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Evidence of Lingual-luring by an Aquatic Snake

HARTWELL H. WELSH, JR. AND AMY J. LIND

Pacific Southwest Research Station, USDA Forest Service, 1700 Bayview Dr., Arcata, California 95521, USA.
E-mail: hwelsh/psw_rsl@fs.fed.us

ABSTRACT.-**We describe and quantify the components of an unusual snake behavior used to attract fish prey: lingual-luring. Our earlier research on the foraging behavior of the Pacific Coast aquatic garter snake (*Thamnophis atratus*) indicated that adults are active foragers, feeding primarily on aquatic Pacific giant salamanders (*Dicamptodon tenebrosus*) in streambed substrates. Juvenile snakes, however, use primarily ambush tactics to capture larval anurans and juvenile salmonids along stream margins, behaviors that include the lingual-luring described here. We found that lingual-luring differed from typical chemosensory tongue-flicking by the position of the snake, contact of the tongue with the water surface, and the length of time the tongue was extended. Luring snakes are in ambush position and extend and hold their tongues out rigid, with the tongue-tips quivering on the water surface, apparently mimicking insects in order to draw young fish within striking range. This behavior is a novel adaptation of the tongue-vomeronasal system by a visually-oriented predator.**

The luring of prey by snakes has been associated primarily with the use of the tail, a behavior termed caudal luring (e.g., Neill, 1960; Greene and Campbell, 1972; Heatwole and Davison, 1976; Jackson and Martin, 1980; Schuett et al., 1984; Chizar et al., 1990). Greene and Campbell (1972) noted that caudal luring was a form of mimicry, which Schuett et al. (1984) called feeding mimicry. Lingual-luring behavior, analogous to that which we described here, has been described in the alligator snapping turtle (*Macroclemys temminckii*) (Drummond and Gordon, 1979) and the snowy egret (*Egretta thula*) (Buckley and Buckley, 1968).

Most research on ophidian tongue use has focused on the chemosensory function of the tongue. In fact two reviews of the behavioral ecology of snakes make no mention of a lingual-luring function (Mushinsky, 1987; Ford and Burghardt, 1993). However, Lillywhite and Henderson (1993) noted the occurrence of a prolonged extension of the tongue observed in vine snakes (e.g., Kennedy, 1965; Henderson and Binder, 1980), a behavior which is described in detail by Gove (1979). Lillywhite and Henderson (1993) listed prey luring as one of several possible hypotheses to explain this phenomenon (but see Keiser, 1975). We know of one other reference to a similar behavior in a laboratory setting (Czaplicki and Porter, 1974). Here we describe and quantify field observations of lingual-luring by a snake for the first time.

We have studied the natural history, behavior, and population dynamics of the Pacific Coast aquatic garter snake (*Thamnophis atratus*) along an approximately 5 km section of Hurdygurdy

TABLE 1. Timed field observations of durations (in seconds) of lingual-luring behavior in the Pacific Coast aquatic garter snake (*Thamnophis atratus*) at Hurdygurdy Creek, Del Norte County, California. Each line represents a different individual. SVL = snout to vent (cloaca) length.

Date	Gender	SVL (mm)	Total obs. time (min:sec)	# of tongue-flicks	$\bar{x}$ length of tongue-flicks	Min-max
9/13/90	F	209	-	-	-	5-11
9/27/94	F	212	15:00	11	8.6	2-17
5/24/95	M	288	-	2	5	5
5/25/95	F	230	-	12	8.3	2-16

Creek in the Smith River drainage of northwestern California since 1986. Our study area and the common behaviors of this species have been described elsewhere (Lind and Welsh, 1994). However, it is important to provide a brief description of Hurdygurdy Creek to provide the appropriate context for the new behavior we describe. Hurdygurdy Creek is a medium-sized (4th to 5th order; Strahler [1957]), fast-flowing, mountain stream that drains 78 km^2 of rugged Douglas-fir forest in the Siskiyou Mountains. Annual rainfall in this basin is approximately 2500 mm and stream discharge is substantial, ranging from about 1.0 cubic meters per second (cms) in the summer to over 100 cms in the winter (McCain, 1994). Mean daily water temperatures range from 5 C in winter to 21 C in summer (McCain, 1994). Hurdygurdy Creek supports several species of anadromous fishes, including chinook and colic, salmon, and steelhead trout, as well as resident cutthroat trout (McCain, 1994).

