THE VOMERONASAL ORGAN OF THE SKINK, SCINCELLA LATERALIS: THE MORPHOLOGY AND ROLE IN PREDATION

by

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Thesis submitted to the Faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree Master of Science in Zoology

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December 1983

Blacksburg, Virginia
I dedicate this thesis to a man who showed me the trail.

Benedictory Chant (Navajo)

Now talking God,
With your feet I walk,
I walk with your limbs,
I carry forth your body,
For me your mind thinks,
Your voice speaks for me.
Beauty is before me,
And beauty behind me,
Above and below me hovers the beautiful,
I am surrounded by it,
I am immersed in it,
In my youth I am aware of it,
And in my old age
I shall walk quietly
The beautiful trail.¹

ACKNOWLEDGEMENTS

I would like to thank the members of my graduate committee, Drs. Robin Andrews, Jack Cranford, and David West, for their assistance and patience throughout the course of this research. I am also grateful to

for the use of his laboratory,

for her guidance through the administrative maze,

for his help and advice on photography, and

to

for facilitating my development as a teacher and for the use of his photography equipment. Special thanks to my friends and conspecifics,

and

, for their moral support and stimulating conversation. This research was partially funded by Sigma Xi, the Virginia Academy of Science, and the Department of Biology, Virginia Polytechnic Institute and State University.
# TABLE of CONTENTS

Dedication ........................................... ii

Acknowledgements .................................... iii

General Introduction .................................. 1

Literature Review ..................................... 3

The Morphology and Relative Size of the Vomeronasal Organ in Ascalobotans and Autarchoglossans
  Introduction ......................................... 21
  Materials and Methods ............................... 23
  Results .............................................. 25
  Discussion ........................................... 29

The Relative Roles of Vision and the Chemical Senses in Prey Detection by Scincella lateralis.
  Introduction ......................................... 34
  Materials and Methods ............................... 37
  Results .............................................. 45
  Discussion ........................................... 49

Literature Cited .......................................... 55
Tables....................................................64
Figures...................................................80
Curriculum Vitae........................................85
Abstract..................................................
GENERAL INTRODUCTION

The vomeronasal organ is a paired chemosensory organ found in or below the nasal capsule in three vertebrate classes (Amphibia, Reptilia, and Mammalia). Because it is most highly developed in squamate reptiles (lizards and snakes), most research on the vomeronasal organ has utilized this taxon.

Morphological studies of the vomeronasal organ include descriptions of macro-structure, the type of cells present, and their innervation and placement within the organ (Pratt, 1848, Bellairs, 1970, Parsons, 1970).

Behavioral studies have used two basic approaches. One approach is to eliminate combinations of vision and the chemical senses and to compare the animal's responses to various stimuli before and after the manipulation (reviewed by Burghardt, 1970). Another approach is to present different stimuli, such as prey or a conspecific, and compare the behavior of the animal to an animal presented the appropriate control. Such behavioral studies have shown that the organ is involved in a variety of behaviors such as mating and predation (Burghardt, 1970, 1980, Chiszar and Scudder, 1980).
The objectives of this study were to describe the vomeronasal organ of the ground skink, *Scincella lateralis*, and to determine the organ's role in the lizard's predatory behavior. The ontogeny of the vomeronasal organ and its relative size in comparison with the vomeronasal organs of other species are described in the morphological section. The relative roles of vision and the chemical senses in prey detection are described in the behavioral section.
LITERATURE REVIEW

MORPHOLOGY

Introduction

The vomeronasal organ or Jacobson's organ has been of interest to biologists for many years. Since its discovery in 1809 by the Dutch surgeon Ludwig Levin Jacobson it has been described in three of the seven vertebrate classes, the Amphibia, Mammalia, and Reptilia (Bellairs, 1970).

The vomeronasal organ is a paired chemosensory structure that is sensitive to non-volatile or slightly volatile compounds that are either inhaled or transferred to the organ by the tongue (Burghardt, 1980). In general, the vomeronasal organ consists of isolated regions or sacs within the nasal cavity, but in some groups (e.g. squamate reptiles) they are completely separate from the nasal capsule (Parsons, 1970, 1971). The vomeronasal epithelium is derived from nasal epithelium during development and is similar to the olfactory nasal epithelium proper. However, in contrast to the olfactory nasal epithelium proper, the primary sensory cells of the vomeronasal organ lack cilia and Bowman's glands (Graziadei, 1977, Parsons, 1970, 1971).
These cells are innervated by the vomeronasal nerve, which terminates in the accessory olfactory bulb. The accessory olfactory bulb is located medially and behind the olfactory bulb, having separate neural connections from the olfactory bulb (Burghardt, 1980). Thus, the vomeronasal organ, vomeronasal nerve, and accessory olfactory bulb comprise the vomeronasal system, a separate sensory system from the olfactory system proper. The following paragraphs briefly review the morphology and function of the vomeronasal organ in amphibians and mammals, followed by a more detailed review of squamate reptiles.

**Amphibians**

In the amphibians, the vomeronasal organ is confluent with the nasal cavity, but the exact location and development varies between orders. In Anura the it exists as a divertriculum on the lower medial side of the nasal cavity and is fairly well developed. In the Urodela the vomeronasal organ is simply an isolated region of vomeronasal epithelium in the posterior half of a lateral sinus (Noble, 1954, Parsons, 1971). Caecillians lack a vomeronasal organ, it is functionally replaced by the retractile tentacle (Noble, 1954). The apparent function of the vomeronasal system in amphibians is to "smell objects" in the mouth (Noble, 1954).
Mammals

Considerable variation exists in the development of the vomeronasal organ in mammals. In general, it is a narrow tubular structure on either side of the nasal septum lying below and anterior to the nasal cavity (Eisenberg and Kleinman, 1972). A small duct may connect the vomeronasal organ to the nasal cavity or to the nasopalatine duct, which joins the nasal and oral cavities (Parsons, 1971). In the prosimians the vomeronasal organ is separate from the nasal cavity but is connected to the oral cavity by the nasopalatine canal (Schilling, 1980). In other mammals such as man the vomeronasal organ is lost or vestigial.

