STIMULUS CONTROL OF CAUDAL LURING AND OTHER FEEDING RESPONSES: A PROGRAM FOR RESEARCH ON VISUAL PERCEPTION IN VIPERS

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ABSTRACT: Quantitative studies of perceptual mechanisms in vipers have focused on chemosensory tongue-flicking, in part because the prevalent sit-and-wait foraging habit provides few other clues about pre-strike prey recognition. Snakes that employ caudal luring offer a unique opportunity to quantify visual perception, and to infer cognitive functions when snakes use caudal luring, pursuit, or sit-and-wait predation depending on prey type. Stimulus control of caudal luring and other prey capture tactics were examined in four phylogenetically distant vipers: the Copperhead (*Agkistrodon contortrix*); the Sidewinder (*Crotalus cerastes*); the Massasauga (*Sistrurus catenatus*); and the Horned Adder (*Bitis caudalis*). While all four species feed on a variety of prey, the luring response of each species is evoked almost exclusively by a certain type of organism, and alternate strategies are used to capture other prey types. Feeding experiments and experimental manipulations using prey-like models suggest that these vipers readily discriminate between different types of prey through visual cues involving shape and/or movement features, and that they have evolved appropriate responses for capturing particular prey taxa. Intraspecific variation in stimulus control between populations of *S. catenatus* suggests that evolution of perceptual mechanisms for prey recognition and appropriate response operates on a fine scale. The potential exists to understand cognitive functions, such as decision making, and the evolution of prey recognition in vipers through studies of caudal luring and differential response to prey stimuli.

INTRODUCTION

Because most snakes experience the world from ground level, the common view is that the role of vision is minor compared to that of chemosensory or tactile modalities (Ford and Burghardt, 1993). Visual perception seems more difficult to evaluate than other mechanisms owing to a perceived scarcity of observable indicators that can be meaningfully interpreted. This problem is especially prominent in studies of vipers, since most of them use a sit-and-wait capture strategy that, until the strike, provides little or no information about prey recognition in the appetitive phase of the foraging sequence. Naturally, most studies of visual prey recognition have used actively foraging colubrids (e.g., Czaplicki and Porter, 1974, 1979; Herzog and Burghardt, 1974; Drummond, 1985; Chiszar et al., 1988a; Garcia and Drummond, 1995). Inroads have been made on very few pitvipers (e.g., Scudder and Chiszar, 1977; Chiszar et al., 1981; Gillingham and Clark, 1981), and almost nothing is known about visual perception in true vipers. Studies on visual release of chemosensory behavior in rattlesnakes tell us that visual cues are important in predatory sequences, but they do not necessarily reveal which visual cues are important in releasing predatory behavior.

The extent to which we can understand a perceptual modality through stimulus control (SC) experiments is exemplified by the well integrated research program on chemosensory aspects of predatory behavior (e.g., Chiszar et al., 1979; 1983a; 1988b; 1992; O'Connell et al., 1982; Furry et al., 1991; Waters et al., 1996). The multitude of well designed experimental studies has provided a robust picture of chemosensory SC in a large number of squamates. But SC research on vipers has focused mainly on mammal prey, perhaps artificially emphasizing the roles of certain sensory modalities in feeding behavior. Diets of vipers are diverse, and various strategies are used for capturing prey (Greene, 1997). Accordingly, we should expect perceptual mechanisms and SC parameters to show concordant diversity, with modalities other than olfaction playing prominent roles for certain prey types. Snakes that differ in feeding ecology may differ in emphasis on cues from a given sensory modality (Chiszar et al., 1986; Cruz et al., 1987). Investigations of the role of vision in predatory interactions are a next logical step, yet no research program exists to study visual SC in vipers. Analyses of responses to visual stimuli can potentially provide new insights to how snakes experience the world—specifically, how they perceive, integrate, and respond to cues in a spatial context.

In this paper I report visual SC research on four species of vipers, *Agkistrodon contortrix*, *Bitis caudalis*, *Crotalus cerastes*, and *Sistrurus catenatus*, with additional insights from current knowledge of other species. Much of this work was performed in a controlled laboratory setting with effective isolation of variables, but I also present findings from non-controlled feeding trials. Until more is known about visual perception in vipers,

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such descriptive and non-experimental data are clearly of value (Ford and Burghardt, 1993). Large numbers of observations on captives often suggest new experimental approaches. Likewise, watching animals in uncontrived situations may reveal phenomena that can be further studied in the laboratory.

SETTING THE STAGE
Research Perspectives

To develop a viable research program for the study of visual perception in vipers, we need behavioral indicators that are ecologically relevant and easily observable. Indeed, we have several to choose from. Orientation toward and initiation of chemosensory examination of prey may provide information about cue recognition (e.g., Scudder and Chiszar, 1977; Chiszar et al., 1981; Gillingham and Clark, 1981). Predatory pursuit is evidence for visual recognition when other cues are eliminated. Predatory striking is an effective indicator of visual discrimination when other variables can be controlled, especially when strikes are directed at prey dummies or animals isolated in containers. Surprisingly, caudal luring (CL) has been entirely neglected as a tool for studying visual prey recognition. Caudal luring is an ambush strategy employed by a relatively immobile predator whose tail display resembles the quarry of a more agile actively foraging predator, thus enticing it into striking range (R. Reiserer, unpublished). This behavior is particularly suited to studies of many viper species and, because it bears features unique among predator-prey interactions, has the potential to tell us things about the mental workings of snakes that other behaviors cannot (e.g., spatial perception).

Perceptual mechanisms in snakes were reviewed by Ford and Burghardt (1993), with a useful discussion of settings and methods. Greene (1973) reviewed defensive tail displays, suggesting experimental methods that apply equally well to studies of CL. Both of these displays are interpretable in a functional, ecological sense, but they may also be interpretable in considerations of cognition. A long and sometimes misinterpreted tradition in the study of cognitive ethology has sought insight into the inner workings of the animal mind (e.g., Uexküll, 1909; Griffin, 1976), and modern students of behavior have extended this ambition into studies of cognition in snakes (Burghardt, 1991, 1996). If it is possible to know what an animal is "thinking," or at least how it decides among alternative modes of responding, we will have to approach the problem through induction, and we must start with description (Tinbergen, 1963), not just of the behavior itself but of how it functions in communications with other animals (Griffin, 1991).

Stimulus Control and Caudal Luring as a Response Variable

For an animal to behave appropriately, it needs simple and accurate behavioral triggers (= cognitive structures sensitive to stimuli) that include a description of things or events (= stimuli) that are often variable and ambiguous in nature. Investigations of these behavioral triggers, whether inherited or learned, are the goal of SC studies. Five levels of SC have been defined (Herrnstein, 1990) and classified from least to most complex: (1) *Discrimination* is the standard level used for SC studies in the laboratory. At this level stimuli are explicitly defined and cannot be generalized or approximated. Chemical or tactile stimuli are examples of such defined categories; (2) *Rote categorization* is the ability to identify exemplars within a category by explicit recognition of each variant. This level is equivalent to possessing an unordered list of possibilities, outside of which identification is not achieved; (3) *Open-ended categorization* allows generalization across categories. At this level the animal can recognize variation in orientation, perceptual distance, apparent size, color, and so forth, yet still categorize the stimulus correctly based on some principle of similarity. The test of this level is demonstration of generalization; (4) *Conceptualization* is the level at which association arises, and the transfer of one stimulus or set of stimuli to an unrelated contingency is possible. Concepts need not be dependent upon learning (Herrnstein, 1990), as often assumed; and (5) *Abstract relation* is the level at which associations between and among concepts occur. This last level is difficult, but not impossible, to test for in nonlinguistic subjects. To clarify the first four levels, I offer some examples using water as the object to be categorized. Snakes probably cannot distinguish between water and vinegar (aqueous acetic acid), or between clean and dirty water through tactile cues, but they might do so using chemosensory or gustatory cues. Thus they may fail to discriminate with one sense but succeed with another. Discrimination is not merely the ability to detect a stimulus, but rather to distinguish it from other categorically similar stimuli. When a single category (e.g., water) is recognized—by a given modality—in several forms (e.g., clear pool, muddy pool, clear stream, clear droplets), but not others (e.g., muddy droplets) because of failure to

generalize, the animal is categorizing by specific recognition, or rote, though recognition of that form may be accomplished by other sensory modalities (e.g., by the tongue). When unfamiliar forms (e.g., muddy droplets) are recognized through generalization from other forms, say by recognition of reflectance properties, the animal demonstrates open-ended categorization. The conceptual level adds associative complexity to general recognition skills, as when an animal comprehends that falling water droplets form pools that can be found by searching. These examples make clear the need to isolate sensory information and to examine modalities capable of comprehensive representation of the environment.

Studies of visual perception, including infrared, may help to penetrate some of the territory that investigations of olfactory discrimination cannot. Although chemical learning has been demonstrated in rattlesnakes (Melcer et al., 1990; Furry et al., 1991), categorizations beyond the level of rote would be difficult to demonstrate with chemosensory experiments. So far, tests of chemosensory SC beyond the level of discrimination have not been attempted. Chemosensory behavior differs between rodent and lizard specialists (Chiszar et al., 1986; Cruz et al., 1987), and we may assume that variation in SC of feeding responses is prevalent. In some predator-prey interactions, olfaction may play little or no role in pre- or post-strike foraging behavior. We need a means of assessing this variation in vipers through indicators of visual prey perception and categorization.

Caudal luring is a way of actively participating in prey capture without expending the energy for active chase, and perhaps of minimizing exposure to the eyes of predators while doing so. The behavior is present in at least 36 species of viperid snakes (references in Ananjeva and Orlov, 1982; Greene, 1992; and reviews by Neill, 1960; Heatwole and Davison, 1976; Strimple, 1992; R. Reiserer and G. Schuett, unpublished), and probably many more. Caudal luring might have evolved from a displacement activity, an inappropriate, contextually functionless behavior that releases nervous tension in a stressful or anticipatory situation (Tinbergen, 1952). More likely, however, it is an intention movement (Daanje, 1950) derived from motor patterns involved in locomotion, a hypothesis first advanced by Greene (1973). In either case it is reasonably assumed that the behavior is associated with anticipation or general neural excitation.

