Lingual Luring by Mangrove Saltmarsh Snakes (*Nerodia clarkii compressicauda*)

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ABSTRACT.—Very few cases of predatory luring by squamate reptiles involve body parts other than the tail. Here, I report the use of the tongue by Mangrove Saltmarsh Snakes (*Nerodia clarkii compressicauda*) to lure prey, a behavior thus far adequately described for only one other snake species. Fishes are the only verified component of the diet of these snakes and are effectively attracted by the luring behavior. Lingual luring by these snakes is particularly unique in that the tongue is curled upon itself distally such that a conspicuous loop is formed at its terminus. The rapid oscillations typical of chemosensory tongue flicks are absent, though the terminal loop does exhibit some vertical and horizontal movement. The duration of luring tongue flicks is significantly greater than the duration of chemosensory tongue flicks.

Predatory luring is a means of nutrient acquisition in which one organism (the predator) produces a stimulus that is attractive to another organism (the prey) that is consumable, in whole or in part, to the predator. This often occurs in the form of aggressive mimicry (Wickler, 1968; Vane-Wright, 1976; Pasteur, 1982; Pough, 1988) or feeding mimicry (Schuett et al., 1984) in which a deceptive signal transmitted by the predator (the mimic) resembles a stimulus produced by an entity (the model) that the prey (the dupe) would normally approach. In successful predatory luring, potential prey perceive the attractive stimulus and approach the predator more closely than they might in the absence of that stimulus. This may or may not result in capture and consumption of attracted prey in a given instance, but it should do so at least occasionally (Dawkins and Krebs, 1978).

Predatory luring by nonavian reptiles is widely reported and is exhibited by members of several groups therein (Neill, 1960; Drummond and Gordon, 1979; Murray et al., 1991). The most common form of predatory luring among reptiles is caudal luring, which is exhibited primarily by snakes and involves motions of the tail tip that cause it to resemble a generalized invertebrate larva suitable as prey for frogs and lizards (Pough, 1988). Predatory luring by reptiles is also achieved through the use of the tongue (i.e., lingual luring), but the taxa involved are few. The most well known example of lingual luring comes from the Alligator Snapping Turtle (*Macrochelys temminckii*), which possesses a bifurcate, wormlike lingual appendage that attracts fish into its mouth (Drummond and Gordon, 1979; Spindel et al., 1987). Czaplicki and Porter (1974) re-ported lingual ''fly-casting'' by two watersnake species (*Nerodia sipedon* and *Nerodia rhombifer*) that flicked the surface of the water with their tongues, causing fish to approach and be captured. However, because the focus of their study was not the luring, the authors' description of the behavior is limited. Some have speculated that the straight, rigid, long-lasting tongue protrusions exhibited by vine snakes (*Ahaetulla, Oxybelis, Thelotornis*, and *Uromacer*) serve to lure prey (Lillywhite and Henderson, 1993). However, Keiser (1975) provided an effective argument against such a function for this behavior as exhibited by *Oxybelis* and perhaps others, at least with respect to arboreal prey, and he found crypticity a more likely role. In addition, there is no evidence to date that those tongue protrusions are attractive to prey, a key component of predatory luring (Strimple, 1992). Recently, a more detailed and convincing account of lingual luring by a snake was provided by Welsh and Lind (2000). They observed neonate and juvenile Aquatic Gartersnakes (*Thamnophis atratus*) quivering the tips of their tongues on the water's surface in streams where the snakes feed upon juvenile salmonid fishes. *Thamnophis atratus*' tongue protrusions during luring are of far greater duration than normal, investigative tongue flicks and are effective at attracting prey (Welsh and Lind, 2000).

Herein I describe lingual luring by another semiaquatic snake, the Mangrove Saltmarsh Snake (*Nerodia clarkii compressicauda*). These snakes are associated rather strictly with Red Mangrove (*Rhizophora mangle*) around the Atlantic and Gulf coasts of the southern half of Florida as well as northern coastal Cuba (Neill, 1965; Ernst and Ernst, 2003). Fish are the only

known component of their diet (Miller and Mushinsky, 1990; Mullin and Mushinsky, 1995) and are the assumed target of the luring. This report involves a species not previously known to lure prey, and certain details of the luring behavior make it unique.