Our earlier research on the foraging behavior of the Pacific Coast aquatic garter snake (*Thamnophis atratus*) indicated that adults are active foragers, feeding primarily on aquatic Pacific giant salamanders (*Dicamptodon tenebrosus*) in streambed substrates. Juvenile snakes, however, use primarily ambush tactics to capture detritus-feeding larval anurans (foothill yellow-legged frog, *Rana boylii*) and juvenile salmonids along stream margins, tactics that include the luring behavior described here. We first observed this unusual behavior in the summer of 1987, and have subsequently observed it on numerous occasions during snake censuses that we conduct at our field site three to five times each year. This behavior, which we identify as lingual-luring, appears to involve a unique combination of body position, tongue position, and duration of the tongue extended with the distal portion quivering (see Gove [1979] for a definition of the tongue quiver).

MATERIALS AND METHODS

While we have observed luring behavior frequently in the field, quantifying the duration of lingual-luring bouts of undisturbed snakes under field conditions has been difficult. Previously, we manually timed the durations of extended tongues for a total of only four undisturbed snakes (Table 1). However, in this study, using video equipment (Sony Hi 8 Camcorder with an 8x zoom lens) we were able to film 24 snakes in the field. for later analysis. Videotaping occurred over five days each August in 1994, 1995, and 1996. All taping occurred under clear skies, between 1000 and 1600 h (Pacific Daylight Time) when full sun was on the creek and the snakes were most active. Our videographer was dressed in camouflaged clothing and used binoculars to locate snakes before creeping slowly from the downwind direction to within filming distance (2 to 5 m). Only video sequences from undisturbed snakes were used in our analysis.

From field observations and initial analysis of the videotapes, there appeared to be three aspects of snake behavior that differed between typical chemosensory tongue-flicking and lingual-luring: the behavior and related body position, the relationship of the tongue-tip to the water surface, and the duration of the tongue-flick. We conducted a frame-by-frame analysis of all taped behaviors where we could observe an individual snake use its tongue in any way. When analyzing the video tapes we used verbal cues from the videographer (i.e., "new snake") and visual cues from the surroundings (i.e., changes in substrates and aquatic habitats) to identify individuals. Each instance of tongue use by a snake constituted a datum, defined here as a tongue-flick after Gove (1979): ". . . the movement of the tongue from its appearance outside the mouth until its complete withdrawal. This corresponds to the 'tongue-flick cluster' of Ulinski (1972)." We timed the duration of each tongue-flick (i.e., the number of video frames for which the tongue was visible [30 frames = one second]). Of the 812 tongue-flicks on the videotapes, 39 were removed, leaving 773 for analysis. In these 39 tongue-flicks, snakes were submerged and engaged in underwater substrate crawling (Lind and Welsh, 1994). These tongue-flicks were all of short duration, and the extended tongue was always in the wa-

ter, and thus contact with water was not independent of the behavior.

