

## Short Communications

Chemoreception in the Feeding Behaviour of Adult American Alligators, *Alligator mississippiensis*

The involvement of chemoreception in the feeding behaviour of reptiles has been studied in lizards, snakes (see Burghardt 1980 for review) and turtles (Grassman & Owens 1984). No experimental investigations of responses to prey chemicals by crocodylians have been reported, although anecdotal accounts suggest they use chemoreception in food recognition (e.g. Neill 1971; Pooley & Gans 1976). We report field experiments demonstrating the use of chemoreception in food recognition by adult American alligators.

Alligators were observed at the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana, during August and September 1988. Experiments were conducted in a 12.5-ha pen, consisting of approximately 70% land and 30% water, containing five male and 15 female alligators maintained together for 15 years. Alligators were maintained on nutria, *Myocastor coypus*, meat placed once a week at a site within 2 m of the water in their enclosure.

In experiments 1-3, alligators were presented with paper bags measuring 13 x 7 x 27 cm containing (1) beef, *Bos* sp. (2) nutria, or (3) western diamondback rattlesnake, *Crotalus atrox*, meat. Control bags contained only paper. Each bag was perforated by 24 holes (diameter = 3.0 mm), spaced approximately 3.0 cm apart. Bags were soaked in tap water for 10 min and filled either with 227 g of meat or folded, water-soaked paper bags. All bags were bound at the bottom and tied closed at the top with a piece of string, approximately 50 cm of which was left free to attach to a rope-and-pulley system in the study pen.

In experiment 4, alligators were presented with an aqueous extract obtained by adding 450 ml of distilled water to 440 g of nutria meat, and filtering. A 5-ml aliquot of filtrate was placed in a hot bath to remove the water. The residue was weighed, indicating a 12 mg/ml solution. Experimental bags were soaked for 2 min in the filtrate; control bags were soaked in tap water.

Alligators were presented with one meat-containing and one control bag during each 10-min session. Sixteen sessions each were conducted in experiments 1 and 2; ten sessions each were conducted in experiments 3 and 4. Experiments 1-4 were conducted consecutively, with from 1 to 22 days intervening between experiments.

A rope 16.5 m long attached to two pulleys was placed over a 13.5-m channel, 2 m deep. One pulley

was attached 0.9 m above the ground to a post on one side of the channel. The pulley on the opposite shore could be moved between two hooks located 1.8 and 0.9 m high on a post. Control and experimental bags were tied 6.8 m apart on the rope while it was in its raised position. The bags were positioned over the water (approximately 3.4 m from either shore). The adjustable pulley was then moved to the lower hook to allow the bags to partially enter the water. Observers were stationed near one of the posts.

During each session we scored: (1) number of alligators visible by flashlight before and after each session; (2) number of mouth contacts alligators made with each bag; (3) latency of alligators to remove bags; and (4) the presence or absence of bags at the end of a session. We observed alligators during all tests by shining a flashlight near the rope, but neither directly on it nor on the bags suspended from it. Alligators always approached the bags while swimming near the water surface, thus their responses could be observed. At the end of each session, we raised the pulley and pulled the bags or their remnants to shore. We removed the bags and string (if either was present) and presented two new bags. The position of control and experimental bags on the rope was counterbalanced with each presentation.

Alligators had been fed 825 kg of nutria meat 5 or 6 days before conducting experiments 1, 3 and 4; they were fed 412 kg of nutria meat 1 day before conducting the experiments, between 1952 and 0223 hours. Air and water temperatures ranged from 22 to 27°C and 24 to 29°C, respectively.

Information by which our subjects could discriminate between conditions was limited, initially, to chemical cues; all materials were contained in or absorbed onto paper bags presented under reduced illumination. Our inability to identify individuals responding under these dimly lit settings, however, poses a constraint to the statistical analysis of our data. The censuses conducted before each session indicated from two to seven alligators in the vicinity of our apparatus, but we do not know how many individuals responded to the materials presented. Our data analyses should be considered with this caveat in mind.