MATERIALS AND METHODS

My initial observations of apparent predatory lingual luring involved two captive-born one-year-old *N. c. compressicauda* (1F, 1M) that were obtained from a commercial supplier and whose parents had been captured at an unknown site in the Florida Keys. To examine the behavior further, I collected three *N. c. compressicauda*, one sub-adult (F) and two adults (1F, 1M), on northern Key Largo in March 1999. None of these wild-caught animals exhibited the putative luring in the three months following capture. Therefore, for the present laboratory study, I focused on 25 captive-bred young (<1 yr old), all descended from the original captive-born luring male and the two wild-caught females. Feeding sessions involving 19 of the offspring were videotaped and analyzed.

Videotaped feeding sessions were conducted on days when subjects were to be fed in accordance with their normal schedule (4–6 guppies every 5–7 days) to ensure sufficient and similar motivation to feed. On this schedule, young *Nerodia clarkii* grow in good health and rarely refuse food. Subjects were videotaped individually in a 5.83-liter plastic shoebox filled with tap water to a depth of 2 cm. A single 20-cm length of 1.7-cm diameter PVC tubing was partially submerged horizontally to provide an anchorage and ambush site for the subject. I added between three and six guppies (*Poecilia reticulata*) to the feeding chamber, usually before transfer of the subject from its home enclosure. Subjects were videotaped during multiple sessions for 15–20 min or until it became apparent that they had little interest in the fish (e.g., attempted to escape for several min). To determine how closely allied the putative luring was with the presence of fish, I made a small set of control observations using a litter of eight juveniles: During the second session of observations of these individuals, I videotaped the subjects alone in the chamber for 10 min before adding four guppies to the water. After the fish were added, I continued videotaped observations for an additional 20 min. The feeding chamber was rinsed thoroughly with tap water between each of these 30-min observation periods.

Videotaped feedings were later examined carefully for instances of putative luring, and a qualitative means of distinguishing this from normal tongue flicking (Gove, 1979) was established. To make a quantitative comparison between normal tongue flicks (NTFs) and putative luring tongue flicks (LTFs), I measured the duration of each LTF and an equal number of NTFs (one NTF chosen pseudorandomly from within ± 2 min of the start of each LTF) by counting video frames in which any part of the tongue was outside the mouth. After converting from number of frames to sec, I calculated the mean durations of the two types of tongue flicks for each subject and used these means to compare the duration of LTFs to that of NTFs using a paired-samples *t*-test. I estimated the size of this difference effect by calculating Cohen's *d* using *t* in a formula that accounts for any correlation between paired measures (Dunlap et al., 1996, Eq. 3). The coefficient of variation (CV) served as a metric of interindividual variability in mean duration of LTFs and NTFs. Spearman rank correlation was used to examine the relationship between the subjects' mean durations of LTFs and NTFs. Data were tested for normality using the method of D'Agostino et al. (1990) and for equality of variance using Levene's test.