We analyzed the videotape data in two ways: (1) descriptive statistics of a frequency distribution of tongue-flick duration; and (2) analysis of variance (ANOVA) of duration of tongue-flick among behavior and tongue-position types. Because we hypothesized that ambush position (i.e., body out of water with the head oriented toward water, and within a few cm of the surface [Lind and Welsh, 1994]) was a primary component of lingual-luring, we lumped all other behaviors (Lind and Welsh, 1994) into an "other behaviors" category for analysis. For the frequency analysis, we split the data into two subsets at a natural break point based on a visual examination of a frequency histogram of the untransformed duration data. We then described the associated behaviors for the two resulting subsets. We used ANOVA to examine the contribution of behavior (ambush or other), tongue position (tips in contact with water or not) (="factors"), and their interaction, toward explaining variation in tongue-flick duration. The data for this analysis consisted of tongue-flick durations by factor combination, with individual snakes (N = 24) treated as blocks. Thus an individual snake could only contribute once to any combination of behavior and tongue position, accounting for potential biases resulting from multiple observations on a single individual (i.e., lack of independence of observations). Since each individual usually exhibited some but not all of the possible combinations, our final data matrix consisted of 41 observations. Tongue-flick durations were natural log transformed prior to analysis to improve normality and reduce the heterogeneity of variances (assumptions of ANOVA).

RESULTS

Description of the Behavior.-We have observed lingual-luring behavior only in neonate and juvenile snakes (see Lind and Welsh, 1994 for age class definitions) of both sexes foraging in relatively shallow stream margins inhabited by young-of-the-year anadromous salmonid fishes (e.g., Table 1). These fishes are primarily steelhead trout (*Oncorhynchus mykiss*) and occasionally chinook salmon (*O. tshawytscha*). Despite numerous observations, we have not seen this behavior associated with adult snakes or any other prey species. Prior to lingual-luring, young snakes approach the water slowly, crawling around and over streamside rocks until they position themselves on rocks at the stream margin with their heads oriented toward the water and 1-2 cm from its surface (Fig. 1) (see also ambush position, Fig. 1 in Lind and Welsh [1994]). This slow, careful positioning is often associated with head swaying, apparently to gain additional parallax (Lillywhite and Henderson, 1993), which may help them locate fish below the water surface in the near vicinity. During this positioning, typical, short-duration, tongue-flicking (sensu Burghardt, 1980) is often observed. Luring behavior appears to be initiated only when one or more fish enters the snake's field of view once it has assumed the ambush position. Snakes then typically orient toward the prey, with the actual onset of luring made apparent by a dramatic change in the length of time the tongue is held extended. Snakes then hold their tongues fully extended with the tips quivering at the water surface for varying lengths of time. The duration of individual episodes of lingual-luring appears to be modulated in response to behavioral changes on the part of the fish prey.

While we have yet to observe an entire successful prey capture sequence, we have observed all of the component parts such that we can reconstruct the entire sequence from multiple partial observations. For example, one of our video sequences documents a snake luring in and then striking at a clearly visible fish, but in this instance missing. In another instance, in the field, we observed a snake lingual-luring for several minutes, then we moved momentarily to record observations on a second snake nearby. We returned to see the first snake, still in exactly the same position, but now with its head held up away from the water, with a newly captured, and struggling, juvenile steelhead. It appears from our field observations, that once initiated lingual-luring behavior is repeated until the snake tires, the fish retreats, or the fish is drawn within capture range. When the latter occurs, the snake strikes in an attempt to capture the fish.

Videotape Analyses.-Typical chemosensory tongue-flicking involves rapid movement of the tongue in and out of the mouth, sampling for molecules from the air and transferring these "captured" molecules, by way of the vomeronasal ducts, to the vomeronasal organ in the roof of the mouth (Halpern and Kubie, 1980). A typical chemosensory tongue-flick (non-luring behavior/tongue positions) in our study snakes had an average duration of 0.43 sec (from videotapes: N = 684, SD = 0.86). The average duration of a luring tongue flick was 4.71 sec (from videotapes: N = 89, SD = 5.07), apparently depending on the response of the fish prey.