The literature on the function of the vomeronasal organ in mammals has been reviewed by Eisenberg and Kleiman (1972). In general, the vomeronasal organ has been implicated in the reception of sex hormones found in urine and glandular secretions. Stimulation of the vomeronasal organ by these compounds is important in intraspecific interactions (Beauchamp et al. 1980, Burghardt, 1980).

Reptiles

The vomeronasal organ is poorly developed in non-squamate reptiles. In crocodilians it is present only in the embryo. In turtles the vomeronasal organ is very
similar to that found in amphibians, that is, it is confluence with the nasal cavity and exists as a isolated region of vomeronasal epithelium (Bellairs, 1970, Parsons, 1971).

The vomeronasal organ is most highly developed in squamate reptiles, being best developed in snakes and variable among lizards. In general, it is a relatively large structure paired structure completely separate from the nasal cavity, and located on either side of the nasal septum anteriorly between the nasal and oral cavities (Parsons, 1970, 1971). Each half of the vomeronasal organ hemispherical in shape, with its ventral surface invaginated by a structure called the mushroom body. This structure nearly fills the center of the vomeronasal organ so that only a narrow lumen remains. The vomeronasal duct leaves the lumen and enters the mouth at the anterior end of the choanal groove. The lachrymal duct also enters the vomeronasal duct just above the choanal groove in most squamates (see Parsons, 1970, for a review of the variation of where the lachrymal duct enters the vomeronasal duct). The vomeronasal sensory epithelium lines the dorsal walls and sides of the lumen. The mushroom body and vomeronasal duct are lined with ciliated epithelium (Bellairs, 1970, Parsons, 1970, 1971). The vomeronasal sensory epithelium
consists of a columnar tri-layered cell arrangement that is a functional structural unit. The first layer is located next to the lumenal surface and consists of supporting cells and bipolar neurons that are covered with microvilli. The second layer is a bipolar cell layer and the third layer is an undifferentiated cell layer that probably functions in cell replacement (Wang and Halpern, 1980).

In squamates, tongue protrusion and retraction bring both volatile and non-volatile substances in contact with internal sensory structures of the vomeronasal organ (Burghardt, 1980). Meredith and Burghardt (1978) simultaneously recorded electrical impulses from the hyoglossus muscle of the tongue and accessory olfactory bulb in *Thamnophis sirtalis* and *T. radix*. Their results indicated that neural activity in the accessory olfactory bulb significantly increases following a tongue flick. Thus, tongue flicking is associated with vomeronasal neural activity.

The methods by which the chemical compounds are transferred from the tongue to the sensory epithelium of the vomeronasal organ is unclear. In reptiles with strongly bifurcated tongues (snakes, varanid, teiid and anguinid lizards), the tongues tips may actually be inserted into the vomeronasal ducts. In lizards with blunt tongues (iguanids,
scincids, geckonids) the cilia that line the vomeronasal ducts and mushroom bodies may transport chemical cues to the sensory epithelium (Bellairs, 1970, Parsons, 1970). However, Gillingham and Clark (1981) found that as the tongue of a snake is retracted into the lingual sheath it contacts processes on the sheath that are elevated as the mouth closes. These processes are located directly beneath the vomeronasal ducts and may actually enter the ducts when the processes are in an elevated position. An experimental group of snakes whose processes had been removed and a control group with intact processes were tested with fish extract and distilled water. The control group was apparently able to detect the extract but the experimental group was not. This study suggests that the tongue need not contact the vomeronasal ducts to effect the transfer of chemical compounds.

BEHAVIOR

Introduction

Many behaviors of reptiles are mediated by chemical cues. These include intraspecific interactions such as courtship, combat, mating, and territoriality, as well as predation and other interspecific interactions (reviewed by Burghardt, 1970, 1980, Chiszar and Scudder, 1980, Madison, 1977).
Reptiles have two pathways for the reception of chemosensory information. Because of this dual system of "olfaction", it is important to define carefully the terms used in chemosensory research. Chemical senses refer to both the nasal and vomeronasal sensory systems. Chemical cues are compounds that stimulate the sensory epithilium of either system. Nasal olfaction refers to chemosensation via the nasal cavity and vomeronasal olfaction refers to chemosensation through the vomeronasal organ.

The presumed functional differences between vomeronasal olfaction and nasal olfaction are that nasal olfaction is a distance receptor of volatile compounds, while vomeronasal olfaction is a contact receptor of slightly volatile or non-volatile compounds (Burghardt, 1980, Cowles and Phelan, 1958, Duvall, 1981). At least some ascalobotan lizards must lick the substrate to obtain chemical cues (Bissinger and Simon, 1981, De Fazio et al., 1877). Tongue contact with prey is a necessary releaser of attack behavior in naive garter snakes (Sheffield et al., 1968). Moreover, direct tongue contact with a prey trail is necessary for successful trailing behavior by garter snakes. When a perforated plastic sheet prevented contact with a chemical trail, tracking was not exhibited (Kubie and Halpern, 1978). However, in snakes and autarchoglossan lizards volatile
compounds can also be detected by the vomeronasal organ. Skinks are able to discriminate conspecifics from other species and the sex of a conspecific, and hungry rattlesnakes are able to detect prey from odors that diffuse through the air (Cowles and Phelan, 1958, Duvall et al., 1980).