The Fisher exact probability test indicates that bags containing meat or meat extract were removed more often than were control bags ( $P < 0.05$  for all experiments, Table 1). Nutria are common in the diet of free-ranging alligators in the area from which our subjects were obtained (Valentine et al. 1972;

Table 1. Responses by alligators to control and meat-containing or extract-treated bags

Experiment no.	No. of sessions	Condition	No. of sessions in which bags first contacted†	$\bar{X} \pm SE$ contacts‡	$\bar{X} \pm SE$ latency for first contact (N)§	Bags removed†
1	16	Control	4*	2.1 ± 0.4*	3.5 ± 0.5 (14)	8*
		Beef	12*	0.9 ± 0.1*	2.4 ± 0.1 (15)	14*
2	16	Control	0*	2.6 ± 0.5*	3.5 ± 0.4 (15)	2*
		Nutria meat	16*	1.3 ± 0.2*	1.9 ± 0.3 (16)	16*
3	10	Control	0*	2.6 ± 0.5*	3.5 ± 0.6 (8)	2*
		Snake meat	10*	1.1 ± 0.1*	2.8 ± 0.4 (10)	10*
		Control	1*	1.1 ± 0.4*	3.5 ± 2.7 (6)	0*
4	10	Control	9*	2.6 ± 0.4*	2.8 ± 0.6 (9)	8*
		Nutria extract	9*	2.6 ± 0.4*	2.8 ± 0.6 (9)	8*

\* Significant difference detected between control and experimental values ( $P < 0.05$ ).

† Fisher exact probability test.

‡  $t$ -test.

§ Mann-Whitney  $U$ -test.

McNease & Joanen 1977), and all our subjects had been raised on this species. Beef is not a natural food for alligators, and snakes are not commonly encountered in analyses of their stomach contents (Valentine et al. 1972; McNease & Joanen 1977).

McIlhenny (cited in Klauber 1972) stated that alligators vigorously shake venomous snakes, including rattlesnakes, before ingesting them, but that non-venomous snakes are swallowed unceremoniously. He suspected that alligators distinguish between snakes on the basis of chemical cues since a skinned rattlesnake carcass was shaken. We failed to observe head-shaking or other unusual reactions during presentations of rattlesnake meat, but the species we used is not one alligators encounter under normal conditions.

The Mann-Whitney  $U$ -test failed to detect differences in the latencies with which alligators contacted experimental and control bags ( $P > 0.05$  for all experiments). Their tendency to contact experimental bags first (Fisher exact probability test;  $P < 0.05$ ), however, suggests that they detected water- or air-borne chemicals from materials presented to them (Table 1).

Observations of the behaviour of alligators during our tests suggests that contact chemoreception is important in food recognition. Alligators grasping control bags opened their jaws and released bags intact on 30 occasions during our experiments. Bags containing meat or treated with meat extracts, on the other hand, were released only 11 times; generally they were removed when first contacted. Since alligators, as with other crocodylians, apparently lack a vomeronasal organ as adults (Sluiter 1992), gustation is probably involved in contact chemoreception of food.

T. Joanen and L. McNease provided valuable support and advice for this study. R. Elsey offered logistical help. A. Bruske, S. Siebenicher, G. Thomas, P. Urruzuno, M. Whiting and A. Yanovsky provided expert field assistance. G. Burghardt, J. Dixon, L. Hayes-Odom and D. Owens commented on previous versions of the manuscript. This research was supported by grants to P.J.W. from the National Geographic Society and Sea Grant.

TIMOTHY P. SCOTT  
PAUL J. WELDON

Department of Biology,  
Texas A & M University,  
College Station, TX 77843, U.S.A.

## References

- Burghardt, G. M. 1980. Behavioral and stimulus correlates of vomeronasal functioning in reptiles: feeding, grouping, sex and tongue use. In: *Chemical Signals: Vertebrates and Aquatic Invertebrates* (Ed. by D. Müller-Schwarze & R. M. Silverstein), pp. 275-301. New York: Plenum Press.
- Grassman, M. A. & Owens, D. W. 1984. Development and extinction of food preferences in the loggerhead sea turtle, *Caretta caretta*. *Copeia*, **1984**, 965-969.
- Klauber, L. M. 1972. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. Vol. 2. Berkeley: University of California Press.
- McNease, L. & Joanen, T. 1977. Alligator diets in relation to marsh salinity. *Proc. Conf. Southeast. Assoc. Fish Wildl. Agencies*, **31**, 36-40.
- Neill, W. T. 1971. *The Last of the Ruling Reptiles: Alligators, Crocodiles and their Kin*. New York: Columbia University Press.
- Pooley, A. & Gans, C. 1976. The Nile crocodile (*Crocodilus niloticus*). *Sci. Am.*, **234**, 114-124.

Sluiter, C. P. 1892. Das Jacobsons'sche Organ von *Crocodylus porosus* (Schm.). *Anat. Anz.* 7, 540-545.  
 Valentine, J. M., Walther, J. R., McCartney, K. M. & Ivy, L. M. 1972. Alligator diets on the Sabine National Wildlife Refuge, Louisiana. *J. Wildl. Mgmt.* 36, 809-815.

