

DETECTION OF FOOD CHEMICALS BY THE AMERICAN ALLIGATOR (ALLIGATOR
MISSISSIPPIENSIS) IN AQUATIC AND TERRESTIAL ENVIRONMENTS.

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John Kennedy Olson, jr.
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Carroll College
Helena, MT 59625



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Jean E. Smith
Jean E. Smith, Ph.D.
Professor of Biology

29 Mar. 1990
Date

John Addis
John Addis, Ph.D.
Associate Professor of Biology

3/29/90
Date

Henry E. Burgess
Mr. Henry Burgess, M.S.
Professor of English

3-29-90
Date

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Abstract

These experiments demonstrated that the American Alligators (Alligator mississippiensis) detected chemicals from food on land and under water. American alligators were offered raw meat or animal carcasses on land and under water where only chemoreception could be used to discriminate between experimental and control materials. Juvenile alligators, tested in indoor tanks, opened cheesecloth packets containing meat more often than control packets when these materials were placed under water and on platforms above the water surface. Adult alligators, tested in outdoor semi-naturalistic enclosures, removed cheesecloth-wrapped meat presented under water, and both meat and raccoon (Procyon lotor) carcasses placed under perforated baskets on land, more than control materials. Juvenile alligators, in aquaria partially filled with water, exhibited more lateral head movements and mouth-opening in response to a water extract of meat than to plain water.

Introduction

Studies of food recognition in reptiles focus on the detection of prey chemicals by snakes and lizards. These investigations demonstrate the efficacy of prey extracts in eliciting predatory attack (review in Burghardt 1980, 1989), the involvement of vomeronasal and olfactory chemoreceptors in food recognition (Halpern and Kubie 1979; Halpern and Kubie 1984), and the general nature of chemicals eliciting feeding behavior (Wang et al. 1988; Schell et al. 1990). The use of chemoreception in food recognition by other reptiles, including crocodylians, has received little attention. The intent of this study is to experimentally verify the chemoreceptibility of the American alligator (Alligator mississippiensis).

Anecdotal accounts suggest that crocodylians detect both air and waterborne chemicals from food. Pooley and Gans (1976), for example, stated that the Nile Crocodile (Crocodylus niloticus) "sniffs out" carrion on land. Neill (1971) observed that the American alligator (Alligator mississippiensis) respond to meat on land and under water by moving its head from side to side, and that blood in the water elicits this response. He suggested that the papillae on the external surface of the jaw contain chemoreceptors used in food detection.

Scott and Weldon (1990) tested adult A. mississippiensis maintained in semi-naturalistic enclosures for responses to

meat chemicals by suspending paper bags containing meat or treated with a meat extract, along with control bags, from a rope over a water channel in a semi-naturalistic enclosure. Meat-containing or extract -treated bags were removed from the rope more often than were controls, indicating that alligators detected meat chemicals. Alligators generally grasped experimental bags first; thus they perceived chemicals prior to contact. Since the materials presented to alligators in Scott and Weldon's study were partially immersed in water, it is not clear whether air or waterborne chemicals were detected.

We report of the ability of juvenile and adult A. mississippiensis to locate food on land and in water by chemoreception. The behavioral responses of alligators to waterborne chemicals from meat are described.

Alligator mississippiensis, in common with other crocodilians, is amphibious, and it encounters food on land and in water. This species is an opportunistic carnivore, preying upon a variety of vertebrates and invertebrates (Giles and Childs 1949; McNease and Joanen 1977) and , at least occasionally, ingesting carrion (Valentine et al. 1972; McNease And Joanen 1977). Our experiments provide information on the natural feeding behavior of alligators in so far as they suggest the use of chemoreception in scavenging carrion.

Materials and Methods

Juveniles

Terrestrial Presentations. Ten alligators, captured during July, 1989, in Cameron Parish, Louisiana, were tested during August, 1989, for responses to food chemicals on land. The total lengths of juveniles used in this experiment and in aquatic presentations ranged from 22 to 33 cm. Subjects were maintained collectively for several weeks in a 4.9 x 0.8 m concrete outdoor enclosure filled with 33 cm of fresh water. They ate beef (Bos sp.) until two weeks before testing.

Subjects were transferred indoors to individual 152 x 56 cm opaque fiberglass tanks containing 10 cm of water several hours before testing. A 41 x 20 x 10 cm concrete block was positioned at a 30 degree angle in the center of each tank, with its lower edge at the water surface and its upper edge situated 10 cm above the water line. The control and the experimental packets were presented 13 cm apart and 1.3 cm from the top edge of the block. The water in the tanks was drained and refilled to its original level several hours before testing.

Cheesecloth packets (100% cotton) containing 10 g balls of beef or a paper towel rolled into a ball were soaked briefly in plain water. One meat packet and one paper packet were presented to each subject during a trial. The packets were held by a rubber band out of the water, 13 cm apart and

1.3 cm from the top of the edge of each block. The side of the platform on which the meat and paper packets were presented was alternated with each subject; their positions were reversed the following day during the second test.