The few studies that have distinguished between nasal and vomeronasal olfaction downgrade the importance of nasal olfaction in squamates. For example, Burghardt and Pruitt (1975) surgically removed tongues of new born (unfed) and adult garter snakes, *Thamnophis sirtalis* and *T. radix*. Feeding in the tongueless neonates, was almost abolished, but the tongueless adults fed, although somewhat abnormally. When the nasal olfactory and visual systems were temporarily rendered inoperative there were no significant differences in feeding behavior for either the tongueless or control adult snakes. Garter snakes with intact olfactory and accessory olfactory nerves can detect and follow a prey trail. When the accessory olfactory nerve is severed the ability to detect and track prey is abolished, but, olfactory nerve lesions do not disrupt this behavior (Kubie and Halpern, 1979). DeKay's snake, *Storeria dekayi*, also loses much of the ability to trail prey and recognize conspecifics after removal of the tongue (Noble and Clausen,
1936). These and studies from the 1920's and 30's (extensively reviewed by Burghardt, 1970) indicate that the VO and tongue function as a single unit and are an important sensory modality in squamates.

RTF can be used to evaluate the response of squamates to chemical cues, as RTF is associated with the level of arousal. For example, lizards that are moving, in the presence of conspecific odors, or investigating novel objects have a greater RTF than individuals that are not moving (Bissinger and Simon, 1979, De Fazio et al., 1977). Concentrated prey surface extracts elicit a greater RTF from snakes than dilute extracts (Burghardt, 1970). Moreover, tongue flicking is associated with trailing behavior by all snakes.

Snake behavior

There are at least two basic predatory repertoires employed by snakes. Chemical cues alone elicit predatory behavior in natricine snakes, while a combination of visual, thermal, and chemical cues are necessary to elicit predatory behavior in crotalids (Burghardt, 1970, Chiszar and Scudder, 1980).

Natricine snakes use chemical cues to identify, track, and direct the strike (Burghardt, 1970). Visual cues alone elevate the rate of tongue flicking and cause orientation to
prey, but fail to stimulate attack behavior. Garter snakes, *Thamnophis sirtalis*, presented with prey sealed in transparent vials, exhibit an elevated RTF and orient to the prey, but do not strike (Burghardt, 1970). Response to a visual stimulus does not seem to be due to the body form of prey, but rather to its movement. Garter snakes ignore dead prey in transparent vials (Burghardt, 1970). However, they increase their RTF, orient to, and repeatedly strike objects saturated with prey surface extracts (Burghardt, 1967, 1970, 1980, Burghardt and Pruitt, 1975, Chiszar et al., 1981).

Chiszar et al. (1981) presented garter snakes all pairwise combinations of four stimuli (a visual stimulus, a visual control, a chemical stimulus, and a chemical control) and evaluated the behavioral response (RTF). The snakes responded to the visual and chemical cues in the same manner, but the response to the combined visual and chemical cues was significantly higher. There was no statistical interaction between visual and chemical cues, although the authors suggested that response to the chemical cues may be additive (Chiszar et al., 1981).

Crotalid snakes use both visual and thermal cues to locate prey and direct the strike. Vomeronasal olfaction is used to track the wounded prey (Chiszar and Scudder, 1980). Rattlesnakes, *Crotalus viridis*, do not respond to chemical
cues alone, but do respond to visual and thermal cues. Furthermore, the response to the visual and thermal cues is not significantly different in the presence or absence of chemical cues. This indicates that visual cues may alert the snake to chemical cues that would otherwise be missed (Chiszar et al., 1981). Normal post strike predatory behavior (elevated RTF, tracking behavior, and ingestion) can usually be stimulated after a predatory strike. Golan et al. (1981) presented rattlesnakes all pairwise combinations of four different treatments (snakes were allowed to strike prey, they were presented prey but not permitted to strike, they were also presented a mouse trail, no mouse trail), and evaluated the RTF and trailing ability. In the strike condition, snakes exhibited an increased RTF whether or not a trail was present. However, when a mouse trail was present the snakes were able to follow the trail. Snakes in the no strike condition did not exhibit an increased RTF and did not follow a mouse trail (Golan et al., 1981). However, the presence of prey odors aids in maintaining a high RTF over time. When observed for thirty minutes, rattlesnakes that struck prey maintained a higher RTF if prey odors were present (Scudder, 1983). The need for visual and thermal cues and a predatory strike to elevate the RTF can be overridden, but only after prolonged
food deprivation. Rattlesnakes after prolonged starvation exhibited an elevated RTF and searching behavior when presented only chemical cues (Chiszar et al., 1981).

Natricine snakes are able to distinguish the preferred prey of their species prior to any feeding experience (Burghardt, 1980). For example, newborn garter snakes exhibited greater responses to extracts of the normal and preferred prey types of their species than to extracts of prey not normally encountered (Burghardt, 1969, 1970, Burghardt and Abeshaheen, 1971). Innate prey preferences show significant geographical, species, and subspecies variation (Arnold, 1977, Burghardt, 1969, 1970, Dix, 1968). This variation is consistent with the known food habits of each species (Burghardt, 1970). For example, neonate Thamnophis elegans from coastal California eat a sympatric species of slug, Ariolimax, and also react to its extract. In contrast, neonate T. elegans from inland areas where the slug does not occur do not eat the slug under experimental conditions nor react to its extract (Arnold, 1977).

Innate preferences are not modified by maternal experience or stimulus deprivation. Gravid garter snakes were fed exclusively on either fish or worms. Their newborn offspring responded to fish and worm extracts in the same manner as neonates previously tested from the same population (Burghardt, 1971).
In contrast to the response of natricines, neonates of three rattlesnake species did not respond at all to extracts of their preferred prey, non-preferred prey, or distilled water controls (Chiszar and Radcliffe, 1977). The results were attributed to the lack of the appropriate visual and thermal cues.

