diving belts. After submerging the bell, the water surface inside it was slapped with a plastic pad to produce a sound (Fig. 1). The sound made underwater could not be heard by an above-water human observer at more than 3 m. Alligator hearing in audible frequencies is roughly as acute as human hearing (Beach, 1944; Higgs et al., 2002), so at the distance of 30–50 m the animals could only hear the water-borne sound.

The first series of tests ($N = 30$) were conducted during 20 May–31 May 2008 in artificial flood control canals in the Everglades of Florida, United States, on sunny or partly cloudy days with air temperatures between 24–28°C. Three canals with large alligator populations were used (two running east-west, 2–4 m wide, and one running north-south, 10–12 m wide). All tests were conducted in early morning because previous observations had shown that, at that time of the day, most alligators were partially submerged and showed little overall activity. Three observers moved upwind along a canal looking for animals or groups of no more than three that were separated by at least 250 m from other alligators. Animals smaller than 1.5 m were ignored. When an appropriate animal or group was found, it was used in the experiment as follows. While observer A was watching the animals from the closest point on the bank of the canal (Fig. 2A), observers B and C positioned themselves neck-deep in the water (so that the animals could not see their movements) 30–50 m from the animals, upwind and downwind along the canal. The observer who had the diving bell (either observer B or observer C, in alternating order) quietly submerged it and 2 min later produced a single sharp slap inside the bell.

Movements of animals in the 1-min periods before and after the sound were recorded; the before period was used as a baseline. Movement was recorded as "1" if at least one animal in a group moved more than a body length in one direction. If the direction changed later, only the initial direction was recorded. If more than one animal in a group moved, only the movement

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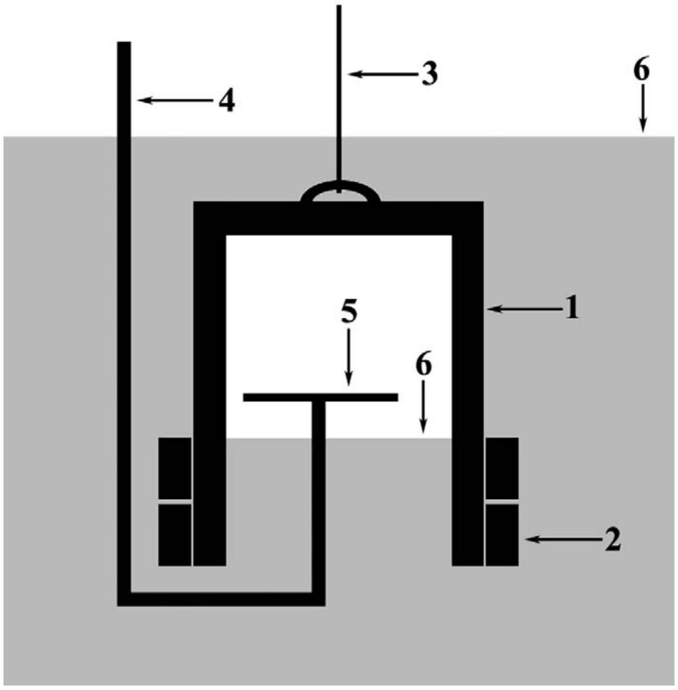

FIG. 1. Schematic drawing of the diving bell used for producing underwater slapping sounds. (1) Metal bucket, (2) extra weights (diving belts), (3) rope, (4) metal handle, (5) plastic pad, (6) water surface.