Such a behavior provides the potential to study what constitutes motivation on a fine scale. By varying stimuli we can chisel away the extraneous information given off by a prey item and examine the effects of many permutations of a feeding stimulus, such as shape, size, color, movement pattern, orientation, and so on. Furthermore, by inducing abrupt cessation of luring, we might investigate the cues involved in detection of a predator (R. Reiserer, unpublished). Caudal luring may, indeed, allow us to explore the cognitive levels achievable by snakes. What can be said when a snake lures for both frogs and lizards? Does it conceptualize them as food, categorize them as separate items of food, or merely discriminate between some common stimulus and no stimulus at all? And what if only one is lured for and the other is pursued?

Caudal luring is not without limitations and challenges. A negative response could mean that a snake does not recognize the stimulus as prey, is not hungry, is sick, has detected the observer, did not see the stimulus, or something else. Conclusions must ultimately be based on positive responses. We can ameliorate this problem to some degree by coupling negative responses to positive ones in ordered sequences to eliminate motivational variables. Statistical comparisons of treatments with multiple trials are also useful. Because CL is, in most cases, restricted to juveniles of a species, investigators must acquire many neonatal specimens. There is a relatively short window of opportunity for studying the behavior in a given subject, so complicated experiments must be done expediently. This circumstance, however, also provides the opportunity to investigate ontogenetic causation of behavior modification. It is yet unknown what physiological changes precipitate cessation of CL. Another potential application for CL is in studies of the evolution of SC. When species that employ CL vary geographically in feeding ecology, they might also show changes in SC of luring behavior.

ANIMAL SUBJECTS AND EXPERIMENTS
Copperhead (*Agkistrodon contortrix*)

Background.—The Copperhead has an extensive range in the United States and a limited one in northern Mexico (see map in Gloyd and Conant, 1990). It occupies a variety of habitats, from woodland to relatively open grassland and swamps in the East to dry deciduous and coniferous forest and arid landscapes in the West. Ditmars (1907) first described CL in the Southern Copperhead (*A. c. contortrix*), but more useful sources are Neill (1948, 1960). Unpublished data (G. Schuett, pers. comm.) and those presented

here indicate that CL is represented in all races of this species. The diet of *A. contortrix* is broad and variable (Fitch, 1960, 1999), both geographically and ontogenetically. Prey include many invertebrate species, amphibians, lizards, snakes, birds, and mammals, the latter making up most of the adult diet in both numbers and mass, while juveniles take mostly other types of prey (Fitch, 1999).

Subjects and husbandry.—Observations of feeding behavior began in 1987 on six neonatal *A. c. phaeogaster* born in captivity, and four wild-collected individuals ranging from neonate to adult size. All originated from Butler and Greenwood counties, Kansas. Subjects were housed individually (captive born) or in groups of two (wild-collected) in 10–30 gal terraria with wood chip substrates and a rock shelter. Photoperiod (12L:12D) and heat (undefined gradient) were provided by 100 W incandescent light bulbs controlled by a timer. Water was provided in dishes ad libitum, and subjects were offered food weekly. Diets were varied among three groupings of two neonates, and consisted of neonatal laboratory mice (*Mus musculus*), frogs (*Acris crepitans*), and Tobacco Hornworms (*Manduca sexta*). Wild-collected snakes were provided all three food types. Further observations occurred on two *A. c. laticinctus* born 8 August, 1992, from a female collected in Love Co., Oklahoma, and five *A. c. phaeogaster* born in September, 1993, from a Douglas Co., Kansas, female. These five neonates were housed communally in a large oval stock tank (ca. L100 x W200 x H64 cm) at the University of Kansas Fitch Natural History Reservation (FNHR), but were later transferred to an indoor facility where they were housed in a plastic tub (L38 x W50 x H15 cm). Frogs (*Rana blairi* and *A. crepitans*) were used in five feeding trials with these snakes, and lizards (*Anolis carolinensis*) were used in seven trials. The *A. c. laticinctus* young were housed in large plastic boxes (L39 x W58 x H15 cm) with naturalistic substrates of leaf-litter and rocks, and sub-surface heating on one side of the enclosure. Photoperiod was similar to that mentioned above, except that low light often illuminated these snakes from another room during scotophase. Weekly or biweekly feedings consisted primarily of frogs (*A. crepitans*, *Hyla chrysoscelis*, *Pseudacris triseriata*, *R. blairi*, and *R. catesbeiana*), but lizards (*Eumeces fasciatus*) and various caterpillars (Lepidoptera larvae) were also offered. Most observations of *A. contortrix* took place in the last five hours of the photoperiod, but those at the FNHR occurred near midday.

Results.—Caudal luring was not observed in my earliest (1987) studies of *A. contortrix*, but different responses to various prey were recorded. Most noteworthy were differences between behavior toward caterpillars and frogs, both in predatory response and in prey handling behavior. The sight of a caterpillar elicited an immediate pursuit response, even from a distance of 50 cm. Copperheads moved toward caterpillars while emitting tongue flicks, swiftly seized them, and struggled with the writhing larvae in an attempt to swallow them as quickly as possible. Release was rare, but when it occurred the snake did not wait for the prey to become immobile before another ingestion attempt. Handling behavior of naive neonates was similar to that of adults. Ingestion times were, in general, short ($\overline{x}$ = 123 sec ± 55 SD, range 31–235 sec, N = 12), unless the larva was doubled over rather than swallowed from one end. Ingestion times for frogs were much longer ($\overline{x}$ = 475 sec ± 179 SD, range 207–741 sec, N = 8), even though prey mass often did not differ. Feeding behavior also differed qualitatively. Snakes adopted an ambush strategy for frogs, sitting still except for tongue-flicking (TF) and head orientations. They seemed, however, not to detect those that were close-by unless they moved. Occasionally, when a frog hopped near or on top of a snake, the snake reoriented in response, sometimes making direct lingual contact with the frog several times, only to have it escape. Indeed, capture success was so low that I began placing five or more frogs in the tank during feeding times. These prey were usually bitten and held. When a snake lost its hold and the prey escaped it was rarely found and ingested. The above observations merit comparison to behavior with mammal prey. The typical response is well known: introduction of a newborn mouse elicits TF, then one or a series of strikes, followed by close lingual examination and eventual (usually head-first) ingestion. In my studies neonatal mice were usually placed near the snake, because when placed at a distance they were frequently ignored. Moving the mouse closer almost invariably initiated predatory behavior.

Observations on the litter of two *A. c. laticinctus*, from Oklahoma and the five *A. c. phaeogaster*, from Douglas Co., Kansas, provided the opportunity to better quantify predatory behavior, with the inclusion of CL as a response. I recorded the response by a subject to a given prey item (frog, lizard, or caterpillar) and the means by which the snake captured the prey animal (Table 1). Success rate in this captive setting provides limited information, but a few features of

Table 1. Prey capture responses from 98 feeding trials with *Agkistrodon contortrix* using three prey types: H = held; R = released; CL = caudal luring; and P = pursuit. Asterisks indicate a shared value (1) also included in another value (14) owing to a combination of responses. Three CL responses were elicited by *Anolis carolinensis*, but those lizards avoided luring snakes and were not captured by that strategy. Only *Rana blairi* responded to CL. Other prey were *Acris crepitans*, *Hyla chrysoscelis*, *Pseudacris triseriata*, *Rana catesbeiana*, *Eumeces fasciatus*, and unidentified green caterpillars. Sit-and-wait predation occurred only for frogs and resulted in all but four frog captures.

Prey animal	Total trials	Total feedings	Prey typically held/released	Possible prey response	# times prey elicited response	# prey captured via response
Frog	51	39	H	CL	26	4
				P	5	0
Lizard	24	17	H or R	CL	3 + 1*	0
				P	14*	14
Caterpillar	23	23	H	CL	0	—
				P	23	23

each capture tactic may have ecological relevance. All caterpillars were captured on the first attempt with little effort, but lizard pursuits were often lengthy. Upon detecting an approaching snake, skinks usually sought shelter under leaves, sometimes evading the snake for >15 min. The snake continued moving to the place where the skink had disappeared and, with elevated TF rate, probed beneath the leaves, sometimes biting the concealed skink (N = 8), but other times pulling back and waiting poised for movement cues (N = 6). Such cues need not have been from the lizard. Rustling of leaves from a concealed lizard could reinitiate probing behavior by the snake. A few times (N = 4), the snake gave up momentarily and assumed a coiled posture where it last detected the skink. Tongue-flicking rate slowly declined to near baseline until movement was detected. The snake continued pursuit when the lizard came back into view (N = 2) or otherwise betrayed its presence. The one instance of CL for a skink appeared to be a misidentification by the snake. The skink had been dropped into the enclosure out of view of the subject and was rustling the leaves when luring began, but when the lizard became visible, luring instantly turned to pursuit. Three other CL events occurred when the only prey present were *A. carolinensis*, and snakes did not pursue these lizards.

Seventy-six percent of feeding trials with frogs elicited CL. The chemosensory probing seen in lizard stalking was not observed for frogs, but *A. contortrix* did use cues from displaced leaves to orient toward hidden frogs. These cues, however, did not result in the same exploratory chemosensory probing seen for lizard prey, and snakes remained stationary rather than pursuing frogs. Five "pursuits" for frogs were recorded, but all were short (< body length), none were suc-

cessful, three occurred after an unsuccessful strike, and each was followed by a bout of CL in the resulting uncoiled (or partially coiled) posture. Two observations of frogs seizing the tail of a snake occurred in the enclosure at the FNHR. Both times several *A. crepitans* and *R. blairi* were present in the tank. In the first case, one subject began to lure and a nearby *R. blairi* hopped over and bit the tail. In the second case, two individuals lured and the only *R. blairi* in the tank responded to one of them. Although *A. contortrix* struck at frogs that were moving (usually adjusting posture after a hop) within striking range, in all cases when a frog was attracted toward a luring snake, the snake waited to strike until the frog bit the tail. In one spectacular sequence, a subject struck and missed one frog and, while outstretched, continued luring. Another recently metamorphosed *R. blairi* approached from behind and seized the tail. The snake turned around part way, continuing to lure while appearing to wait for the next cue. Another bite by the frog caused the snake to advance another increment, and the snake struck the frog upon its third tail attack.

Although they elicited luring in *A. contortrix*, *A. crepitans* and *P. triseriata* were apparently not attracted to the tail lure (but see *S. catenatus* below), and all attracted frogs were ranids. One of the most intriguing observations was of a juvenile *A. c. laticinctus* successfully luring its sibling. The two subjects were sitting 15 cm apart when a *R. blairi* was introduced. When one snake began to lure for the frog, the other immediately swung its head around and advanced toward the lure with an elevated TF rate. The luring snake stopped moving its tail as its sibling arrived at the lure, and the pursuer made lingual contact with the tail a few times before withdrawing.