Chemical cues received by the vomeronasal organ may stimulate courtship, male combat, and aggregation (Burghardt, 1970, 1980). Male *Thamnophis sirtalis* increase their RTF in response to compounds secreted from the backs of oestreus females. These compounds are pheromones (Burghardt, 1980) and their production can be hormonally stimulated (Crews, 1976, Kubie et al., 1978). Newly shed female *Thamnophis radix* treated with oestradiol benzoate several days prior to ecdysis are sexually attractive to males. Moreover, untreated females are also sexually attractive if they are housed with a treated female. Thus, the compounds appear to be transferred by contact (Kubie et al., 1978).

The use of the vomeronasal system in social interactions among snakes is less well known than its use in predation. Experimental manipulation of the sensory systems of garter snakes led Noble (1937) to conclude that vomeronasal olfaction was at least as important as nasal
olfaction during intraspecific interactions of snakes. For example, Andren (1982) demonstrated that the vomeronasal system may be the primary mediator of sexual behavior in *Vipera berus*. The vomeronasal mucosa of dominante *Vipera berus* males that had successfully tracked and courted females and had participated in male combat were anesthetized with Xylotape. When reintroduced into the enclosure containing conspecifics, these males were unable to trail oestrous females or subordinate males. Moreover, treated males did not exhibit courtship behavior when they encountered a female and fled when they encountered males (Andren, 1982).

**Lizard Behavior**

Saurians are divided into two groups, the Ascalobota and Autarchoglossa (Camp, 1923). The Ascalobota include lizards with simple tongues and relatively undeveloped vomeronasal systems (e.g. Iguanidae, Agamidae, and Gekkonidae). The Autarchoglossa include lizards with modified tongues (forked to varying degrees) and well developed vomeronasal organs (Scincidae, Teiidae, and Anguidae). Ecological and behavioral differences between these groups classically have been associated with the degree of development of the vomeronasal system and different reliances on vision and chemosensation in recognition of prey and conspecifics (Stamps, 1977). For
example, ascalobotans exhibit a lower RTF during activity, than do autarchoglossans (Bissinger and Simon, 1979).

Both ascalobotan and autarchoglossan lizards use a variety of visual cues, including prey size, movement, color and pattern, for the location and recognition of potential prey. Visual cues alone cause orientation and attack behavior. *Anolis lineatopus* attacked live prey sealed in transparent tubes (Curio and Mobius, 1978). When presented combinations of moving vs non-moving or large vs small prey, the ascalobotan *Anolis carolinensis* and the autarchoglossan *Eumeces fasciatus* consistently prefer moving prey over non-moving prey regardless of size (Burghardt, 1964). In contrast, a riparian species, *Anolis aquaticus*, attacks dead as well as living prey (Goodman, 1971). Goodman suggests that response to non-moving prey may be to differentiate between potential prey and other moving objects in streams.

Coloration and pattern also helps lizards to identify potential prey. *Anolis carolinensis* attack unicolored insects more readily than multicolored insects. This behavior appears independent of palatability or smell (Sexton, 1964). Newborn *Sceloporus malachiticus* avoid eating unpalatable milkweed bugs. This response may represent innate avoidance of aposmatically colored prey or a preference for unicolored prey (Reznick et al., 1981).
Color pattern and movement also direct the predatory attack. *Eumeces laticeps* bite large beetles just behind the head, using the the color contrast between the head and thorax as an directional cue. The direction of movement is used as an attack cue. Lizards consistently attack the head region when the prey is moving in a forward direction. When directional cues and color cues are contradictory the lizards revert to the use of color contrast only (Cooper, 1981).

The ability of ascalobotan lizards to detect prey using chemical cues is unknown. Autarchoglossans presumably can use chemical cues to detect prey, but few studies provide data to support or refute this view. Researchers in the 1930's eliminated combinations of the sensory systems used in prey detection by autarchoglossans. The results of these studies were contradictory and provide little information (see Burghardt, 1970, for a thorough review of this literature). However, the autarchoglossans *E. fasciatus* and *E. inexpectatus* exhibit innate responses to chemical extracts of potential prey (Loop and Scoville, 1972, Burghardt, 1973).

Chemical signals are important mediators of social communication among autarchoglossans and, to a lesser extent, among ascalobotans (Bissinger and Simon, 1981,
Chemical cues may function in conspecific recognition, sex
discrimination, and territorial behavior. *Eumeces*
*fasciatus*, simultaneously exposed to odors of conspecifics
and *S. lateralis* responded to a conspecific with an
increased RTF and snout dip rate, but did not respond to *S.
lateralis* (Duvall et al., 1980). *Scincella lateralis* and *E.
laticeps* are able to discriminate the sex of a conspecific
by chemical cues alone. Male *S. lateralis* were attracted to
female odors, but repelled by male odors, while females were
attracted to males, but responded randomly to female cues
(Duval et al., 1980). Post-reproductive *E. laticeps*
exhibited higher RTF to cotton swabs containing conspecific
odors than to a distilled water control during the first
twenty seconds of testing. In addition, testosterone-treated
males exhibited a higher RTF to estrogen-treated females than
to normal males, but two treated males attacked swabs
containing chemical cues of treated males (Cooper and Vitt,
1983).