RESULTS

Description of the Behavior.—The luring tongue flick of *N. clarkii compressicauda* comprises three phases similar to the protrusion, oscillation, and retraction phases that Ulinski (1972) outlined for flick clusters (here referred to as tongue flicks; Gove, 1979), except the oscillation phase of a tongue flick is replaced by a luring phase. This luring phase, like the oscillation phase of Ulinski (1972), overlaps the protrusion and retraction phases. The protrusion and luring phases are most notably characterized by an immediate and persistent curling of the distal portion of the tongue. Upon leaving the margin of the mouth, the tongue tip bends upward and makes contact with the rostrum in the vicinity of the junction between the rostral and internasal scales (Fig. 1A); this is diagnostic of the behavior. Further protrusion of the tongue while its tip remains in contact with the rostrum results in the formation of a terminal loop (Fig. 1B). The bifurcation point touches or nearly touches a slightly more proximal portion of the tongue, and the two tines are forced apart laterally. Remaining curled, the tip of the tongue then breaks contact with the rostrum as protrusion continues (Fig. 1C–D). After some time, the tongue is retracted back into the mouth, the tip uncurling in the process. During the protrusion and luring phases, some slow, low-amplitude vertical movement of the tongue usually occurs. During the luring phase, the
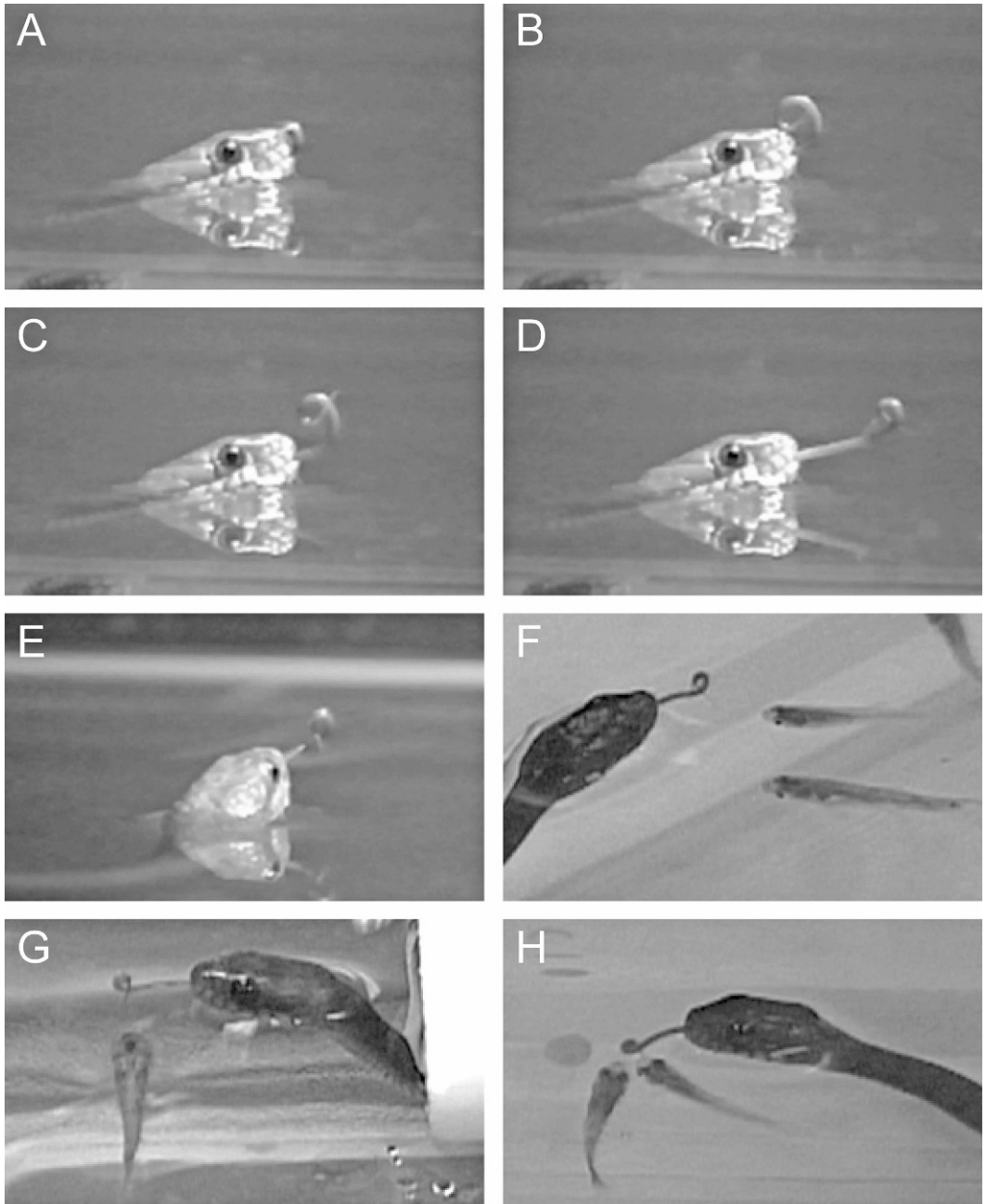
Fɪɢ. 1. (A–D) Sequence of noteworthy points in the protraction phase of a luring tongue flick by *Nerodia clarkii compressicauda*. (E) Lateral deflection of the tongue during the luring phase. (F–H) Attraction of fish toward the tongue during the luring phase. Images are unaltered except for cropping and global changes to size, brightness, and contrast. The retraction phase (not shown) follows the luring phase and involves uncurling of the terminal loop as the tongue is withdrawn into the mouth.

completeness of the tongue loop is often decreased and increased alternately; this is tightly linked to the vertical movements. Lateral deflection (Ulinski, 1972) and twisting of the tongue will often also occur during the luring phase (Fig. 1E), and in many cases the terminal tongue loop is bent toward fish in the vicinity. As one would expect, not every LTF is executed

well. False starts occasionally occur whereby the tongue is retracted prematurely, before the terminal loop is completed or protruded beyond the snout. In other cases, the terminal loop remains stuck to the snout for part or all of the duration of the LTF. Also, near-complete uncurling occasionally occurs well before the onset of retraction, resulting in a protruded tongue only slightly upturned.