(Received 26 June 1989; initial acceptance 11 May 1989;  
 final acceptance 17 July 1989;  
 M.S. number AS-636)

### Acoustic Characteristics of Alarm Calls Associated with Predation Risk in Chickadees

The possibility of coding of information concerning some aspects of the nature of the predator and/or the degree of predation risk in alarm calls needs to be addressed in a variety of species, especially under field conditions. Here, I report evidence that the degree of risk from aerial predators in Mexican chickadees, *Parus sclateri*, is associated with significant differences in pitch in a single kind of alarm call, and discuss context-specific variation of alarm calls of some other avian and mammalian species.

As part of a study of the chickadee's vocal repertoire (Ficken, unpublished data), I observed flocks of four to six Mexican chickadees, usually associated with over 30 other individuals of several different species on 5 and 6 October 1985 and 5-10 October 1986 at Rustler Park in the Chiricahua Mountains (Cochise County), Arizona. I used a Sony Professional Walkman cassette tape-recorder, and either an Electrovoice Soundspot microphone or a Nakamichi CM-100 cardioid microphone, and analysed vocalizations with a Kay 7800 Digital Sona-graph (150-Hz filter band width).

During the study many hawks were migrating through the area, and about two hawks per hour were sighted near the study flocks. The chickadees gave high-pitched calls (termed 'High Zees' by Ficken & Witkin 1977), typical of many passerines and often referred to as 'aerial' predator calls (Marler 1955). In response to these calls, all flock members immediately stopped moving and became silent.

I recorded 12 bouts of calling from at least eight different flocks (in numerous other cases, calls were heard but not recorded). In five cases, the context was unknown, as the predator was not observed. Before I measured sonagrams, I divided the contexts of calling into two categories based on presumed risk of the predator to the chickadees. The low risk category included two cases of hawks (*Accipiter* spp.) that were flying very high and not near the flocks, one call given when a Steller's jay, *Cyanocitta stelleri*, flew over the flock very suddenly

(the chickadee's response was probably one of initial 'mistaken identity', as these calls are not usually given to this species), and one to a *Buteo* sp. flying high over a flock (chickadees usually did not call in response to these hawks which pose little danger to small birds). High risk included sharp-shinned hawks, *Accipiter striatus*, flying within 30 m of the flock. These hawks feed on small birds.

As the calls are given in a series consisting of nearly identical calls, I measured only the first call in each series. Because of the trend for higher pitched calls in high risk situations for black-capped chickadees, *P. atricapillus* (Ficken & Witkin 1977), I predicted higher pitch in calls in high risk situations in Mexican chickadees. In all cases, only one chickadee in the flock called. Calls were coded and measured 'blind' as to their context. The alarm calls of the Mexican chickadee are distinguished easily from other species in the flocks because of their rapid frequency modulations (Ficken, unpublished data). Only once did another species call.

Calls given in the high risk situation were significantly higher pitched than those in the low risk situation, and there was no overlap in pitch between the two risk categories. No significant difference occurred in the duration of the individual calls, but larger samples might reveal a tendency for longer durations in high risk situations (Table 1). In the low risk cases, normal movement and calling seemed to resume more quickly than in the high risk cases.

Table 1. Comparison of high zee calls in low and high risk situations in Mexican chickadees

	Highest frequency (kHz)	Lowest frequency (kHz)	Duration (s)
Low risk	8.7	7.5	0.13
	8.5	7.2	0.13
	8.7	6.7	0.17
	8.5	6.8	0.14
High risk	9.0	7.7	0.18
	9.0	8.0	0.22
	9.2	8.0	0.13

Mann-Whitney *U*-test, one-tailed,  $U=0$ ,  $P=0.028$  for highest and lowest frequency;  $U=5$ ,  $P=0.43$  for duration.

Seyfarth et al. (1980) suggested that vervet monkeys, *Cercopithecus aethiops*, 'name' predators by giving calls that are specific for different predators; response to the calls also differs according to the kind of predator. This type of call specificity is probably unusual.