Ascalobotans may also use chemical cues to recognize
conspecifics. Juvenile *Sceloporus jarrovi* lick the
substrate more often in cages which previously contained
another lizard or in a novel clean cage than was observed
in the home cage (Defazio et al., 1977, Bissinger and Simon,
1981). Sceloporines are also able to recognize conspecific chemical signals but appear unable to distinguish sex by chemical cues. *Sceloporus occidentalis* responded to conspecific exudates with an increased rate of substrate licking, followed by visual displays, but did not differentiate exudates by sex (Duvall et al., 1979, 1981).
The Morphology and Relative Size of the Vomeronasal Organ in Ascalobotans and Autarchoglossans

INTRODUCTION

The vomeronasal organ is a paired chemosensory organ located in the roof of the mouth in squamate reptiles. The macro-structure, micro-structure, and embryonic development of the organ are well known (Parsons, 1970, and included references). The vomeronasal organ, the tongue, vomeronasal nerve, and accessory olfactory bulb are parts of the vomeronasal system (Burghardt, 1980). The tongue transfers chemical compounds from the air or substrate to the vomeronasal duct, from which they are transferred to the organ. Chemical compounds stimulate the sensory epithelium, and these impulses are transferred to the accessory olfactory bulb of the brain by the vomeronasal nerve. The destruction of the vomeronasal nerve abolishes normal feeding behavior in snakes (Kubie and Halpern, 1979). Tongue flicking is also associated with neural activity in the accessory olfactory bulb, and thus the vomeronasal organ (Meridith and Burghardt, 1978).
The vomeronasal organ is developed to varying degrees within the squamates; snakes generally have well developed a vomeronasal organ, while the vomeronasal organ of lizards is more variable (Bellairs, 1970, Parsons, 1970). The degree of vomeronasal development among lizard families has been associated with the relative importance of chemosensation in the detection of prey, conspecifics, and other chemical stimuli in their environment (Burghardt, 1970). Lizards with a poorly developed vomeronasal organ are thought to be primarily visually oriented, and those with a well developed vomeronasal organ are thought to be chemically as well as visually oriented (Parsons, 1970). Differing dependence on vision and the chemical senses is associated with the major subdivision of lizards, i.e. the Ascalobota and the Autarchoglossa (Bissinger and Simon, 1979, Stamps, 1977). The Ascalobota are thought to be visually oriented, have poorly developed vomeronasal organs, blunt tongues, and low rates of tongue flicking (e.g. Iguanidae, Xantusiidae and Gekkonidae). Autarchoglossa are thought to be chemically oriented, have a well developed vomeronasal organ, elongate tongues, and high rates of tongue flicking (e.g. Scincidae, Anguidae, Varanidae).

One objective of this study was to describe in qualitative terms the vomeronasal organ in the ground skink,
Scincella lateralis, and other lizards. The second objective was to quantify the ontogenetic change in size of the vomeronasal organ in *S. lateralis*. The third objective was to test the hypothesis that the size of the vomeronasal organ is larger in autarchoglossan than in ascalobotan lizards.

**MATERIALS and METHODS**

All specimens (Table 1) were killed with sodium pentobarbital and the following external measurements taken: 1. body mass (g), 2. snout-vent length (mm), and 3. head width at the widest point (mm). Immediately after these measurements were taken, the entire head or the nasal region was removed, preserved in Bouin fixative, and decalcified in Kristensen fluid. Tissue was dehydrated in an ethanol series to either xylene or toluene and embedded in paraffin. The tissues were sectioned at 10 or 20 microns and stained with Mallory's triple stain (Humason, 1972).

Measurements of the vomeronasal organ (mm) were taken with an ocular micrometer of a dissecting microscope. Four measurements were taken on the last section containing a complete dorsal projection of the vomer bone (Figure 1). 1. Vomeronasal capsule length (VOC) was the distance from the dorsal projection of the vomer to the anterior plate of the septo-maxilla. 2. Vomeronasal capsule height (VOH) was the
distance from the basal plate of the vomer to the dorsal plate of the septo-maxilla. 3. Vomeronasal organ length (VOL) was the distance from the anterior plate of the septo-maxilla to the end of the vomeronasal sensory epithelium on the same line as the measurement vomeronasal capsule length was taken. 4. Vomeronasal sensory epithelium thickness (VOE) was the maximum thickness of the sensory epithelium on the same line as measurements 1. and 3 above. Ontogenetic series were available only for Scincella lateralis and Sceloporus undulatus. Data from Eumeces fasciatus and Eumeces inexpectatus were combined in all analysis.

VOC and VOE were used to make interspecific comparisons of vomeronasal size and sensory capabilities, respectively. I have assumed that the thickness of vomeronasal sensory epithelium is related to the sensitivity, kinds or numbers of chemical compounds that are perceived (see discussion).

Statistical Analyses

The relationship between independent and dependent variables was evaluated using least squares linear regression (Ray, 1982). Head width was used as an index of body size to minimize differences in body shape among species. Differences between slopes and intercepts were determined with multiple range tests (Sokal and Rohlf, 1969).
RESULTS

Intraspecific comparisons

Each vomeronasal organ of *Scincella lateralis* is located in a bony capsule (Figure 2). The vomer forms the ventral and posterior walls of each cavity, the septo-maxilla forms the anterior, dorsal, and labial walls, and the nasal septum forms the lingual wall. The organ almost completely fills this cavity. Each vomeronasal organ is roughly hemispherical and consists of vomeronasal sensory epithelium, mushroom body, a lumen, vomeronasal duct, and a vomeronasal nerve. The sensory epithelium forms the dorsal and lateral sides of the organ. A vomeronasal nerve innervates this epithelium and terminates in the accessory olfactory bulb. The ventral surface of each vomeronasal organ is invaginated by the mushroom body, which leaves a narrow lumen. The mushroom body consists of a cartilage concha covered with a thin layer of ciliated epithelium. This epithelium has no apparent sensory function (Parsons, 1971) and is not innervated by the vomeronasal nerve. The duct of the vomeronasal organ leaves the lumen anterioventrally on the labial side of the organ and terminates in the choanal groove on the roof of the mouth.
The lachrymal duct enters the lingual side of the vomeronasal duct as it enters the choanal opening. Little connective tissue or other supportive tissues occur between the vomeronasal organ and the bony capsule.