Discussion.—Copperheads clearly used both visual and chemical cues to detect skinks (first visual, then chemical), and the same appeared true for caterpillars. Pre-strike behaviors for these two prey animals were nearly identical, but post-strike behaviors differed. Skinks (and *Anolis*) were either held while envenomation took effect or struck and released, while caterpillars were engulfed as quickly as possible. Some sort of discrimination occurred, but it is unclear which sensory modality was responsible. The one observation of an *A. contortrix* attracted to the lure of its sibling suggests that information could be integrated by a combination of visual (initial stimulus = chemosensory releaser) and chemical (feeding response releaser; the dupe did not attack the tail) modalities (e.g., Gillingham and Clark, 1981; Chiszar et al., 1983b). The behavior of the duped snake was precisely that of predation on caterpillars, and this observation argues for visual recognition of larval insects. Frogs and some lizards were held after the strike, and the simple question arises: when was the "decision" to hold the prey made? This question cannot be satisfactorily answered at present, but clearly *A. contortrix* categorize frogs differently than skinks or caterpillars prior to the strike. Caudal luring might be a particularly beneficial response in *A. contortrix* populations that depend on anurans during early life, since frogs seemed nearly undetectable via olfaction. Some frogs, however, may be more easily detected via chemosensation, such as the subterranean *Gastrophryne* (Fitch, 1999).

Observations of *A. contortrix* searching for hidden lizards raise tantalizing questions. Are *A. contortrix* capable of conceptualizing with respect to prey? When skinks were beneath leaves they did not present any visual cues attributable to the lizard itself. The leaves were, in fact, the signal generators. Copperheads seemed to readily associate the "behavior" of leaves to the presence of a skink. If chemical cues were the main locator stimuli, then snakes would probably continue searching instead of waiting for a visual cue (sometimes coiling up nearby). Similarly, snakes were cued to the presence of frogs by leaf movements when the frog was not in view, but behavior toward concealed frogs differed from that toward skinks, in that pursuit (but not orientational exploration) was inhibited with frog prey. This observation raises the possibility that inhibition of pursuit was influenced by the snake's prior experience with, and expectations of, the prey present, and that the SC linked to leaf movement is an association contingent upon prior experience with the prey animal.

Associative relationships between objects and stimuli are the hallmark of the conceptual level of SC, and it seems hard to deny that *A. contortrix* reached this level in associations between leaves and skinks (and likely frogs).

These observations suggest a further extension of cognitive research in snakes (and other squamates) to encompass mental capacities, such as object permanence, currently thought to occur only in some higher vertebrates (e.g., Doré and Dumas, 1987). Without the capacity to attribute continued existence (object permanence) to a prey animal that has moved out of their perceptual field, snakes would presumably discontinue predatory behaviors (i.e., CL, pursuit) soon after prey were out of sight, yet *A. contortrix* often continued the predatory sequence (see later discussion). Such behavioral versatility goes beyond categorization, and requires a rich cognitive representation of objects and events (Etienne, 1984) in addition to acute recognition skills. Copperheads showed evidence of keen recognition skills, but they appeared not to categorically recognize *A. carolinensis*. Or did they? These lizards frequently moved by jumping (saltations) and they adhered to the walls of the enclosure just as frogs sometimes did. By using skinks as a model lizard and human criteria for grouping, these snakes failed to correctly categorize *Anolis*, but they may not have done so by their own criteria. This is an interesting reminder that animals need not categorize things as we do. They may categorize more by behavioral cues than by morphology—if it moves like a frog, it is a frog.

Massasauga (*Sistrurus catenatus*)

Background.—The Massasauga ranges across a broad diagonal band of grassland that stretches from southern Ontario and New York to southeastern Arizona and northern Mexico (see map in Ernst, 1992). In the northern and central United States, *S. catenatus* is found in fairly moist to swampy habitats, but southwestern inhabitants occupy dry desert grasslands. The diet of this rattlesnake is geographically and ontogenetically variable, and includes invertebrates, fishes, amphibians, reptiles, birds, and mammals (reviewed by Ernst, 1992). Juveniles from eastern populations include frogs in their diet, but those of desert regions feed primarily on lizards (Lowe et al., 1986; Holycross and Mackessy, 2002). Caudal luring was described by Schuett et al. (1984) in the eastern race (*S. c. catenatus*), but the behavior is ubiquitous (see below).

Subjects and husbandry.—Feeding observations were made on ten *S. c. tergeminus* neonates (group 1) born 17 August 1991 to a female from Russell Co., Kansas (a mesic region). Sexes were determined by H. Fitch to be 1:1. Neonates were housed individually in plastic tubs (L51 x W27 x H20 cm) with screen lids, sand and gravel substrate, a rock shelter, and a water dish. Heat and photoperiod were controlled automatically, as indicated above for *A. contortrix*. Nine of these snakes were divided into three subgroups of three individuals, and each subgroup received a diet of neonatal laboratory mice, frogs, or lizards (*A. crepitans* and *E. fasciatus*), or a mixture of mice, frogs, and lizards. Additional experiments were conducted on 17 (10 male: 7 female) captive bred neonatal *S. c. edwardsii* from five litters (group 2) born at Arizona State University in the fall of 1996 (donated by A. Holycross). The parents of these snakes were collected in Cochise Co., Arizona (a xeric region), and were long-term captives from H. Greene's collection at the University of California, Berkeley (UCB). Desert Massasauga neonates were housed at the Field Station for Behavioral Research (FSBR) at UCB. Enclosures and substrates were similar to those of *S. catenatus* above, except that enclosure lids were omitted to allow introduction of prey items without disturbance. A thermal gradient was provided by subsurface heat tape and additional heat was supplied by 100 W incandescent light bulbs suspended 60 cm above the substrate. Ambient temperature was 22–26°C. Photoperiod was controlled automatically (12L:12D) with both incandescent and flourescent fixtures. Two of these snakes had fed on neonatal mice and were excluded from feeding experiments, but the others were ingestively naive when feeding trials began. All conclusions are based on trials that occurred in the latter half of the photoperiod.

Methods: Feeding trials.—In group 1, six subjects were exposed to frogs and lizards, but three of those also received mice as prey. Feedings occurred weekly and subjects were exposed to one lizard or two frogs at a time. Feeding behavior was noted for interesting cases, but no attempt was made to determine the frequency of responses. In group 2, timed feeding trials took place in the home enclosures, with blinds in front of the enclosures to reduce visual disturbance from observers. Enclosures were situated on a concrete floor and the blind (700 cm tall) spanned the room. Twelve healthy, ingestively naive snakes were selected and equally partitioned for feeding trials using two prey types, lizards and frogs. Two phases of feeding

experimentation followed. For the first phase, I chose prey species that either occur in the natural environment of *S. c. edwardsii*, or are represented by close analogs. Anuran species were *Scaphiopus couchii* and *Spea hammondii*, and lizard species were *Uta stansburiana* and *Sceloporus occidentalis*. Food animals were abundantly available from laboratory reared stock or from local populations. Both feeding treatment groups received one trial per week for two weeks, totaling 12 trials per treatment. In the second phase, I experimented with two other frogs (*Hyla regilla* and *H. squirella*) and another lizard (*Anolis sagrei*) obtained locally or from a dealer. Initially, two treatments were designated, one for each prey type, but it soon became clear that the snakes would not feed on frogs. After two weeks, subjects in the frog feeding treatment were, by necessity, allowed to begin feeding on lizards and young mice. Phase two feeding trials with frogs coincide with a mixed diet for snakes in the frog treatment, but the lizard treatment did not receive other prey. An additional 18 trials per treatment gave a total of 30 trials.

Results: Feeding trials.—Caudal luring was observed 16 times in group 1 neonates, always for frogs (*Acris*). Frogs were attracted close enough to bite the tail lure on two occasions. In one case, the frog jumped onto a wall of the enclosure and maneuvered itself so that its head and body were oriented downward toward the luring snake poised on top of a rock slab. The frog lunged from approximately 18 cm and bit the tail. The frog was seized and held, as was typical for all frog predations. In the other case, the luring snake's attention was apparently focused on one frog when another approached and bit the tail; the snake turned its head, but the frog escaped before the snake could strike. In five additional instances, frogs did not actually bite the tail, but oriented toward it and approached the subject, whereupon they were bitten. *Sistrurus catenatus* seemed much less likely than *A. contortrix* to wait for an approaching frog to bite the tail before striking, and luring seemed to be used to coax the frog close enough to allow a strike. Ten feedings on skinks (*E. fasciatus*) all resulted from pursuit and capture. Stalking included both fast and slow advances, and capture times ranged from a few seconds after introduction to about 30 min.

The behavior of neonatal *S. c. tergeminus* from mesic habitats in Kansas differed from that of *S. c. edwardsii*, the desert form. The former lured for and fed on frogs but pursued lizard prey, whereas the latter lured for lizards and did not eat frogs. During the first

12 frog feeding trials in group 2 subjects, only two were struck (not bitten and held), but no ingestion took place. In the subsequent 18 trials no frogs were struck. The refusal of frogs did not appear to be due to a lowered threshold for detecting or responding to frogs. Indeed, frogs frequently elicited alert behavior (TF and head orientations), and occasionally a short pursuit. Caudal luring was never observed during any frog presentation, even though the hylids appeared sufficiently animated to elicit the behavior (e.g., in *S. c. tergeminus*). Luring for lizards was observed 13 times during feeding trials (but many more times in non-experimental trials), with four probable prey attractions. Attracted lizards were struck before reaching the snake and never actually bit the tail. Head orientation and deliberate movement toward a luring snake was considered successful CL. Struck lizards were most often held, but occasional releases usually resulted in successful trailing and ingestion. Although *A. sagrei* were the main feeder lizards for *S. c. edwardsii*, only once did that lizard elicit CL. The locomotory behavior of these arboreal lizards differed from ground-dwelling species, and their movement pattern may generally be insufficient stimulus for CL (but see *A. contortrix,* Discussion above).