We found snake body position, tongue position, and duration of tongue-flicks were closely linked. Both descriptive analysis of frequency data and quantitative assessments of tongue-flick duration, demonstrated that the use of the ambush position in combination with the

FIG. 1. Juvenile Pacific Coast aquatic garter snake (*Thamnophis atratus*) in ambush position using lingual-luring (photo by A. Lind).

tongue extended and the tongue-tips quivering on the water was different from the other behavior/tongue-flick combinations. Specifically, the two subsets of tongue-flick durations that we derived by separating the untransformed frequency distribution of 773 tongue-flicks at a natural break point (Fig. 2: <1.77 sec and ≥1.77 sec) showed pronounced differences in behavior and tongue position frequencies. In the long duration tongue-flick group (≥1.77 sec), 82% of the bouts were ambush with tongue-tips quivering on the water and 18% were all other behavior/tongue position combinations (Fig. 2, lower inset). Only 6% of the bouts in the short duration group (<1.77 sec) were ambush with tongue-tips on the water and 94% were other behavior/tongue position combinations (Fig. 2, upper inset). Comparison of mean tongue-flick durations among behavior and tongue-position categories using ANOVA showed a significant interaction between behavior and the tongue-position. Snakes flicked their tongues the longest when in ambush position with their tongue-tips on the surface of the water (behavior X tongue position, $F_{1,14} = 8.07$, $P = 0.013$) (Fig. 3). We consider these results strong evidence of lingual-luring, which is exhibited specifically in the ambush position, involves long-duration tongue-flicks with the tips quivering on the water surface, and is associated with the stalking of aquatic prey, usually salmonids. These results support our hypothesis that lingual-luring is in fact a unique new foraging behavior. While we have not quantified prey response to lingual-luring, we have observed positive responses by fish on numerous occasions in the field. These observations, coupled with an extensive videotaped sequence where a fish is clearly drawn in by a luring snake, constitute evidence that lingual-luring attracts fish.

DISCUSSION

Previous observations of apparent lingual-lur-ing in snakes were made during laboratory experiments with two species of water snake (*Nerodia rhombifer* and *N. sipedon*) (Czaplicki and Porter, 1974). Czaplicki and Porter (1974) described lingual-luring (which they called flycasting), in which neonate snakes tongue-flicked the water surface near potential prey items while floating the front 1 / 5th of their bodies on the surface of 5 cm deep pans of water containing goldfish. They emphasized that the tongue-flicks barely broke the surface of the water (much as a small insect might) which attracted the goldfish and resulted in successful captures. This behavior