Context and Efficacy of Luring Tongue Flicks.— All of the 25 subjects observed in this study exhibited LTFs. I observed the behavior only in the presence of fish, and it was often exhibited during a subject's first encounter with this prey. Subjects most often produced LTFs while in the water (96% of all LTFs) with their head either above (89%) or below (11%) the water's surface, though on a few occasions (4% of all LTFs), the subject exhibited the behavior while perched atop the ambush tube. During many (33%) of the LTFs produced with only the head above the water, the terminal tongue loop made contact with the water's surface. Subjects were usually motionless for at least a short period (1– 2 sec or more) prior to initiating LTFs, and their entire body remained motionless while the tongue was protruded.

Fish often approached the subject's tongue during LTFs (Fig. 1F–H), and attraction, though not quantified, seemed to me to be strongest when the terminal loop was deflected downward far enough to touch the surface of the water. On four videotaped occasions, a fish struck at and bit the tongue during the luring phase. In three of these four cases, the subject immediately struck at the fish, albeit unsuccessfully; in the fourth case, the subject did not respond. On 10 other videotaped occasions, the subject aborted an LTF and immediately struck at a nearby fish that had not bitten the tongue. Two of these 10 strikes resulted in capture of the fish, one of which was clearly attracted to and approaching the protruded, curled tongue of the subject at the time. In addition to this, one subject that was never videotaped also attracted and captured a fish once as a direct result of an LTF.

Exhibition of Luring Tongue Flicks Relative to Fish Presence.—During the 10-min control observations of eight subjects with no fish present, no LTFs were observed. However, seven of the eight subjects exhibited LTFs after fish were added (Fig. 2). Three of the subjects initiated LTFs almost immediately upon the addition of fish (12, 15, and 23 sec afterward), and two others did so before 3.5 min had passed. Two of the three remaining subjects that exhibited LTFs, first doing so at 5.3 and 13.1 min post-addition, had captured fish earlier in the trial, necessarily delaying the onset of the behavior
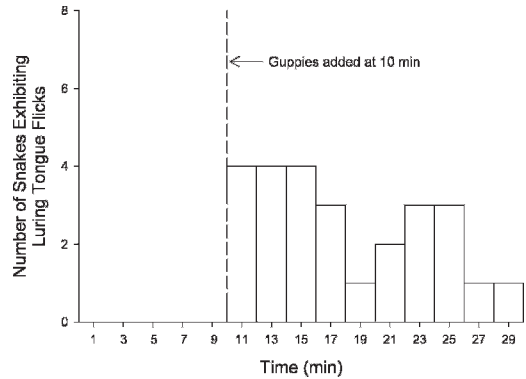

FIG. 2. Frequency distribution of latencies of luring tongue flicks exhibited by eight juvenile *Nerodia clarkii compressicauda* during 30-min individual observation periods. Each snake was alone in a feeding chamber during the first 10 min of the observation period. Four guppies (*Poecilia reticulata*) were added to the feeding chamber 10 min after observations began.

for at least a short time during prey handling and swallowing.

Comparison between Durations of Luring Tongue Flicks and Normal Tongue Flicks.—Videotaped observation sessions involving 19 of the 25 subjects yielded a total of 188 LTFs, which were analyzed along with an equal number of NTFs. The duration of NTFs ($N = 188$) ranged from 0.08–1.02 sec, whereas LTFs lasted from 0.22– 35.3 sec (Fig. 3). Subject mean durations of NTFs averaged 0.31 ± 0.033 sec (mean ± 95% CI, $N = 19$), whereas those of LTFs averaged 10.95 ± 2.31 sec. These means differed significantly ($t_{18} = 9.70$, $P < 0.0001$), with an extremely large effect size ($d = 3.08$). Interindividual variation in mean duration of LTFs (CV = 43.82) was nearly twice that of NTFs (CV = 22.09), and the variances of these two groups of means differed significantly (Levene's test, $F_{1,36} = 12.39$, $P = 0.0012$). Mean duration of LTFs was not significantly correlated with that of NTFs ($r_s = 0.042$, df = 17, $P = 0.864$).