Vomeronasal organ measurements are linearly related to head width (HW) (Table 2). The slopes of all regressions were significantly different from zero (P<0.05). The slopes for VOC, VOH, and VOL versus head width were not significantly different from one another (F=0.88, df=2, P>.05). In contrast, the slope for VOE versus head width was significantly lower than all others (F=35.97, df=1, P<.05).

The absolute size of the vomeronasal organ increases during ontogeny, but its relative size decreases. For example, the organ (VOL) is 2.5% of the SVL of the smallest juvenile (16 mm SVL, 2.9 mm HW) and 1.31% of the SVL of the largest adult lizard (48 mm SVL, 6.2 mm HW).

**Interspecific comparisons**

The vomeronasal organ of *Sceloporus undulatus* is qualitatively similar to the vomeronasal organ of *Scincella lateralis*. However, it differs in the placement and development of several structures (Figure 3). The mushroom body of *S. undulatus* projects from the anterior wall of the
vomeronasal capsule, whereas, in *S. lateralis* it projects from the ventral wall. Supportive tissues and ciliated epithelium surrounding the concha of the mushroom body appear relatively thicker in *S. undulatus* than in *S. lateralis*. Vomeronasal sensory epithelium of *S. undulatus* is extremely thin or lacking along the extreme dorsal and ventral surface of the lumen. In *S. lateralis*, a thick layer of sensory epithelium covers the entire lumenal surface. Additionally, the amount of supportive tissue between the vomeronasal organ and the capsule is greater in *S. undulatus*. Finally, the lachrymal duct of *S. undulatus* enters the vomeronasal duct dorsal to the choanal opening. In contrast, the lachrymal duct and the vomeronasal duct enter the choanal groove simultaneously in *S. lateralis*.

The vomeronasal organs of other species utilized in this study are also shown in Figure 3. In general, the vomeronasal organs of these species are morphologically similar to those of *S. lateralis* and *S. undulatus*.

The relationship between VOE and VOC (Table 3) was used to compare the sizes of the vomeronasal organ in ascalobotans and autarchoglossans. Both the *S. lateralis* data and the *S. undulatus* data provide regressions significantly different from zero (*P*<0.05). Neither the slope nor intercept of the relationship between VOE and VOC
for S. lateralis were significantly different from the slope or intercept for S. undulatus (slopes, F=1.08, df=1, 46, P>0.05, intercepts, F=1.92, df=1, 46, P>0.05). I therefore assumed that this relationship between VOE and VOC does not differ among all species. Combining data for all the species, I calculated a common regression line (VOE = 0.1398 + 0.0749 VOC), and then compared the residual values among groups (ascalobotan or autarchoglossan) and among species.

The mean residual for ascalobotans (-0.0241) and the mean residual for autarchoglossans (0.0068) were significantly different (\(X^2=9.29, \text{df}=1, P<0.05\), Kruskal-Wallis test). This indicates that vomeronasal sensory epithelium thickness is greater in autarchoglossans than in ascalobotans. Moreover, there were significant differences among species (\(X^2=23.14, \text{df}=5, P<0.05\), Kruskal-Wallis test, Table 4).

The mean residual for Ophisaurus ventralis was significantly larger than any other species (\(Z=2.12, \text{df}=1, P<0.05\), Wilcoxon 2-sample test). The mean residuals for Scincella lateralis, Hemidactylus turcicus, and Eumeces were not significantly different from one another. (\(X^2=1.17, \text{df}=2, P>.05\), Kruskal-Wallis test). The mean residuals for Xantusia vigilis and Sceloporus undulatus were marginally different (\(Z=1.94, \text{df}=1, P<0.053\), Wilcoxon 2-sample test).
The mean residuals for *X. vigilis* and the *Eumeces* were not significantly different (Z=0.00, df=1, P<0.05, Wilcoxon 2-sample test), but the *Eumeces* were significantly different from *S. undulatus* (Z=2.72, df=1, P<0.05, Wilcoxon 2-sample test).

**DISCUSSION**

The amount of the lumenal surface that is covered by the sensory epithelium and the thickness of sensory epithelium exhibits considerable variation. Sensory epithelium covers most of the lumenal surface (excluding the mushroom body) and is relatively thick in *Scincella lateralis*, *Eumeces faciatus*, *E. inexpectatus*, *Ophisaurus ventralis*, and *Xantusia vigilis*. The sensory epithelium thickness of *O. ventralis*, an autarchoglossan, far exceeds that of any other species in this study (Figure 2) and is similar in thickness to that of garter snakes (about 300 microns, Gillingham and Clark, 1981). The vomeronasal sensory epithelium appears to be even better developed in *Varanus* where it extends down into the vomeronasal duct (Pratt, 1948). In contrast, the sensory epithelium of *Sceloporus undulatus* thins considerably on the uppermost dorsal and lowermost ventral surface of the lumen. In *Hemidactylus turcicus* the sensory epithelium thins only on
the ventral surface. Thus, the functional surface area of sensory epithelium is less in *S. undulatus* and *H. turcicus* than in the other species utilized (Figure 3).