Trials began at 2200 and ended at 0500 h. the following day; the room was dark throughout the trials. Tanks were inspected and the displaced and damage packets were noted. The mean water and air temperature were 26 C and 31 C, respectively.

Adults

Terrestrial tests of alligators' responses to food chemicals were performed during August and September of 1989 in a semi-naturalistic 1.7 ha. enclosure at the Rockefeller Wildlife Refuge in Grand Chenier, Cameron Parish, Louisiana. The enclosure, which consisted of 30% water and 70% land, housed 20 male and 40 female alligators for 15 years. The total lengths of adults used in this experiment and in the aquatic presentations ranged from 2.1 to 3.4 m. Alligators were fed 6% of their total body weight in ground nutria (Myocastor coypus) meat once a week during the day at a site near the shore of a water channel in their enclosure. They were fed between 3 and 5 days before the beginning of each experiment.

Four stations were established several meters from the alligators' regular feeding site. Vegetation was removed and a layer of sand 9 cm deep was deposited over four 114 x 94 cm

areas 1.4 m apart and 1.1 m from the shore of a channel in the enclosure. A perforated wicker basket (66 x 41 x 22 cm) tied with a rope to a wooden stake was placed at the center of each station; the contents of the baskets could not be seen.

Ground horse (Equus sp.) meat and raccoon (Procyon lotor) carcasses were presented to alligators in separate experiments. Alligators do not ordinarily prey upon horses, although alligator attacks on equines have been observed (Kellogg 1929). Alligator stomach content analyses indicate that raccoons are consumed occasionally (Giles and Childs 1949; McNease and Joanen 1977).

Horse meat was presented to alligators during four overnight trials conducted over 10 days. The horse meat was kept refrigerated before use. During each trial, 1550 g of meat was placed under each of two randomly chosen baskets; the two control baskets contained a roll of newspaper. After the second trial, fresh sand was deposited at each station, and the positions of the meat and paper-containing baskets were changed.

Nine raccoon carcasses (1.7-7.6 kg), obtained as roadkills in Cameron Parish, Louisiana, were kept frozen in plastic bags and thawed 6 h before being used. A carcass was placed under each of the two randomly chosen baskets; control baskets contained a roll of newspaper. Two carcasses and corresponding controls were presented during each of the four

nights in which tests were conducted; in addition, one carcass and control was presented on one night.

Materials presented to adults in terrestrial tests were carried into the enclosure contained in plastic bags and placed under the baskets from the end facing away from the channel; thus, nearby alligators were not permitted prior visual access to the materials. Dried vegetation was placed around the base of the baskets to further conceal their contents. The sand around the baskets was smoothed to permit animal tracks to be read.

Trials began at 1830 h and ended at 1000 h the following day, when the position and contents of each basket were noted. At the end of each trial, the contents of each basket were removed, and the baskets were rinsed with plain water and allowed to dry. The mean air temperature at the beginning and end of the trials was 27 C and 24 C respectively.

Juveniles

Aquatic Presentations. Ten juvenile alligators used during the terrestrial presentations were tested during August for their ability to locate food under water. Subjects were maintained individually and tested indoors in the fiberglass tanks described above. They were fed beef until two weeks before testing. The tanks were drained and filled to 13 cm with fresh water. Subjects were allowed to acclimate in their tanks for several hours before testing began.

Cheesecloth packets containing 40 g of beef or paper towel rolled into a ball were soaked briefly in plain water. One meat-containing packet was placed in the center of a plastic dish (diameter = 9.0 cm; height = 1.6 cm) in one corner of each tank. A paper-containing packet was placed in a dish in the opposite corner at the same end of the tank; the rims of the two dishes were 35 cm apart. A weight of 50 g was placed on the top of each packet.

The side on which the meat and paper-containing packets were placed was changed for each successive individual. This experiment was conducted over one night.

Trials began at 2200 h and ended at 0500 h the following day; the room was dark throughout. The packets removed from the dishes or opened were noted. The mean temperature of the water was 25 C.

Adults

Five male and 15 female alligators were tested during June and July for their ability to locate food under water. Subjects were maintained and tested in a 13 ha. enclosure consisting of 30% water and 70% land. The alligators used in this experiment had been transferred to this enclosure during May, 1989; they previously had been maintained together in a similar pen for 15 yrs. Nutria meat, amounting to 6% of the alligators' combined weight, was provided once a week at a regular site on land 1 m from a canal in the enclosure.

Four stations, each consisting of two stakes placed 2 m apart, were established 15 m apart and 1 m from shore of a 12.7 m wide channel in the study pen. The site at which the alligators' routinely fed was 90 m from the closest station and it was not visually accessible from the experimental stations.

Alligators were presented with 1200 g rolls of nutria meat wrapped in cheesecloth. A comparable weight of oyster shells wrapped in cheesecloth served as the control. Each cheesecloth bag was bound by a light cotton string tied to a 5.5 m rope. A loop at one end of the rope was tied to a stake.

Two to four stations were used during each test, with meat and control bags placed at alternate stations. The bags were placed underwater between 0900 and 1030 h and examined four hours later. The mean water temperature was 27 C.