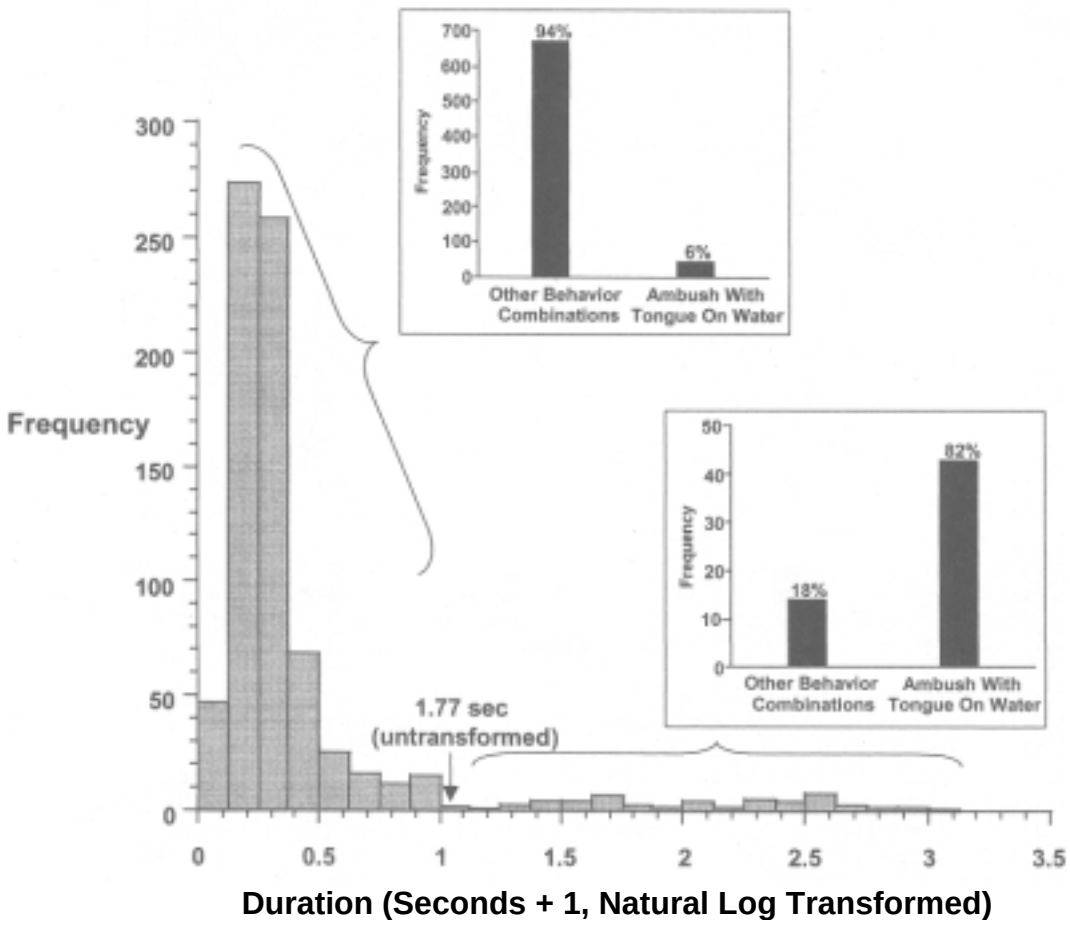

FIG. 2. Durations (in seconds +1 log transformed) of 773 tongue-flicking bouts from 24 individual snakes derived from a frame by frame analysis of videotapes. Untransformed data were divided at 1.77 sec duration, where a natural break in the distribution of data occurred. Inset graphs describe the frequency of observations on either side of the divide that were associated with each of the behavior and tongue-flick categories analyzed (see text).

occurred in an artificial setting with prey not natural to these snakes, and Czaplicki and Porter (1974) did not distinguish these luring tongue-flicks from those typically exhibited by snakes stalking prey in other situations (e.g., they made no mention of extended tongue-flick durations). Consequently, it is not possible to determine whether these putative luring events differed quantitatively (i.e., in duration) from typical chemosensory tongue-flicks, and therefore whether they were intentional (true feeding mimicry) or fortuitous (accidental feeding mimicry).

We have now observed the lingual-luring behavior described in this paper repeatedly in the field. It appears to differ from other long duration tongue-flicking that has previously been described (see Gove, 1979; Mushinsky, 1987; Ford and Burghardt, 1993), with the possible exception of arboreal vine snakes (e.g., genera *Oxybelis, Ahaetulla, Thelotornis,* and *Uromacer*), and rough green. snakes (*Opheodrys aestivus*) (see Gove, 1979; Lillywhite and Henderson, 1993; and references therein). Several authors have described prolonged extension of a rigid tongue in vine snakes which they associated with defensive situations, and that may also occur during prey-stalking (Kennedy, 1965; Keiser, 1975; Gove, 1979; Henderson and Binder, 1980). Lillywhite and Henderson (1993) noted prey-luring was one of several possible hypotheses proposed to explain this behavior but Keiser (1975), for example, argued that a luring hypothesis was not supported, favoring one of crypsis.