The importance of variation in the surface area and thickness of the vomeronasal sensory epithelium is indicated by the fine structure of this tissue. The vomeronasal epithelium is divided into "columnar baskets". These columns consist of three different cell layers: a supportive cell layer on the luminal surface, a bipolar neuron layer whose dendritic elements invade the supporting cell layer, and a basal undifferentiated cell layer which generates the bipolar layer (Wang, and Halpern, 1980). Each column is surrounded by a sheath of connective tissue, which probably prevents stimulation of neighboring columns. Columns are thought to be functional units (Wang, and Halpern, 1980), and are possibly individual receptors. In garter snakes the supportive cell and the basal cell layers are relatively thin (one cell, and four to six cells thick, respectively, when compared to the bipolar layer (twenty to thirty cells thick). Thus, variation in the thickness of the vomeronasal sensory epithelium is probably due to differences in the thickness of the bipolar neuron layer. A reduction in thickness in this layer could be due to smaller or fewer cells. If it is due to fewer cells, then fewer
dendritic elements would reach the lumenal surface and the sensitivity of the receptor would be reduced.

Receptors may be differentially sensitive to particular classes of chemical compounds (Moulton and Tucker, 1964). Thus, a larger surface of sensory epithelium would presumably contain more sites for the reception of chemical compounds and thus enable a more detailed analysis of those compounds than a smaller surface area (Moulton and Tucker, 1964). Thus, lizards with reduced vomeronasal sensory epithelium thickness and surface area may have fewer receptors in a column. These lizards could respond to a fewer chemical compounds and would possibly be less sensitive to those compounds than lizards with more surface area and thicker vomeronasal sensory epithelium. However, the specificity and sensitivity of the vomeronasal organ is unknown.

An objective of this study was to test the hypothesis that the relative size of the vomeronasal organ is larger in autarchoglossan lizards than in ascalobotan lizards. Comparison of the residual values for ascalobotans and autarchoglossans from a common regression equation indicates that the vomeronasal organs of autarchoglossans are larger than those of ascalobotans. Measurements of all of the species utilized in this study, except Hemidactylus
turcicus, as well as qualitative descriptions of the vomeronasal organs of other ascalobotans and autarchoglossans add additional support to this conclusion. The vomeronasal organs of anoles and chameleons (ascalobotans) are vestigial or lacking (Haas, 1947, Parsons, 1970, Pratt, 1948). On the other hand, the vomeronasal organ of Varanus (autarchoglossan) is well developed (Pratt, 1948). However, observations on H. turcicus suggest that the relative size of the vomeronasal organ may be related to ecology as well as systematic relationships.

The vomeronasal sensory epithelium thickness of H. turcicus (ascalobotan), does not differ from Scincella lateralis or Eumeces (autarchoglossans), and its mean residual is ranked higher than these skinks (table 4). The relatively great thickness of the vomeronasal sensory epithelium of H. turcicus may offset the observed reduction in surface area reported earlier. A thicker epithelium would increase the number of receptors present, thereby increasing the number of dendrites reaching the lumenal surface, and thus increase the sensitivity of the tissue. The vomeronasal sensory epithelium thickness of X. vigilis, another ascalobotan, is not significantly different from the epithelium thickness of Eumeces and was marginally not
different from *S. undulatus*, (P<0.053). This indicates that aphantobots that are secretive and nocturnal such as *H. turcicus*, and possibly *X. vigilis*, have well developed vomeronasal organs and chemosensory abilities, despite their taxonomic position. Thus, my results suggest that the relative size of the vomeronasal organ is associated with the ecology of a species, and that the degree of development of the vomeronasal organ is a continuum rather than a dichotomy.
The Relative Roles of Vision and the Chemical Senses in Prey Detection by *Scincella lateralis*.

INTRODUCTION

Autarchoglossan lizards (scincids, varanids, and anguids, Camp, 1923) use both vision and the chemical senses to detect prey. Although visual and chemical senses may be used independently to release predatory behavior, the manner in which they interact is unknown. Thus, the objective of this study was to evaluate the relative roles of vision and the chemical senses in the predatory behavior of the ground skink, *Scincella lateralis*.

This study consisted of a sequence of three experiments. The first experiment tested the hypothesis that *Scincella lateralis* use both visual and chemical cues to detect prey. I predicted that ground skinks would respond to both the visual or chemical stimulus of prey and that a combination of these stimuli would elicit an even greater response. The second experiment tested the hypothesis that *Scincella lateralis* exhibits a greater response to a concentrated chemical stimulus (normal prey).
than to a disturbance control or to a novel chemical stimulus.

The combined results of the first two experiments indicated that the predatory behavior of ground skinks is primarily motivated by visual cues. Experiment III thus tested the hypothesis that visual cues initiate a sequence of predatory behavior, which will persist in the absence of visual stimuli if appropriate chemical cues are present.

*Scincella lateralis* was used in these experiments because it is generalized insectivore that appears to have well developed chemosensory abilities. For example, ground skinks are able to distinguish the sex of a conspecific by chemical cues alone (Duvall et al. 1980). This species is a common member of the forest floor litter community in the southeastern United States.

I did not attempt to distinguish between nasal and vomeronasal olfaction. The few studies that have made this distinction report that nasal olfaction is relatively unimportant in squamates. For example, when the vomeronasal system is rendered inoperative by removing the tongue, anesthetizing the organ, or cutting the vomeronasal nerve and the olfactory system left intact, snakes are unable to recognize conspecifics or feed normally (Andren, 1982, Burghardt, 1980, Burghardt and Pruitt, 1975, Kubie and
However, when the nasal olfactory system is rendered inoperative by plugging the nostrils or cutting the olfactory nerve and the vomeronasal system left intact, snakes are able to recognize conspecifics and feed normally (Andren, 1982, Burghardt, 1980, Burghardt and Pruitt, 1975, Kubie and Halpern, 1979). I therefore assumed that vomeronasal olfaction was the primary sensory modality of the chemical senses in my experiments. Response to chemical stimuli was measured, in part, by the rate of tongue flicking (RTF).