Juveniles

Responses to Meat Extract. Observations of alligators during routine feedings and preliminary tests indicated, as Neill (1971) had described, that they sweep their head laterally and open their mouths or snap when fresh meat or meat-tainted water is presented. Six juveniles used in previous experiments were tested during August for responses to water-borne chemicals from beef. An extract was prepared by adding 41 l of water to 940 g of ground beef and filtered. The concentration of solutes in the extract was determined by

removing a 4 ml aliquot, placing it into a preweighed tube, and heating it at 100 C for 24 h. The residue weight indicated a 3.8 mg/ml solution.

Alligators were removed from their concrete tank 3 h before testing began and placed individually in 26 x 51 cm glass aquaria with 11 cm of water. The sides of each aquarium were covered with paper; a wire screen was placed on top of each aquarium. A one-way mirror and two 15 W light bulbs were placed over each tank. The lights over each tank were turned on 20 min before each trial began and they remained lit throughout the 20 min trial period.

On the first day of testing, a 100 ml aliquot of either beef extract or plain water was poured into the alligator's aquarium. On the following day, it was given the other treatment. The number of times the alligator swayed their head and opened their mouth while underwater were recorded each minute for 20 min.

Results

The twenty trials that were run testing juvenile alligators response to terrestrial presentations resulted in all twenty meat-containing packets being removed from the concrete platforms. All but two of the meat packets were opened, while none of the control packets were removed or opened. The Mann-Whitney U-test indicates that significantly more meat-containing packets were opened ($P \leq 0.05$).

Terrestrial tests of adult alligators resulted in all nine of the carcass-containing baskets being displaced from their stations and their contents removed. One of the control baskets was removed with its contents; the others had not been disturbed. Alligator tracks were the only ones observed. The Fisher exact probability test indicated significantly more carcass-containing baskets were disturbed ($P \leq 0.05$).

The aquatic presentations to the juvenile alligators resulted in nine of the meat-containing packets being removed or opened. Eight of the control packets were disturbed but none was opened. The Mann-Whitney U-test indicates that significantly more meat-containing packets were opened ($P \leq 0.05$).

The aquatic presentation of materials to adult alligators resulted in eleven of the 18 meat-containing bags being removed; only one of the control bags was removed. The Mann-Whitney U-test indicated that significantly more meat-containing bags were removed ($P \leq 0.05$).

The juvenile alligators response when presented with meat extract averaged 78.8 head waves and 58.2 mouth-openings during the 20 min trials. Only one subject exhibited head waving and mouth opening during plain water presentations, resulting in an overall average scores of 0.7 and 1.5 per 20 minute trial; the individual in this case had been presented with meat-extract the previous day. The Mann-Whitney U-test detected a significantly greater number of head waves and mouth openings to meat extract ($P \leq 0.05$).

Discussion

Juvenile and adult alligators selectively removed meat wrapped in cheesecloth or contained under baskets in all terrestrial and aquatic tests. Since juveniles were tested individually, statistical treatment of data from experiments in which they served as subjects was routine. Adults, on the other hand, were tested collectively in their seminaturalistic enclosures. Our failure to account for the responses of individual adults may have resulted in a violation of the assumption of independence for our analysis; thus our results should be considered with this caveat in mind. Nonetheless, our experiments with adults provide results more readily related to the behavior of free-ranging individuals, given the setting in which they were tested.

Neill (1971) reported that A. mississippiensis sweeps its head from side to side when presented with food in water or on land, and that blood introduced into the water is sufficient to elicit this behavior. Our experiments confirm that lateral head movements are exhibited by juvenile alligators presented with food chemicals in water, and that mouth-opening is elicited as well. The open-mouth head movements of alligators in response to meat extract is reminiscent of the feeding behavior of aquatically foraging snakes, e.g., natricines (Drummond 1979) and the yellow-bellied sea snake (Pelamis platurus; Hydrophilidae) (Weldon

1989), where open-mouth head "search" movements are displayed in water laden with food chemicals.

The chemosensory organs mediating alligators' responses to food substances have not been identified, but several anatomical structures are known or suspected by which chemicals could be perceived. All crocodylians possess a complex arrangement of nasal cavities lined with an olfactory epithelium for detecting airborne chemicals (Parsons, 1967). Yearling alligators exhibited heightened gular pumping to airborne presentations of skin gland secretions from adult conspecifics and to several synthetic compounds suspected of occurring in these exudates (Johnsen and Wellington 1982); these chemicals likely were perceived by olfaction. Similar studies should be performed on alligators' responses to chemicals from food.

Post-hatchling crocodylians lack vomernasal organ (Sluiter 1892; Parsons 1967), which mediates responses to food chemicals in snakes and lizards (Halpern and Kubie 1984). They do, however, possess taste buds on the tongue (Bath 1906), and, in A. mississippiensis, these organs have also been observed on the posterior palate (Ferguson 1981). The gustatory responses of crocodylians to food chemicals, and Neill's (1971) claim that papillae on the external jaw surface of alligators contain organs used in food chemical detection, remain to be investigated.

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