Methods: Experiment 1.—This experiment was conducted in two parts to test whether movement or gross shape differences between lizards and frogs influence the performance of CL (part 1), and to examine the influence of fast and slow movement on the striking response (part 2). In part 1, experimental manipulations took place in an arena made of a large plastic tub (L150 x W75 x H25 cm) filled with sand (8 cm deep) and small gravel. The bottom and frame were removed from a 10 gal terrarium (L51 x W25 x H30 cm) and this assembly formed a central chamber in the arena. A blind (150 x 150 cm) minimized disturbance, allowing top side observation and videotaping from a horizontal distance of ca. 1 m and a vertical elevation of ca. 2 m, or lateral side observation from a distance ca. 1 m. Ten subjects were selected for random presentation of six stimulus conditions and one non-stimulus condition. Subjects were placed in the arena chamber and allowed ≥ 30 min to acclimate. Stimuli were used to elicit CL and other predatory behavior as follows: two live animal conditions were scored positive or negative during the first five min of presentation: (1) two lizards were released into the outer arena, and (2) five toads were released into the outer arena. In the remaining conditions, two prey dummies were used, a dowel rod

(50 mm x 9 mm dia.) and a polystyrene foam sphere (25 mm dia.). Each dummy was pulled by a thread in a rectangular path around the outer arena so that it stopped where it started. The dummy's movement was guided by vertical posts, near three corners of the arena, that kept it from contacting the glass chamber. The remaining four stimulus conditions were as follows: (1) dowel rod pulled in long, fast (lizard-like) increments, (2) dowel rod pulled in short saltatory (frog-like) increments, (3) sphere pulled in long, fast increments, and (4) sphere pulled in short saltatory increments. At the end of each frog treatment (while frogs were still present), a dowel was pulled once or twice around the arena to elicit CL. This procedure was used heuristically to determine whether the subject was sufficiently motivated to lure for potential prey. Data were discarded and the trial re-performed the following day (N = 1) if CL could not be provoked. All subjects were either returned to their home enclosures after an experimental session and another subject was placed in the arena, or they were left in the arena overnight and presented with a different stimulus on the following day. Thus all stimulus conditions occurred on different days, and presentation order was varied between subjects. Friedman's repeated measures analysis of variance (ANOVA) on ranks was used in conjunction with the Student-Newman-Keuls method of pairwise comparisons to evaluate differences between treatments. Part 2 of this experiment tested the same 10 individuals for the tendency to strike at a moving dowel. Each subject was tested once in its home enclosure. The dowel was lowered into the enclosure by the attached thread and was left stationary for several minutes. With the aid of a guide wire, the dummy was pulled in a path that brought it within striking distance of the subject (3–5 cm). Two treatments consisted of (1) a fast drag (ca. 0.75–1 m/s) and (2) a slow drag (ca. 0.1–0.2 m/s). Wilcoxon Signed Rank Test was used to compare treatments.

Results: Experiment 1.—In part 1, dummies that moved in fast, long, linear intervals elicited luring more often than those that moved by saltation (Fig. 1). Significant statistical differences were found ($\bar{x} = 32.8$, $df = 5$, $P < 0.001$), so all pairwise comparisons were tested to find the pattern of significance between treatments (Fig. 1). Once during a trial and twice in post-trial sessions with three of the ten subjects, a mixed strategy of luring and pursuit occurred with lizards as stimuli. Stationary CL always preceded this mixed strategy, and twice it followed attempted strikes. The snakes slowly stalked lizards while undulating their
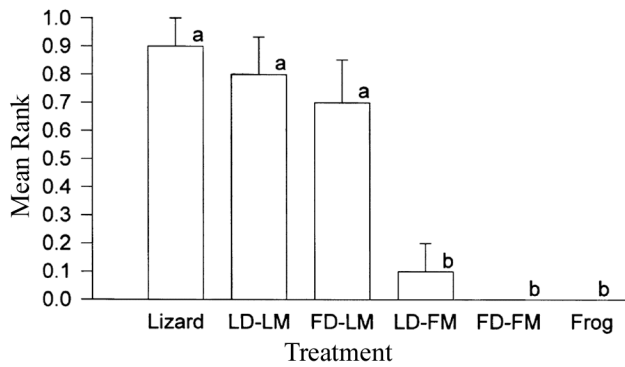
Fig. 1. Mean ranked responses of 10 Desert Massasaugas (*Sistrurus catenatus edwardsii*) to six stimulus conditions. L = lizard; F = frog; D = dummy; M = movement. Treatments marked with the same lowercase superscript do not differ at the 0.05 significance level, but differ from alternatively marked treatments.
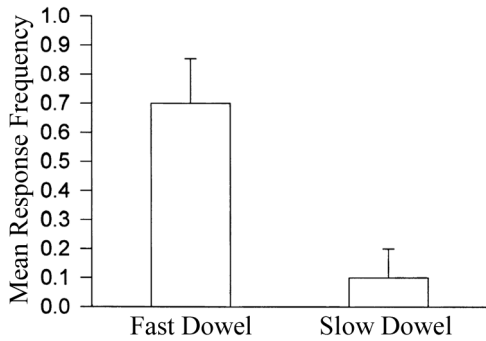

Fig. 2. Prey dummy striking by 10 Desert Massasaugas (*Sistrurus catenatus edwardsii*). Dowel = 50 mm X 9 mm diameter.

tails and TF occasionally. Visual tracking and TF occurred in trials with frogs, but not CL. In part 2, *S. catenatus* struck fast moving prey dummies significantly more often than they struck slow moving ones ($P = 0.0165$, Fig. 2).

Methods: Experiment 2.—When Experiment 1 was complete, there were five individuals from group 2 that were never exposed to young mice. While feeding the other subjects I noted that visual cues from neonatal mice seemed ineffective for releasing predatory behavior in naive snakes, while chemosensory cues appeared necessary for stimulating feeding behavior. As young snakes gained more experience with mice, however, they exhibited behaviors (e.g., stalking from a distance) that suggested visual recognition. Experiment 2 was designed to test whether naive *S. catenatus* learned to use visual cues associated with nestling mice. The five subjects were tested in three sequential phases. Condition 1: a neonatal mouse (≤ 1 week old) was inserted into a 25 ml vial
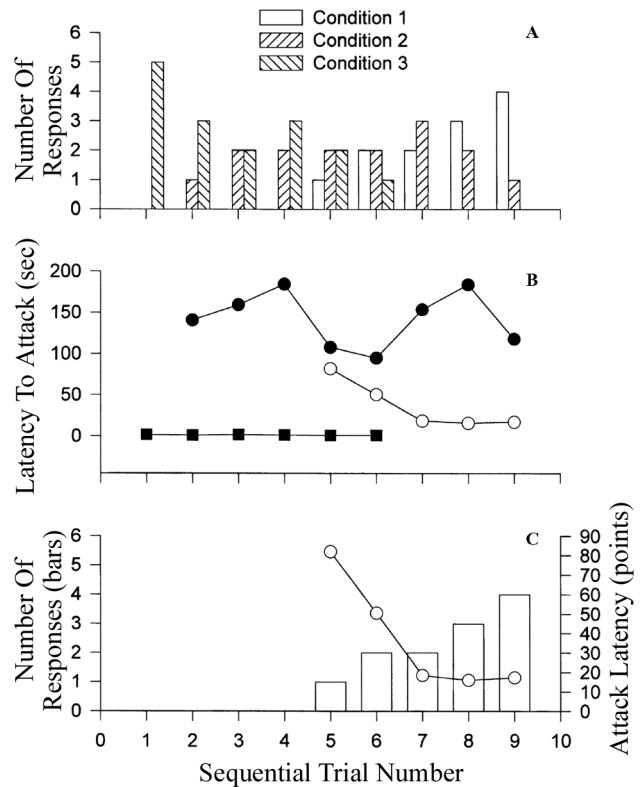

Fig. 3. Learning of mouse visual cues by five naive Desert Massasaugas (*Sistrurus catenatus edwardsii*). (A) Number of responses during three stimulus conditions. (B) Mean attack latency for each stimulus condition. Condition 1 = neonatal mouse in vial 10-12 cm from snake (open circles); Condition 2 = naked neonatal mouse 10-12 cm from snake (solid circles); Condition 3 = neonatal mouse placed 1-2 cm from subject (solid squares). (C) Response frequency and attack latency in Condition 1 plotted together. Bars = numbers of responses; points = mean latency to attack. Number of observations used to calculate mean attack latency are provided by the corresponding response frequency bar.

with forceps and a tight fitting cork was used to seal it in. The vial was placed 10–12 cm from a subject and left for 5 min. If the snake failed to approach, the trial went to Condition 2: the mouse was removed and placed in the shallow depression left by the vial. If the snake failed to approach within 5 min, the trial went to Condition 3: the mouse was moved with forceps to a distance of 1–2 cm. If the snake showed no interest or was frightened, the mouse was removed, but the trial was counted as one in the succession and the subject was moved on in the trial order. Besides two refusals, all subjects were provided reinforcements (the mouse) after each trial. Each individual was tested nine times, with at least 7 days between successive trials. Latency to attack was determined using a stopwatch, and was scored either as time to strike (conditions 2 and 3) or

time to close (≤ 1 cm) chemosensory examination (for condition 1). Spearman's rank order correlation was used to analyze the effects of experience on response frequency.

Results: Experiment 2.—Differences in feeding behavior toward neonatal mice clearly varied with experience (Fig. 3). There was a significant association between experience (i.e., sequential trial order) and frequency of response for condition 1 ($r_s = 0.95$, $P < 0.05$). Latencies to attack (Fig. 3b) showed a decreasing trend for condition 1 and no trend for conditions 2 and 3. Snakes never struck at mice in vials, and chemosensory examinations were very short (ca. 5–10 sec). After brief examination, snakes turned away without lingering.