Gove and Burghardt (1983) described a specialized tongue-flick they observed in three fam-

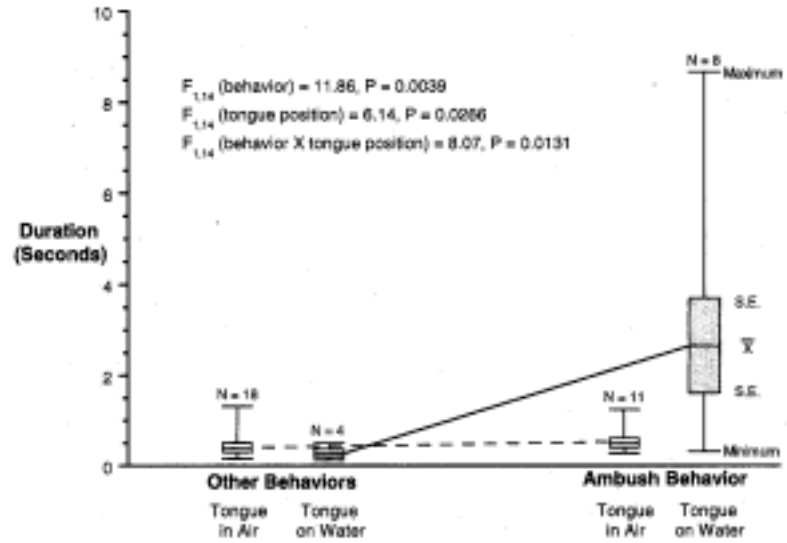

FIG. 3. Mean durations (+one standard error and the range) of tongue-flicks by behavior and tongue position categories. Since each of the 24 individuals exhibited some but not all of the possible combinations our final sample size was 41. Lines show the interaction between ambush position, tongue-tips on the water, and extended durations of tongue-flicking (=lingual-luring).

ilies of snakes that ". . . involves slow oscillations and long extensions . . .", which they noted appears ". . . when snakes are disturbed or threatened, and seem to serve as ritualized warning displays." Their description of this tongue-flick behavior, while superficially similar to the lingual-luring we describe here, emphasized slow oscillations in association with maximum extension, and an associated defensive context (Gove and Burghardt, 1983) (for more detailed analysis see Gove [1979]). They interpreted these long-duration tongue-flicks as serving ". . . either to scan the environment or to concentrate low-level odorants," and place them in either a social or defensive context (Gove and Burghardt, 1983). Specifically, Gove (1979) argued that slow-motion tongue-flicks in *Nerodia sipedon,* with its brightly contrasting red tongue and black tips, "serve as warning devices" when these snakes are disturbed (Gove, 1979). Pacific coast aquatic garter snakes have a red tongue with black tips similar to that described for *Nerodia sipedon* (Gove, 1979). We have observed slow-motion tongue-flicks in *T. atratus* when they are disturbed or handled, which match closely the description of Gove (1979), and we believe are likely warning displays. However, these "displays" are distinct from lingual-luring. While the bicolored tongue may act as a signal in warning displays, we believe that this brightly-contrasting color scheme also may serve as a visual cue to attract fish during lingual-luring. The lingual-luring we described here, while of long-duration, differs markedly from the long-duration tongue-flicks described by Gove and Burghardt (1983) in that only the tongue-tips move, and the movements are rapid and applied to a small area at the water surface (matching Gove's [1979] description of a "distal quiver'): Furthermore, this behavior is exhibited during focused ambush stalking of underwater prey, and not in the presence of a potential mate, rival or predator. .

The high variation in duration we observed with these lingual-luring tongue-flicks (Fig. 2) may be an expression of the range of possible responses between predator and prey. For example, luring duration may be longer when prey is in close visual proximity to the snake and appears to be responding, and shorter when the prey is further away and do not appear to be responding. Given, however, that lingual-luring does attract fish, we believe that it follows that this behavior has the capacity to increase foraging success and thereby enhance fitness.

Although it is not possible for us to definitively say that the lingual-luring behavior we observe by these snakes has no intentional or incidental chemosensory role, we believe that there are contextual aspects associated with this behavior that would negate or severly limit such a role. For example, the lingual-luring in our snakes is associated with flowing waters, and it is often directed at fish that are not only underwater and some distance away (upwards of 0.5 m), but that are positioned downstream of the ambushing snakes. Consequently, while a che-

mosensory explanation for this behavior may be conceivable, we believe the abiotic factors associated with ambush foraging adjacent to a cold, fast-flowing stream make such an explanation highly unlikely.