DISCUSSION

The unique tongue flicks described here likely do not function particularly to enhance chemosensation. Lingual taste buds are apparently absent in snakes (Morgans and Heidt, 1978; Young, 1997); thus, there should be no gustatory benefit to holding the tongue out of the mouth for long periods. One possible vomerolfactory benefit to lengthy protrusions might be an increase in the concentration of chemicals on the tongue, making weak chemical stimuli more detectable upon transfer to the vomeronasal organ (Keiser, 1975). If that were in operation,
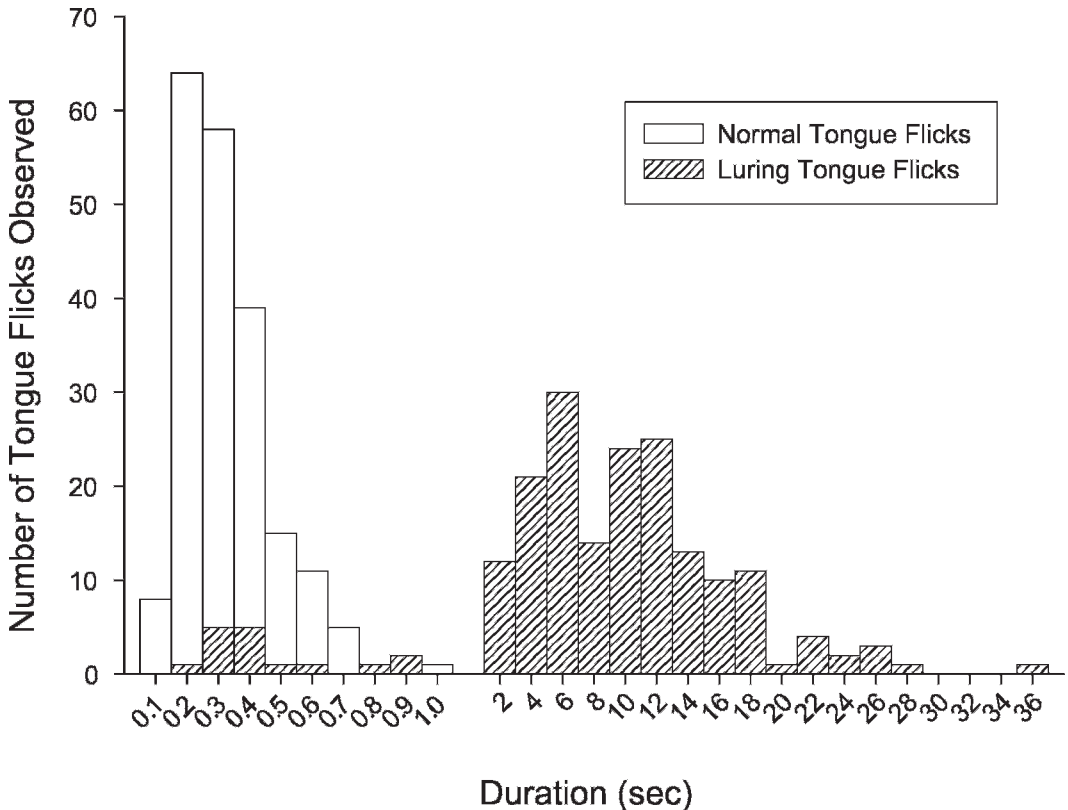
F<small>IG</small>. 3. Frequency distribution of durations of normal tongue flicks ($N = 188$) and luring tongue flicks ($N = 188$) exhibited by 19 neonate and juvenile *Nerodia clarkii compressicauda*. Different bin widths are used below (0.1 sec) and above (2 sec) the gap on the x-axis to prevent variation in normal tongue-flick duration from being hidden within a single bar.

one would expect to see this behavior under almost any circumstance in which the collection of chemical information might be important, but this has not been the case. Alternatively, these tongue flicks might function as an antipredatory signal (Gove, 1979). Although I did not explicitly test this hypothesis here, I have never observed this behavior in contexts that elicit defensive behaviors, such as musking (Gove, 1979; Gove and Burghardt, 1983). Contrary to both hypotheses, I have observed these tongue flicks only in the immediate context of foraging. This is exemplified by the control observations in the absence of fish, during which numerous normal flicks, but no tongue protrusions of the other type, were observed. As soon as prey were presented, however, the subjects began to exhibit frequently the prolonged, curled-tip tongue protrusions. The continued exhibition of normal tongue flicks during the period when fish were present suggests to me that a motivation to acquire chemical information existed but was not being satisfied, to notable extent anyway, by the lengthy, curled protrusions.