Discussion.—Like *A. contortrix*, *S. catenatus* discriminated between frogs and ground-dwelling lizards. However, *S. c. edwardsii* showed no interest in eating frogs and did not lure for them. Luring for lizards may be derived in *S. c. edwardsii* or lost in *S. c. catenatus* and *S. c. tergeminus*, but the necessary phylogenetic data are not yet available to make this determination. In the published description of CL in *S. c. catenatus* (Schuett et al., 1984), only frogs were used as prey, and my sample of lizard feedings (N = 10) for *S. c. tergeminus* was too small to establish that lizards do not stimulate CL. There is, nevertheless, good evidence that geographical variation in SC of CL occurs in this species. Because the desert environments inhabited by *S. c. edwardsii* are relatively recent formations (Fredrickson et al., 1998), the data presented here suggest that a rapid change in SC has occurred, such that in desert populations there has either been a transfer of SC (for both CL and feeding response) from frogs to ground-dwelling lizards or a deletion of frogs from the category of prey. The change in SC of CL most likely resulted from a shift in the movement pattern that releases the behavior, rather than being specifically tied to "lizard" morphology (evidenced by low CL response to *Anolis*). Interestingly, this SC transition does not appear to be complete. *Sistrurus c. edwardsii* retains a low frequency of stalking behavior for lizard prey. Other SC changes (e.g., chemosensory) are probably associated with that suggested here. Part 2 of Experiment 1 further implicates movement as a primary factor in visual prey recognition, and suggests that simplified representations of prey are common. Fast moving dowels elicited striking, but slower dowels were struck less frequently, suggesting that speed influences resolution. The sudden appearance of an appropriately sized object may trigger reflexive striking, whereas slower objects can be resolved by the sensory and nervous systems.

In this study, two out of 10 frogs bit the tail of luring *S. c. tergeminus* neonates, but snakes did not always let frogs (*Acris*) approach the tail before striking. In the previous report on CL in this species (Schuett et al., 1984), snakes struck only following a tail bite by the frog (*Rana* spp.). *Sistrurus c. edwardsii* never let lizards bite the tail, nor did *C. cerastes* (R. Reiserer, unpublished), but *A. contortrix* did. Variation in this behavior might be either geographical or prey-specific, with some feature of ranid frogs producing the necessary stimulus for behavior variation. Logically, rattlesnakes should be less inclined than rattleless vipers to let an animal bite the tail tip, because trauma to the rattle button could result in a less effective lure or perhaps a damaged or deformed rattle in later life. However, because frogs (especially small ones) have weak, toothless jaws (Duellman and Trueb, 1994), bites by frogs may not pose as much threat of damage as lizard bites.

Experiment 2 generated a mouse visual cue learning curve for *S. c. edwardsii* (Fig. 3c). Stalking behavior observed in *S. c. edwardsii* that had learned to recognize neonatal mice was similar to that observed in *A. contortrix* stalking caterpillars or skinks. Tongue-flicking was first initiated, followed by pursuit. In *A. contortrix*, however, the behavior was performed by naive as well as experienced snakes, whereas *S. c. edwardsii* apparently needed conditioning before the response to mice was initiated. An obvious ecological explanation is that in nature a snake would never encounter a neonatal rodent in a well lit situation and, therefore, would have no need for inherited visual recognition of that prey. Interestingly, there are no obvious learned components to CL in snakes. Further explorations might reveal conditioned CL responses, but artificially reduced success rates (i.e., enclosure experiments) and even an apparent aversive stimulus (striking glass) did not seem to diminish the behavior. These data support the view that a mosaic of innate and plastic responses characterizes feeding behavior in vipers.

Sidewinder (*Crotalus cerastes*)

Background.—The Sidewinder is restricted to desert habitats in the southwestern United States and northern Mexico (see maps in Campbell and Lamar, 1989; Ernst, 1992). This species is typically associated with Creosote (*Larrea tridentata*) flats and wind-swept dunes, but it also occurs on rocky substrates.

Crotalus cerastes is the only rattlesnake that partially buries down (= crater formation) in loose substrates in a manner similar to that of African viperine sand-dwellers. The behavior is functionally associated with hunting and thermoregulation (Brown and Lillywhite, 1992). Adult *C. cerastes* feed mainly on rodents and lizards (H. Greene, pers. comm.), but birds and snakes are also eaten (Funk, 1965). Juveniles feed primarily on lizards, which are usually held following the strike, and an olfactory SC study suggests that they rely more heavily on vision than chemosensation during predatory encounters with lizards (Chiszar and Radcliffe, 1977). A description of CL in this species awaits publication (R. Reiserer, unpublished).

Subjects and husbandry.—Details of husbandry are described elsewhere (R. Reiserer, unpublished), but were similar to those of *S. c. edwardsii*. Experiments took place at The University of Kansas Animal Care Unit.

Methods: Experiment 1 (Movement Variation).—Observations of 54 neonatal *C. cerastes* were made either in the individual housing enclosures or in a wooden box arena (L122 x W122 x H38 cm) lined with a layer of plastic sheeting. The inside walls were covered with paper. Sand formed the substrate and the center was occupied by a glass chamber (L51 x W25 x H30 cm). Caudal luring was provoked either by live prey or by prey dummies. Five individuals were chosen at random from 12 neonates that consistently lured when presented with prey or prey dummies. Each subject was tested three times (in a given treatment) for 1 min by presenting a blue dowel rod (50 mm length x 9 mm diameter = D-1), glued to a length of beige thread. The three trials of each treatment were performed in random order with respect to all other trials. Some subjects received more than one trial per day, but not of the same treatment. The rules I used were: (1) if the subject lured during the first trial in a given day, it could receive a second trial after 30 min had elapsed, but if it did not lure in the first trial it was returned to its home enclosure, and (2) if the next trial in a subject's scheduled order was of the same treatment, no second trial was performed on that day. Upon placement in the arena, snakes were allowed to acclimate for at least 30 min, or until they formed a resting crater. The dummy was lowered into the observation arena and dragged for approximately 90 cm along the wall that was directly in front of the subject. The dowel was hidden from view by a blind until it reached the sand. Observations were made through

cracks (ca. 2 cm wide) between the draped paper. Four treatments, each consisting of three trials, were administered to each of the five subjects. Treatments consisted of: (1) a smooth, slow movement of the dowel (ca. 1 cm/sec), (2) a smooth, fast movement (ca. 50 cm/sec), (3) a fast, jerky movement (ca. 50 cm/sec), and (4) a control in which the dowel was lowered into the enclosure but left stationary. Response to the stimulus was scored as either presence (1) or absence (0) of tail undulations, and blocks of data for each snake were scored as ranks (0–3). No attempt was made to score the intensity of the display, but most luring episodes were vigorously performed. For this and the following experiments, Kruskal-Wallis one-way ANOVA on Ranks was used across treatments and pairwise comparisons (significance = 0.05) were made using Student-Newman-Keuls test.

Results: Movement Variation.—Caudal luring was observed at least once among all treatments that involved movement of the dowel (Fig. 4a). However, the average number of positive responses differed significantly between the slow and the fast movements ($H = 16.4$; $df = 3$; $P < 0.001$). Pairwise comparisons showed that both fast movement treatments differed from slow and no movement treatments, but these pairs did not differ from each other.

Methods: Experiment 2 (Length Variation).—To test whether sensory bias exists toward objects that resemble lizards more than other organisms, this and the following five experiments were conducted. Trials were performed in the observation arena as described for the last experiment. Methods were similar except that a different set of randomly chosen subjects was tested, there were five treatments instead of four, length of the blue dowel was varied instead of movement, and the "no movement" treatment was replaced with a no stimulus (NS) treatment in which no dowel was placed in the enclosure. The latter treatment consisted of a 1 min observation of the snake before a trial in which a stimulus was given. Treatments involved dowels of the following dimensions (length x diameter): (1) 10 x 9 mm (D-0), (2) D-1, (3) 100 x 9 mm (D-2), and (4) 400 x 9 mm (D-3). The speed of the motion used was standardized to the fast, smooth motion from the previous experiment (ca. 50 cm/sec).

Results: Length Variation.—Length was an important factor in eliciting a luring response ($H = 21.6$; $df = 4$; $P < 0.001$; Fig. 4b). Pairwise comparisons produced the following groupings of treatments that did not differ significantly from each other, but differed between groupings: (D-0, D-3, NS) and (D-1, D-2).
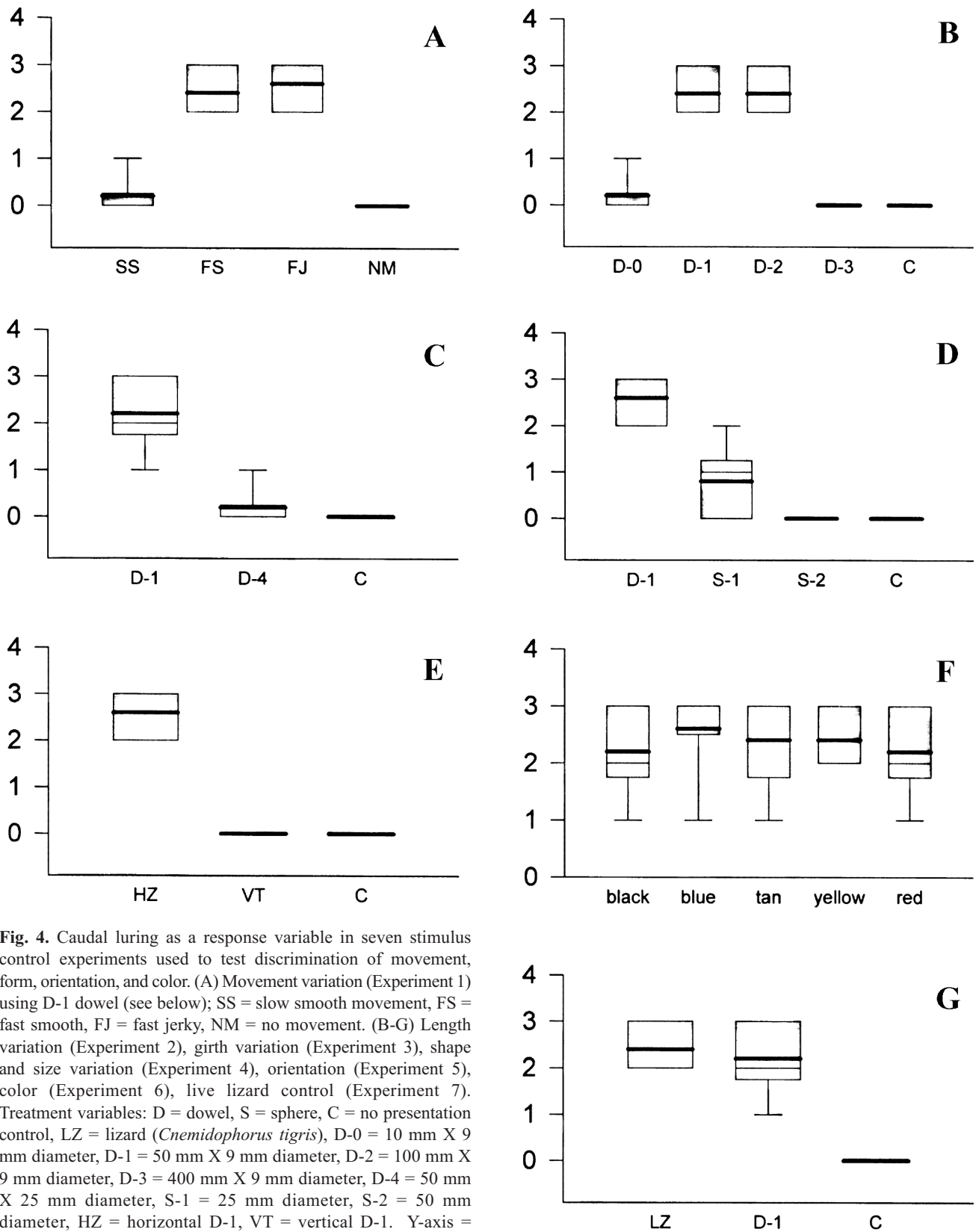
Fig. 4. Caudal luring as a response variable in seven stimulus control experiments used to test discrimination of movement, form, orientation, and color. (A) Movement variation (Experiment 1) using D-1 dowel (see below); SS = slow smooth movement, FS = fast smooth, FJ = fast jerky, NM = no movement. (B-G) Length variation (Experiment 2), girth variation (Experiment 3), shape and size variation (Experiment 4), orientation (Experiment 5), color (Experiment 6), live lizard control (Experiment 7). Treatment variables: D = dowel, S = sphere, C = no presentation control, LZ = lizard (*Cnemidophorus tigris*), D-0 = 10 mm X 9 mm diameter, D-1 = 50 mm X 9 mm diameter, D-2 = 100 mm X 9 mm diameter, D-3 = 400 mm X 9 mm diameter, D-4 = 50 mm X 25 mm diameter, S-1 = 25 mm diameter, S-2 = 50 mm diameter, HZ = horizontal D-1, VT = vertical D-1. Y-axis = response rank in A–G. Box plots represent mean (thick line) and 5th (thin line), 10th, 90th (box), and 95th (bar) percentiles.