In some species, different major categories of alarm calls may be given in a consistent manner according to a general context. For example, in ground squirrels, *Spermophilus* spp., very different vocalizations are reported for aerial and ground predators (Balph & Balph 1966; Melchior 1971; Sherman 1985). Owings & Hennessy (1984) noted that 'aerial' predator calls in ground squirrels are usually given when raptors arrive low and fast; another type of call is often associated with mammalian predators that usually come less suddenly. Sometimes 'aerial' calls are given when a mammalian predator is close. Thus, the type of call is not indicative of a particular 'class' of predators, but rather is associated with the degree of 'urgency' of response required. Similarly blue tits, *Parus caeruleus*, gave a 'scolding' kind of call to life-size models of a hawk close by and the 'aerial' call to a small model mimicking the hawk at a greater height (Klump & Curio 1983). Both black-capped and Mexican chickadees give different kinds of calls when mobbing a stationary predator than when a hawk flies over (personal observation).

In chickadees, consistent variation within a single call category provides the possibility of communicating degree of risk. These alarm calls are simple acoustically so coding possibilities are limited to pitch and duration. In chickens, *Gallus domesticus*, differences occurred in grosser aspects of acoustic structure of 'aerial' type calls given to predators and harmless objects (Gyger et al. 1987). In the black-capped chickadee, *P. atricapillus*, high zees were lower pitched and of shorter duration in response to a nearby mink, *Mustela vison*, (presumably low risk; it appeared suddenly, but elicited only a short burst of calls), than to a flying sharp-shinned hawk or a perched northern saw-whet owl, *Aegolius acadicus*, although sample sizes were small (Ficken & Witkin 1977). Smith (1977) noted that these high-pitched alarm calls, although typically given to hawks, rarely if ever, 'name a single class of predator' and my observations on chickadees support this observation. However, variation in the pitch of an acoustically simple call may encode information concerning the relative degree of 'risk' or 'urgency'. This system differs from that reported in some other species in that this fine-grained information is encoded in a single type of signal.

The Southwestern Research Station of the American Museum of Natural History provided facilities during this study. I thank James Popp for his helpful comments.

MILLICENT SIGLER FICKEN

Department of Biological Sciences,  
 University of Wisconsin-Milwaukee,  
 Milwaukee, WI 53201, U.S.A.

### References

- Balph, D. M. & Balph, D. F. 1966. Sound communication of Uinta ground squirrels. *J. Mamm.*, 47, 440-450.  
 Ficken, M. S. & Witkin, S. R. 1977. Responses of black-capped chickadee flocks to predators. *Auk*, 94, 156-157.  
 Gyger, M., Marler, P. & Pickert, R. 1987. Semantics of an avian alarm call system: the male domestic fowl, *Gallus domesticus*. *Behaviour*, 102, 15-40.  
 Klump, G. M. & Curio, E. 1983. Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. *Bird Behav.*, 4, 78-81.  
 Marler, P. 1955. Characteristics of some animal calls. *Nature, Lond.* 176, 6-8.  
 Melchior, H. R. 1971. Characteristics of arctic ground squirrel alarm calls. *Oecologia, (Berl.)*, 7, 184-190.  
 Owings, D. H. & Hennessy, D. 1984. The importance of variation in sciurid visual and vocal communication. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. A. Murie & G. R. Michener), pp. 169-200. Lincoln, Nebraska: University of Nebraska Press.  
 Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim. Behav.*, 28, 1070-1094.  
 Sherman, P. W. 1985. Alarm calls of Belding's ground squirrel to aerial predators: nepotism or self-preservation? *Behav. Ecol. Sociobiol.*, 17, 313-323.  
 Smith, W. J. 1977. *The Behavior of Communicating*. Cambridge, Massachusetts: Harvard University Press.

(Received 20 March 1989; initial acceptance 30 May 1989;  
 final acceptance 30 June 1989;  
 M.S. number AS-616)

### Statistical Evidence for Aggressive Response to Red by Male Three-spined Sticklebacks

A classic example of a sign stimulus as defined by Tinbergen (1948) is the aggressive response of the male three-spined stickleback, *Gasterosteus aculeatus*, to intruding males who have developed the red breeding coloration (ter Pelkewijk & Tinbergen 1937). The male will even attack a crude fish-shaped dummy with a red belly introduced into his territory. But oddly enough, statistically significant positive evidence with controlled experiments still seems to be lacking for this widely known example of a social signal (Baerends 1985). Here, I report the results of relevant experiments done some time ago at the University of Leiden.

The conditions under which the sticklebacks were maintained have been described by van Iersel (1953). The fish, captured while migrating from the sea to their breeding places in Holland in small, shallow, freshwater streams, were stored in dense numbers in a large tank filled with running water at 10°C to keep them at a low level of breeding activity. In spring, single male fish were placed in