When one also considers that fish are clearly attracted to these tongue movements, and that captures do result, it becomes apparent that this unique behavior functions primarily as a predatory lure.

The duration of luring tongue flicks exhibited by the *N. c. compressicauda* studied here appears to be somewhat greater than that of the *Thamnophis atratus* studied by Welsh and Lind (2000). However, the occurrence and extent of curling of the tongue tip of *N. c. compressicauda* are what make its lure particularly unique. The luring tongue flicks of *T. atratus* also significantly exceed its normal tongue flicks in duration, but its lure differs from the curling lure of *N. c. compressicauda* in that the tip of the tongue of *T. atratus* remains relatively straight and quivers (Welsh and Lind, 2000). Furthermore, the *T. atratus* tongue apparently always touches the water during luring, whereas the *N. c. compressicauda* tongue did so only some of the time here. Despite these differences, which may or may not be trivial, the luring tongue flicks of both species occur in the same context (sensu

Gove and Burghardt, 1983) and are effective in attracting prey.

The specific function of the terminal loop was not directly studied here and is thus unknown, but it may simply be to increase the conspicuousness of the luring tongue flicks. The curling might additionally make the tongue resemble, via semi-abstract mimicry (Pasteur, 1982; Pough, 1988), any number of invertebrates that are preyed upon by fishes in the mangroves. The formation of the terminal loop causes the two tongue tines to point divergently, and this may make the lure even more conspicuous and possibly increase the tongue's resemblance to an invertebrate by simulating antennae, cerci, or other appendages.

Caudal luring is exhibited almost exclusively by neonate and juvenile snakes, but adults of four species have been observed using their tail in a manner attractive to prey (Greene and Campbell, 1972; Heatwole and Davison, 1976; Carpenter et al., 1978; Jackson and Martin, 1980). Greene and Campbell (1972) and Heatwole and Davison (1976) hypothesize that cessation of luring behavior may be related to ontogenetic diet shifts, and they point out that those species that do lure as adults do not change their diet with age. *Thamnophis atratus* undergo an ontogenetic shift in prey type, and lingual luring in that species is exhibited only by neonates and juveniles (Welsh and Lind, 2000). *Nerodia clarkii compressicauda* eat only fish throughout life, with an ontogenetic diet shift that is chiefly restricted to changes in the relative proportions of smaller and larger fishes (Miller and Mushinsky, 1990). Thus, one would expect that their lingual luring might continue into adulthood. One adult *N. c. compressicauda*, the original captive-born male, was observed occasionally throughout its life in a feeding chamber similar to the one used to collect the data analyzed here. This individual exhibited lingual luring well into adulthood, as late as five years of age. Like the observations of caudal luring by adult snakes, which are limited to one or a few individuals (Greene and Campbell, 1972; Heatwole and Davison, 1976; Carpenter et al., 1978; Jackson and Martin, 1980), my observation of lingual luring by one adult *N. c. compressicauda* indicates only that the behavior may occasionally be exhibited by adults. It remains to be seen whether adults exhibit predatory luring nearly as often as do neonates and juveniles. An ontogenetic change in prey size (Miller and Mushinsky, 1990) or an experience-related increase in prey capture skills (Krause and Burghardt, 2001) could eliminate any advantage the lingual luring might provide. In addition to such possible correlates of aging, a limited adjustment to captivity (Ford, 1995)

may also have contributed to the absence of lingual luring among the three wild-caught snakes examined in 1999.

All of the young snakes used for this study belonged to the same paternal family, a fact that limits the validity of my findings considerably. This is partly improved upon by stimulus-control experiments currently underway that involve subjects born to several wild-caught females that were already pregnant at the time of capture. Most of these offspring have lured during the few observation sessions completed thus far (unpubl. data), but these new subjects also originated from the Florida Keys. A study of possible geographic variation in the foraging behavior of *N. clarkii* is now in progress and draws from populations elsewhere in the species' distribution. Until such work is completed, one can conclude only that lingual luring is exhibited by at least some individual *N. c. compressicauda* in the southernmost populations.

The use of captive-reared animals for this study enabled me to control the environment experienced by my subjects. All subjects were isolated upon birth, and many of them exhibited lingual luring the first time they encountered potential prey. Therefore, it is clear that learning is not required for this behavior to occur, at least among members of the populations studied by me thus far. Despite this, I found considerable variation among individuals in mean duration of luring tongue flicks. Whether or not such variation is heritable awaits investigation.

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