Methods: Experiment 3 (Girth Variation).—Trials were performed as indicated above using another set of randomly chosen subjects. Three treatments were administered using (1) D-1, (2) a 50 x 25 mm dowel (D-4), and (3) NS.

Results: Girth Variation.—Girth and/or volume also appeared to be an important mediator of CL ($H = 11.7$; $df = 2$; $P < 0.01$; Fig. 4c), and post hoc comparisons resolved differences between D-1 and D-4. The D-4 treatment did not differ significantly from the NS treatment.

Methods: Experiment 4 (Shape and Size Variation).—Treatments consisted of (1) D-1, (2) a 25 mm dia. styrofoam sphere (S-1), (3) a 50 mm dia. sphere (S-2) made from wadded up paper wrapped with tape, and (4) NS. Trials were similar to the preceding experiments in other respects except that the dowel and small sphere were blue and the large sphere was gray.

Results: Shape and Size Variation.—Size and shape factors influenced CL ($H = 15.7$; $df = 3$; $P < 0.001$; Fig. 4d). The following significance groupings were found by pairwise comparisons: (D-1) differed from (S-1, S-2, NS).

Methods: Experiment 5 (Orientation).—Trials were administered in the housing enclosures of the subjects because this facilitated stabilization of the vertical dowel by resting it against one wall of the enclosure. However, the dowel (D-1) was about half the distance from the subjects as in other experiments, and traveled about half the distance during the trial. The dowel and a guide wire were lowered into the enclosure and left stationary near the wall opposite the subject. Thirty minutes elapsed before the trial was performed, at which time the dowel was either (1) erected into a vertical orientation and moved smoothly along on the guide wire, or (2) dragged in a horizontal orientation facilitated by a different position of the guide wire. If the snake was cratered near one of the short walls of the enclosure, it was disturbed with a long wire and left for 30 min or more to resettle. Observations were made from behind a paper blind (52 cm tall) that spanned the room.

Results: Orientation.—Orientation was very influential in mediating CL ($H = 13.5$; $df = 2$; $P < 0.001$; Fig. 4e). Vertical orientation compared with the NS treatment, producing no luring responses.

Methods: Experiment 6 (Color Variation).—Treatments were similar to those of the length variation experiment, except that color was the dependent variable. Treatments were administered using five D-1 dowel rods, four of which were painted either black, blue, yellow or red; a fifth dowel was left unpainted (= tan) and was similar in color to the sand substrate.

Results: Color Variation.—Color was not a significant factor in SC of CL ($H = 1.37$; $df = 4$; $P = 0.849$; Fig. 4f).

M*ethods: Experiment 7 (Live Lizard Control).*—The preceding experiments demonstrated that objects within a range of sizes elicit CL in young *C. cerastes*. The following experiment compared a D-1 dowel to live lizards using five subjects. Treatments and trials were similar to those in other experiments, except that one treatment consisted of placing a live, well-heated lizard (*Cnemidophorous tigris*) into the observation arena and observing the snake's response during a 1 min period. Because the lizard's movement could not be controlled, the trial timer was started when the lizard began to explore. This treatment supplied a continuous stimulus so the dowel rod treatment was extended to 1 min (or until CL was provoked) of discontinuous but smooth movements along one side of the arena, resembling the explorations of a lizard. A NS treatment was also performed for comparison.

Results: Live Lizard Control.—Differences found with ANOVA ($H = 10.3$; $df = 2$; $P < 0.01$) were due to the NS treatment. The dowel and lizard treatments did not differ significantly (Wilcoxon Signed Rank test, $P = 0.750$; Fig. 4g).

Discussion.—These experiments are discussed with reference to additional findings to be published elsewhere (R. Reiserer, unpublished). Experiment 1 correlated well with CL episodes in snakes presented with live prey. Caudal luring intensity decreased when movements by lizards were slight or absent, even when those animals were in close proximity and in full view of the snake. The latter observation suggests that the prey recognition system of *C. cerastes* lacks resolution. Because dowel rod dummies can elicit the same CL response as live lizards, it follows that legs, heads, and tails are either superfluous information or cannot be resolved visually. Movement pattern was not adequately addressed in Experiment 1. The fast, jerky movement used in one treatment did not resemble saltation, but rather the starts and stops of a ground-dwelling lizard, thus both of the fast movement patterns were lizard-like. Other ecologically relevant locomotor patterns (e.g., climbing) may be difficult to reproduce in the laboratory (but see below). Both *C. cerastes* and *S. catenatus* struck very slow moving lizards when they passed nearby, but slow moving dowel rods were usually ignored. This observation needs to be substantiated systematically

for *C. cerastes*, but if resolution increases with proximity (as suggested for *S. catenatus*), then the eyes, rather than the nervous system, are implicated in filtering of information. Fast movement of dummies may blur distinctions of shape, but that type of movement was precisely what triggered the most vigorous CL responses. Besides relatively fast movement, object dimensions and orientation were key SC parameters. Very short (perhaps insect-like) and very long (perhaps snake-like) dowels are clearly not as stimulatory as those of medium length. *Sistrurus catenatus* did not differentiate between fast moving spheres and fast moving dowels, but *C. cerastes* returned a significantly lower response rate for spheres than for dowels. Shape differences may be a more important SC parameter in the latter species. The fact that *C. cerastes* showed no bias for a particular color is not surprising. Desert lizards preyed upon by *C. cerastes* exhibit variation in coloration, ranging from highly cryptic earth tones to vivid splashes of reds and blues (Stebbins, 1985). The above experiments indicate that olfaction plays a minor role in predation on lizards. Further evidence comes from trailing success when juvenile *C. cerastes* released lizards after a strike. These lizards were almost never ingested, an observation that fits well with known chemosensory capacities of this species (Chiszar and Radcliffe, 1977).

Horned Adder (*Bitis caudalis*)

Background.—This small viperine inhabits arid lands in southern Africa (see map in Broadley, 1983). Its diet consists largely of lizards, but also includes amphibians, snakes, birds, and rodents, with variation attributed to age, sex, and geography (Shine et al., 1998). Caudal luring in *B. caudalis* was first noted by FitzSimons (1962), but has not been formally described. This species uses sidewinding locomotion and buries itself in sand with only the top of its head showing.

Subjects and husbandry.—Five adult *B. caudalis*, four males and one female, were observed in the same arena described above for *S. catenatus*. These animals had been captive in the animal facility at UCB for more than a year when trials began. During that time, many feedings of these snakes (rodents and terrestrial geckos) failed to elicit CL (D. DeNardo, pers. comm.). General husbandry was similar to that of *Bitis peringueyi* given by Reiserer and DeNardo (2000). Briefly, snakes were housed in 10 gal terraria with sand substrate, a subsurface heat gradient, 12L:12D photoperiod, and 22°C ambient temperature. Behavioral experiments took place at FSBR in the same arena described for *S. c. edwardsii*, except that gravel was sifted from the substrate, leaving sand (8 cm deep).

Methods.—The purpose of experimentation was to provoke CL and to examine differences in foraging behavior when *B. caudalis* were alternatively presented with lizards or mice. During experimentation, subjects were placed in the central chamber of the arena and allowed to acclimate at least overnight. Before and after each subject was introduced to the arena, a dilute ammonia solution was used to clean the inner chamber and was sprayed over the substrate surface and allowed to evaporate. During all animal trials (except for one with a lizard), a non-perforated Plexiglass sheet was placed on top of the central chamber. Trials occurred in the latter half of the photoperiod. Stimulus conditions were as follows: (1) two *U. stansburiana* were released into the outer arena. The first 10 min of behavior were scored from videotape that ran continuously during extended sessions, with only the first trial on any given individual (5 total) used in quantitative comparisons with mouse feedings; (2) one dark colored mouse was introduced into the outer arena for 10 min, and observations were audio taped; and (3) a dowel (D-1) was pulled around the arena, as in *S. catenatus* experiments, and the trial was recorded on videotape. Tongue-flicking and head orientations were counted for all presentations, and other behaviors were also noted. Baseline TF rate (= 0.0 per min) for snakes that were partially buried was established from videotape and numerous observations when no stimulus was present.