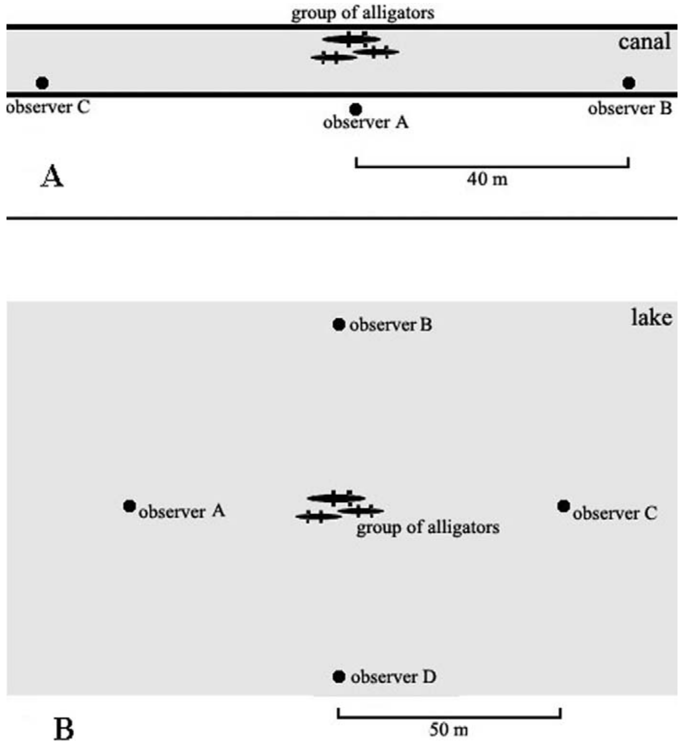

FIG. 2. Setups used in the experiments. (A) Setup used in canals. Sound was produced underwater by observer B or C in alternating order. (B) Setup used in large lakes. Sound was produced by one of the observers, with compass directions used in consecutive order.

of the first animal was counted. Movements within a 180° arc of the direction towards the sound were then scored as movements towards the sound; all movements in other directions were scored as movements away from sound. The proportion of movements toward the sound expected by chance would be 180 : 360 = 1 : 2.

I used the McNemar test (Markman, 1978) to test for a significant change in the number of movements after the signal and the binomial test to find if the proportion of movements towards the signal was significantly greater than expected by chance.

The second series of tests was performed in large lakes (all larger than 1 km^2) in the Savannah River Delta, South Carolina, United States, on 3–10 June 2008 ($N = 12$) and on 24 April – 9 May 2009 ($N = 9$), and in Lake Okeechobee, Florida, United States, on 01–03 April 2010 ($N = 6$). All tests were conducted in early morning on sunny or partly cloudy days with air temperatures between 20–26°C.

Four observers in inflatable kayaks, 100–200 m from shore, moved across shallow portions of lakes selecting focal animals or groups in the same way as described above. When an animal or a group was chosen, the observers positioned themselves in cardinal directions (Fig. 2B) at a distance of approximately 50 m from the animal (estimated visually). One observer (cardinal directions used in consecutive order) used the diving bell to produce an underwater slapping sound in the same way as during the canal experiments described above.

Movements of animals were recorded and analyzed in the same way as in the first series of tests, but the binomial test was performed: movements within a 90° arc of the direction towards the sound counted as positive (+), all other movements as negative (−), and the rate of movements toward the sound expected by chance was 90 : 360 = 1 : 4.

RESULTS

In the canal experiments, alligators were immobile during the 1-min period before the sound in all tests ($N = 30$) except for one. In 16 tests (11 out of 20 in canals running east-west, 5 out of 10 in the wider canal running north-south), at least one animal started swimming towards the source of the sound along the canal and moved more than a body length. No movements away from the sound were observed. The number of animals that moved was significantly higher after the signal than before ($P = 0.001$). The proportion of animals that moved towards the signal was significantly higher than expected by chance ($P = 0.0001$).

In the lake tests, alligators were immobile during the 1-min period before the sound in all tests ($N = 27$) except two. The number of animals that moved after the signal was 12 ($P = 0.007$). In 10 tests, the first animal to move did so towards the source of the sound and moved more than a body length. Animals that moved in other directions were observed twice. The proportion of animals that moved towards the signal was significantly higher than expected by chance ($P = 0.004$).

DISCUSSION

The results suggest that American Alligators have a directionally biased response to water-borne sounds, which means that they are likely capable of locating the source of a sound signal transmitted through the water. It would be physically difficult for the animal to locate the source of sound underwater by using the differences in time of sound arrival or in amplitude between left and right sides of the animal's head, so it is likely that alligators use other methods such as a sound pressure gradient system (Rheinlaender et al., 1981).

Floating alligators normally have their ear opening positioned above the water surface. Their ability to locate the sources of water-borne sounds suggests that such sounds are perceived through skull bones rather than through the auditory canal.

My results support the recent suggestion that slaps are used by alligators primarily as the means of long-distance communication in continuous aquatic habitats, where they carry much further than air-borne sounds, and that they serve as location beacons for infrasound signals (Dinets, 2011).

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