Drummond (1979) challenged the strictly chemoreceptive paradigm of snake foraging established by Burghardt (1968) (see also Burghardt and Pruitt, 1975) by demonstrating the importance of visual cues for amphibious foraging snakes (see also Drummond, 1985). In fact, Drummond (1983) noted that *T. couchii* (=*T. atratus*; see Rossman and Stewart, 1987 for taxonomic changes) was able to detect prey underwater at greater distances than three other species of garter snakes he tested. Furthermore, Schaeffel and deQueiroz (1990) reported that *T. couchii* (=*T. atratus*) had an unusual adaptation to enhance underwater visual acuity that involved constricting the pupils. It is probable that the role of the vomeronasal system is of secondary importance for many aquatic foraging snake species, especially those using lotic waters, such as the *T. atratus* population at our study site, where chemoreception can be compromised or prevented altogether by strong water currents and low water temperatures. Lillywhite and Henderson (1993) indicated that many arboreal snakes that are diurnal ambush predators depend heavily on vision for orientation to objects, and often exhibit associated behavior such as head swaying to gain additional parallax.

The garter snakes at our study site show a diet-related ontogenetic shift from predominately sit and wait predators as neonates and juveniles to active foragers as adults (Lind and Welsh, 1994). In addition to this shift in predatory mode (Huey and Pianka, 1981), our observations suggest that these snakes are also able to shift between, or integrate, visual and chemosensory modalities, depending on the microhabitat they are foraging in (e.g., in, under, or adjacent to the water), and the type of prey they are pursuing (i.e., fish, frogs, or salamanders). Similarly, Lillywhite and Henderson (1993) noted that diurnal active arboreal foraging snakes may be visually oriented or may use a combination of olfactory and visual stimuli (see also Holtzman, 1998). It may be that arboreal and aquatic habitats (especially lotic aquatic habitats) share abiotic attributes that present similar problems to snakes, such as the rapid diffusion of chemical signals. These situations may have favored the parallel evolution and refinement of a visual sensory modality over a chemosensory modality. If this is indeed the case, then an inclusive phylogeny of ophidian relationships based on the range of extant tongue-flicking behaviors (e.g., Gove, 1979) would need to include a derived clade (or clades) of visually-oriented, prey-lurers or stalkers. The tongue-luring behavior we describe here, and that also may occur in vine snakes and rough green snakes (Gove, 1979; Lillywhite and Henderson, 1993), can be considered a novel application of the tongue-vomeronasal system by visually-oriented snake predators. This unique use of what is typically a chemoreceptive organ in snakes, appears to fit the definition of a behavioral exaptation (Gould and Vrba, 1982).

Although we have observed lingual-luring behavior from May through September (the period of greatest snake activity), it may be less frequent during that part of the season when the more easily captured larvae of the foothill yellow-legged frog (*Rana boylii*) are abundant (unpubl. data). Consequently, we suspect the use of lingual-luring may vary considerably with changes in the relative densities of tadpoles and juvenile salmonids. While it is well established that particular species of snakes can show considerable geographic variation in foraging behavior (e.g., Arnold, 1977, 1981a, b, c; Drummond and Burghardt, 1983) and other life history attributes (e.g., Shine, 1987), it is less well documented that both seasonal, and individual, variation in traits such as prey choice and associated foraging behavior can exist within single populations of snakes (H. Welsh, pers. obs.; H. Greene, pers. comm.).

Given the fact that we have observed lingual-luring in neonate snakes at Hurdygurdy Creek, we suspect it may be innate in this population. However, we cannot eliminate the possibility that the behavior is learned. Therefore we hope to test this hypothesis by rearing and observing naive offspring for evidence of lingual-luring.

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