Results.—Both qualitatively and quantitatively, the response of *B. caudalis* was different for mice and lizards. All but one lizard trial were performed on snakes that were, to some extent, buried in the sand, but snakes that struck at a prey item became exposed. Pre-strike TF was never observed in trials with lizards, whereas it occurred in all trials with mice (Table 2). Slight head orientations were common in mouse trials, but never occurred in lizard trials. Snakes never advanced toward a lizard, even when it was close by, or following an attempted strike, but one snake made a slow advance toward a mouse following a strike attempt. Neither mice nor dowel presentations elicited CL, but two individuals lured in lizard trials. Additional CL captured on videotape confirmed the function of the tail movements. Lizards ran directly toward the lure and tried to penetrate the glass wall, sometimes snapping at the tail through the glass.

Table 2. Responses of five *Bitis caudalis* to three stimulus conditions. CL = caudal luring; TF/min^p = pre-strike tongue-flicks per min; TF/min$_p$ = post-strike tongue-flicks per min; HO = head orientation. Superscripts indicate sample size lower than 5: a (N= 1), b (N = 3). Other data given as number of occurrences or average ± SD. Lizards = *Uta stansburiana*. The blue dowel was 50 mm x 9 mm diameter.

Stimulus	CL	Pursuit	Strikes	TF/min^p	TF/min$_p$	HO
Lizard	2	0	3	0	4[a]	—
Mouse	0	1	3	5.3 ± 2.2	24.0 ± 5.1[b]	5.0 ± 5.4
Dowel	0	0	—	0	—	0

When snakes struck at lizards on the other side of the glass, they remained motionless for some time usually without TF, but TF occurred when snakes struck at mice behind glass.

Tail undulations (tail-wagging) occurred in *B. caudalis* in the presence and absence of prey, but those tail movements are clearly distinct from CL with no presently known function. They were associated with forward progression (i.e., a mobile snake) and postural adjustments; tail motions ceased and resumed with body motions. All five subjects showed this behavior, which was also noted by other researchers who worked with these particular animals (J. Luna, pers. comm.). The behavior may serve to draw attention to the tail end of a snake in motion, perhaps to direct a predatory attack to the harmless end so the dangerous end is free to strike. During one observation both tail wagging and CL were observed. The snake had been moving around in the arena prior to introduction of two lizards (*Uta*), and continuous tail wagging occurred during forward progression of the snake. When the lizards were introduced they began to wrestle with each other. The snake stopped moving and slowly descended into the sand with its head oriented toward the lizards. After a few moments the tail appeared about 15 cm behind the snake's head and began rapid undulations. There were two other instances in which burial immediately preceded CL, but in these cases the subject had been luring earlier; a lizard came close and the snake struck the glass; after a few minutes the snake reburied itself and continued to CL.

Discussion.—These data should be interpreted with caution in the light of small sample of snakes, artificial conditions, and trauma from striking the glass terraria. However, I generated more than 20 hours of videotape on predatory interactions with lizards, and recorded numerous additional CL episodes. Another study on the same subjects was conducted by D. DeNardo and J. Luna (unpublished) in which the researchers fed terrestrial geckos to all five snakes, five times each, and videotaped each of the sequences. These snakes were routinely fed mice during regular maintenance, and behavioral observations were noted (D. DeNardo, pers. comm.). Mouse feedings often, but not always, elicited TF prior to the strike, whereas no pre-strike TF occurred in any of 20 gecko feedings. Snakes often became alert, orienting their heads to some degree toward the prey mouse. Sometimes, however, they remained motionless during mouse feedings, yet the mouse was struck, and subsequently ingested, when it came close to the snake. The latter observation suggests plasticity in responses to prey, and that *B. caudalis* can appraise a situation, rather than having only hard-wired feeding responses. Experimental evidence suggests that *B caudalis* assess their prey visually and respond to different stimuli with situation-specific behavior. Many dowel presentations in non-experimental trials never elicited CL. Horned Adders differed from rattlesnakes in several respects, and may have a more complex prey recognition mechanism (see below).

When CL occurred, *B. caudalis* were always at least partially buried, and when they were not, they sunk themselves down before beginning to CL. This same behavior was described for *Cerastes vipera* by Heatwole and Davison (1976), and might indicate intentionality in these snakes (see General Discussion). *Bitis caudalis* never reburied themselves soon after striking at a mouse (in 3/3 strikes), but did so for lizards (in 2/3 strikes), suggesting that the snakes were making some sort of visual assessment about different prey types.

GENERAL DISCUSSION

Although vipers feed on a large variety of prey (e.g., Campbell and Soloranzo, 1992; Greene, 1992; McCoy and Censky, 1992; Sazima, 1992; Shine et al., 1998), studies of feeding behavior have usually been restricted to rodents. Sit-and-wait predation might be less prevalent than is currently accepted, especially in juveniles that depend on non-mammalian prey. Variability in foraging strategy within species or individuals may prove to be a valuable source of infor-
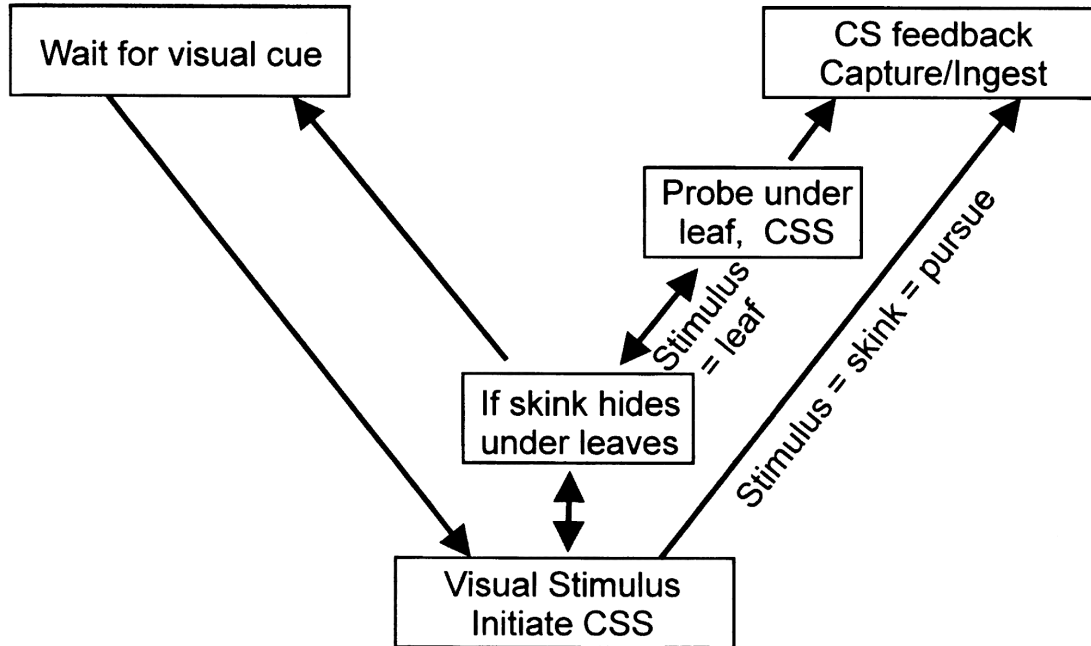
Fig. 5. Simplified schematic of juvenile *A contortrix* responses to skink and leaf movements. CS = chemosensory; CSS = chemosensory searching.

mation about the sensory and central nervous system (CNS) capabilities of vipers, and snakes in general. But we will not capitalize on this potential source of knowledge if researchers are unwilling to do feeding experiments with alternative prey, and to sit for long periods to watch their subjects.

Experiments on SC help us to understand the cues involved in release of predatory behavior, but these contrived experiments have limitations, and some of the most interesting insights from this work came from observing snakes in semi-natural laboratory settings. Copperheads associated the movements of leaves with the presence of prey, and they did so in such close proximity that it is difficult to attribute their responses to a lack of sensory resolving power (either visual or chemosensory). Such observations raise challenging questions. Does *A. contortrix* retain a mental picture of the skink while it is hiding in the leaves? Is the leaf perceived as animate or inanimate? What sensory modality provides the necessary information about leaves and skinks? Do they indeed conceptualize, or is there a simpler, more conventional explanation? A simplified schematic representation of *A. contortrix* feeding on skinks (Fig. 5) raises further questions. Is it simpler to attribute such a feedback system to a hard-wired contingency network, espe-

cially when all of the omitted complexities are added to the model? Or is it more parsimonious to credit snakes with mental machinery capable of interactive associations and CNS-based representations of prey?

Alternative research paradigms, such as the Piagetian theory of object permanence (e.g., Doré and Dumas, 1987), while never applied to non-avian reptiles might provide additional insights, though adaptation of methods to studies of snakes will be necessary. Current theory (see Etienne, 1973; 1984) recognizes three categories or degrees of object permanence in non-human animals: (1) through stereotyped searching postures or movements, various predatory species of invertebrates and unspecified lower vertebrates have developed special devices to increase the chance of further contact with prey that has disappeared from the perceptual field. Such responses are of limited duration, involve objects of immediate survival value, and are thought to result from adaptation that does not involve specialized cognitive structures; (2) learned responses to object disappearance in standardized spatiotemporal experimental contexts. This category was identified in domestic chickens, pigeons and rabbits (non-predators). A search pattern is first learned by trial and error or training, but the pattern is only repeated in the experimental setting;

and (3) spontaneous, active, and flexible searching for an object that has disappeared. Plasticity results from an integrated cognitive structure that develops slowly in the subject and may go through several recognizable stages. This degree of object permanence has been demonstrated in primates, cats, dogs, and some birds (Etienne, 1973, 1984). Caudal luring seems, at first, to fit the first category, but the plasticity in search behavior of *A. contortrix* does not. Predatory behavior of an invertebrate model (larval dragonfly) was the main impetus for description of that category (Etienne, 1984), and feeding mimicry (Schuett et al., 1984) is a much more intricate predatory interaction than that described for dragonfly larvae. Dumas (2000), citing Dumas and Doré (1989, 1991), suggests that object permanence is a fundamental cognitive component of predation, although it is clear that the cited papers refer only to predation in cats. We know so little about object representation in lower vertebrates that it seems premature to classify the complex behavioral repertoires of snakes with those of invertebrates and, indeed, Etienne's (1973) tripartite classification of object permanence may turn out to be better portrayed as a continuum.

Higher order cognitive skills are rarely attributed to reptiles, and demonstrations of learning have been infrequently pursued (Burghardt, 1977). *Sistrurus catenatus* learned to associate the physical appearance of a neonatal mouse (an ecologically foreign stimulus) and its reinforcing consequences (a meal). This experiential modification of SC influenced an existing behavior pattern (pursuit predation) that the snakes possess without conditioning when presented with other prey. The learning experiment presented herein was not adequately controlled, but this might have been easily done with a designated control group of another five naive snakes, by presenting only the mouse in a vial over the same number of presentations that the experimental group received. Degree of hunger presents a potential problem in such studies, and I may not have adequately controlled for motivation to feed. The neonatal mice presented were small (< 4 g) meals compared to what the snakes (ca. 25 g) were capable of swallowing, but the feeding interval was short and satiation might have resulted in two refusals.

Experiments using prey dummies demonstrated that *C. cerastes* and *S. catenatus* have simple rules governing prey recognition (at least from a distance). However, these snakes generalized across exemplars (e.g., different colors of the same sized dowel, different

lizard species, etc.), suggesting that their simple rules include some principle of similarity and perhaps represent categorization at the fourth (open-ended) level of SC. The strong influence of orientation on SC of CL in *C. cerastes* does not conflict with the latter interpretation. Humans use orientation cues to make categorizations (e.g., horizontal plane below = floor, above = ceiling, vertical plane = wall), but we also incorporate other cues that can supercede orientation, and it is this capacity that has not been demonstrated for snakes. *Crotalus cerastes* and *S. catenatus* struck fast moving prey dummies. Slow movements rarely elicited striking for dowels, but slow moving lizards (even behind glass) were often struck. Further experimentation is needed to determine whether proximity increases resolution, but other evidence suggests that it does. Lizards too large to be ingested sometimes elicit CL in *C. cerastes*, but when those lizards approach the snake, CL stops (R. Reiserer, unpublished). Preliminary evidence suggests that *B. caudalis* has more acute prey recognition skills than the other snakes tested. Perhaps features characteristic of lizards, but absent in dowel dummies are important. *Bitis caudalis* is a lizard specialist (Shine et al., 1998) that feeds on both fast-moving lacertids and slow-moving gekkonids, and this ecological context may have favored more acute, or simply different perceptual skills for prey recognition.

By burying themselves before CL, *B. caudalis* also shows evidence of higher-level cognitive skills, but many questions remain. Do these snakes make a "decision" to lure for the lizard? Do they "intend" to conceal themselves, and are they being deliberately deceptive (in addition to the deception of CL)? There may be no way to know, but the response seems "intelligent" and is certainly ecologically relevant. Burghardt (1991) presented evidence for intentionality in the Eastern Hog-nosed Snake (*Heterodon platirhinos*), based on experiments that demonstrate visual assessment of a threat by death feigning snakes (Burghardt and Greene, 1988), and I suggest that there is equally strong testimony for intentionality in *B. caudalis* based on visual assessment of prey.

Caudal luring in rattlesnakes was stimulus-dependent, and tail movements stopped soon after prey or dummy movement ceased. Both *B. caudalis* and *A. contortrix* sometimes lured when there was no discernable prey movement (*Bitis*, N = 1), or when the prey had been out of view (or absent) for some time. Lingering caudal movement was most pronounced in *A. contortrix*, with residual movements up to 20 min

after prey were removed. Always, however, there had been prior stimulation, and the probing behavior (luring without any apparent stimulus) described for *Acanthophis antarcticus* (Chiszar et al., 1990) was never witnessed. Copperheads performed luring motions twice in the absence of prey, but both times the lighting was dim and the movement of my foot (seen through semi-clear plastic) outside the enclosure triggered the behavior. I could instigate tail movement by motioning with my foot, and the undulations diminished when I held still. These and other observations discussed herein suggest that (1) CL releasing cues are both very specific and very general, depending on their context (e.g., see gaping responses in nestling birds, Tinbergen and Kuenen, 1939/1957), (2) general movement produces undefined expectancies of food, (3) some image or impression of prey is retained in the nervous system of the snake after the prey is gone (see e.g., Etienne, 1973, 1984), and (4) the observer is unwittingly influencing the behavior being studied. Caution is warranted in assuming that stimuli are absent, and observation is probably best done from behind a blind or through a remote video monitor.

Caudal luring studies might also provide information about the search images of species lured by the tail. *Acris crepitans* did not respond to the CL of *A. contortrix*, but did to the CL of *S. catenatus*, suggesting that different lures might evolve some specificity beyond that of "larval insect." Not all lures are equally attractive to a given prey animal. Therefore, recent criticisms (e.g., Sisk and Jackson, 1997; Tiebout, 1997; Rowe et al., this volume) of the hypothesis that rattle evolution involved enhancement of the CL (Schuett et al., 1984) are premature. I found differences in attraction among 13 lizard species to the CL of *C. cerastes* (R. Reiserer, unpublished), one of which (*Sceloporus undulatus*) was the subject used by Sisk and Jackson (1997). Their attractant for these lizards was a model of *Sistrurus miliarius* with a mechanically propelled tail and detachable sclerophymae (terminal caudal scales) patterned after *C. cerastes* and *Agkistrodon piscivorus*. Lizards bit the tail of their model, but this result is difficult to evaluate because tail movement by the model only crudely resembled CL (see model design, Sisk and Jackson, 1997). Furthermore*, S. miliarius* is known to CL for frogs (Jackson and Martin, 1980), but not for lizards. Tiebout's (1997) criticisms are more substantial, but caution is warranted until more data are available concerning attraction of the lure to the most targeted animal(s).

Geographic variation in CL has the potential to provide information about ecologically relevant evolutionary changes in the processing of stimulus information by snakes. We expect evolutionary ecological changes involving feeding biology to rapidly track environmental changes, and this seems to have happened in the SC of CL in *S. catenatus*. The arid environments inhabited by *S. c. edwardsii* are very recent formations (less than 11,000 years old), and as little as 18,000 years ago most of New Mexico was vegetated by montane coniferous forest, with the modern Chichuahuan Desert then covered in coniferous woodland (Martin, 1963). The present distribution of *S. catenatus*, and fossil evidence from Kansas and Texas (Holman, 1979, 1981, 2000), suggest that the species originated in the eastern United States, and thus that dietary habits are derived in the desert form.

The experiments and observations herein present a suggestive, but incomplete, picture of visual SC in four distantly related vipers. Some features of foraging behavior seemed invariant, while others showed flexibility and/or appear to be mediated by learning. A thorough discussion of invariant, flexible, and learned behaviors is beyond the scope of this paper and will be the topic of a subsequent manuscript. The emerging picture, however, portrays both complexity and simplicity in the cognitive skills of vipers, with inter- and intraspecific differences in SC well rooted in ecology. Much of our reluctance to attribute complex cognitive capacities to vipers and other snakes probably has much to do with their limbless bodies and sedentary lifestyles, and researchers have been much more willing to grant higher mental faculties to turtles and other reptiles (Burghardt, 1977). By virtue of their morphologies, ecologies, and habits, vipers present unique research challenges, but they also offer unique opportunities for studying how cognitive processes evolve and function in limbless, sedentary tetrapods.

A RESEARCH PROGRAM

In this section I recommend some methods and tools for further study of visual prey recognition and SC. Progress with these techniques will, no doubt, spur the development of new methods that increase the sophistication of visual SC and cognitive research.

(1) Watch both adult and young individuals in natural or semi-natural encounters with a variety of prey. Ask where feeding cues are coming from. Is the stimulus associated with the morphology of the prey animal, something the animal is doing, or is it derived from some other information available to the subject?

Use natural objects and create complex habitats for subjects (e.g., Savitzky, 1992; Savitsky and Burghardt, 2000). We seldom want prey to hide from our subjects, but wild snakes face such problems and have likely evolved responses to such contingencies.

(2) Devise controlled laboratory experiments that test hypotheses derived from observations. Isolate sensory modalities using special enclosures and prey (predator) dummies. Simulate movement patterns, shapes, sizes, orientations, and colors of both prey and non-prey species, using as many variations as possible, and try motions, shapes, and orientations that do not mimic natural situations. Glass is completely effective in the isolation of radiant infrared sensory information (pers. observ., using PalmIR infrared imaging camera, Raytheon Systems), and subjects or prey can be sealed into terraria so that no chemical information is available. Stimulus control experiments should be conducted with subjects on clean or sterile substrates. Vibrational cues can be minimized by keeping subjects on solid foundations. Arenas should be large to allow assessments of spatial variation in SC.

(3) Experiment with all sensory modalities. Snakes may integrate many senses into behaviors that seem dominated by one sensory system. Stimulus control of infrared imaging by pitvipers might share features with visual SC (e.g., Theodoratus et al., 1997). Thermal cues are integrated into the visual centers of the forebrain (Berson and Hartline, 1988), and may function as a spatial sense comparable in many ways to vision.

(4) Design experiments to test for learning (see Burghardt, 1977). The visual sensory system of snakes may be better suited to learning studies than other modalities, with fewer hard-wired responses associated with stimuli. Because spatial information is so variable, vision may be well integrated with parts of the CNS that function in the development of cognitive associations. Experiments with snakes would probably best focus on ecologically relevant behavior patterns, rather than pushing of levers or blinking lights that signal forthcoming rewards.

(5) Use blinds and/or remote video monitoring when viewing subjects. Some subjects never fully acclimate to a human presence, and threatening situations positively inhibit CL (R. Reiserer, unpublished).

(6) Videotape everything. Some patterns are only evident after many viewings of a behavior, or when videotapes are viewed at high speed.

(7) Use technology. Enclosures can be designed to incorporate a video monitor that displays real or animated images to the subject. With the power of computer animation techniques rapidly becoming accessible to non-specialists, such a setup would allow unprecedented control over visual stimuli, while isolating all other variables. Prey images could also be instantly replaced with the image of a moving predator, or an image could be constructed such that a predator rendering is presented at different distances in the background while prey are represented in the foreground. Cautionary measures, however, should be taken to adjust for possible resolution differences between images on a nearby screen and natural ones.

(8) Acquire samples large enough to allow statistical analysis, and design experiments to answer specific questions. Caudal luring data are often binary (i.e., present vs absent) and require appropriate statistical considerations.

(9) Use only healthy animals. Snakes that are not feeding regularly are poor subjects. Snakes that feed too regularly, however, may not exhibit appetitive behaviors. Balancing these two issues is important to successful research. Pay attention to daily and yearly cycles, and do not use animals going through shedding cycles. Variation in tendency to CL is expected in any sample and, when asking questions about SC and prey recognition, choosing subjects that are inclined to CL does not invalidate experiments.

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