Tongue flicking is associated with neural activity in the accessory olfactory bulb, and thus the vomeronasal system (Meredith and Burghardt, 1978). RTF can be used to evaluate the response of lizards to chemical cues, because an increased RTF is associated with different levels of arousal. For example, concentrated surface extracts of prey elicit a greater RTF than dilute extracts (Burghardt, 1970, 1973). Moreover, tongue flicking is associated with trailing behavior by all snakes (Burghardt, 1970, Chiszar and Scudder, 1980). Thus, the tongue flicking response is a direct behavioral assay of the use of vomeronasal olfaction.
MATERIALS AND METHODS

Source and maintenance of lizards in Experiments I and II.

Adult *Scincella lateralis* were collected at Hilton Head, South Carolina, during April and June, 1982, and individually marked by toe clipping.

The lizards were housed in groups of five to ten in 26.5 H x 50.5 L x 30 W cm cages. The substrate was bark mulch or sawdust with small pieces of plywood provided for basking sites and places to hide. Fluorescent Vita-lights provided illumination and 100 watt light bulbs provided both light and heat from 0900-1600 hours. Windows provided a natural photoperiod. Lizards were fed daily on meal worms, crickets, and cockroaches. The food was dusted periodically with a mineral-vitamin supplement. Water was provided *ad lib.* in petri dishes and cages were sprayed daily to elevate the humidity.

General experimental protocol of Experiments I and II.

Lizards were introduced into the test arenas two days before testing to acclimate them to experimental conditions. The test arenas were white plastic tubs (13 H x 29 L x 19 W
cm) with a thin layer of sawdust substrate. A small piece of plexiglass permitted the lizards to hide and still be observed. Lizards were not fed, but water was provided in plastic petri dishes. A plastic cylinder was placed near the petri dish to familiarize the lizards with the cylinders used in testing (see below).

General lighting was provided by Vita-lights (L:D 12:12). Heat lamps (40 watt spot lights, lit from 0900-1600 hours) were hung 10 cm above the substrate in each arena for thermoregulation. The ambient temperature during testing was 29 °C (preferred body temperature of Scincella lateralis is 27°C-29°C, Hudson and Bertram, 1966). An observation blind was placed in front of the test arenas to reduce disturbance by the observer.

Specific test procedures are given in the following experimental descriptions. Testing procedures common to Experiments I and II were as follows. Baseline tongue flicks (Table 5) were recorded for a five minute period before testing. The test cylinder was then lowered into the middle of the test arena. The following observations were recorded during the five minute test period: RTF, orientation time, time spent at the cylinder, bumps, and lunges (terms defined in Table 5). Responses were voice recorded on a cassette recorder and transcribed later. At
the end of test the cylinder was removed. After the day's testing the lizard was returned to its home cage. To reduce habituation, at least one week separated successive tests on any one lizard. All testing took place between 1000 and 1300 hours, during the peak of the lizards activity.

**Experiment I**

The four treatments were: 1. disturbance control, 2. a chemical stimulus, 3. a visual stimulus, and 4. a simultaneous visual and chemical stimulus (visual/chemical). Visual and chemical stimuli alone or in combination were presented in transparent plastic cylinders (2.5 cm H x 2.6 cm D, test cylinders). Air was pumped through the cylinders during testing (see next paragraph). The disturbance control was a clean empty test cylinder. The chemical stimulus was a perforated test cylinder in which a live adult cockroach (*Blattella germanica*) was placed for five minutes before testing, and then removed. During testing, a live cockroach was present in the air line near the pump (line cylinder). The visual stimulus was a sealed test cylinder containing a live cockroach. The visual/chemical stimulus was a perforated test cylinder containing a live cockroach, and a cockroach in the line cylinder.
The test cylinders were lowered into the test arenas on small diameter plastic tubes. The tubes were attached to a 110 volt Carol aquarium pump. During testing air was pumped at a rate of 0.17 cm³/s through the tubes into the test cylinders or just above them (visual test). For the visual/chemical and chemical treatments another cylinder (line cylinder) was connected to the tube near the pump. This experimental design follows Chiszar et al. (1981). Each lizard were tested on all four stimuli in a standardized rotation schedule (Table 6). Tests were conducted from May through July, 1982.

Experiment II

With the following exceptions, methods were the same as used in Experiment I. The test arenas were placed in an environmental chamber (L:D, 12:12, 29°C:20°C). The concentrated chemical stimulus was prepared by placing the test cylinder in a plastic bag containing fifteen adult cockroaches for fifteen minutes. Additionally, air was pumped over fifteen adult cockroaches in the line cylinder during testing. The novel chemical stimulus was a 1 part per 1000 aqueous methyl sulfide solution. A round piece (2.6 cm. dia.) of filter paper saturated with the novel stimulus was placed inside of the test cylinder. Air was pumped through the test cylinders during testing.
Tests with the concentrated chemical stimulus were conducted on September 11 and 12, 1982. Five lizards were presented the concentrated chemical stimulus and five were presented with a disturbance control control on September 11, 1982. On September 12, the lizards that were previously presented the chemical stimulus were presented the control and vice versa. I assumed that testing on the first day would have no effect on the response the second day. Tests with the novel chemical stimulus were conducted on October 12, 13, 18, and 19, 1982. Ten lizards from the previous experiment plus eight additional lizards were used in this experiment. The ten lizards that had already been tested with the concentrated chemical stimulus and the control, were presented only the novel stimulus on October 18 and 19, 1982. The eight previously untested lizards were presented the novel stimulus and a disturbance control on October 12 and 13, 1982.

Experiment III

One hundred freshly caught adult *Scincella lateralis* (mean snout-vent length = 42.3 mm, standard error = 0.319 mm) were purchased from Snake Farm in La Place, La. on May 11, 1983. Lizards were maintained in three 61 W by 122 L by 61 H (cm) terraria prior to testing. The substrate in these
cages was a mixture of sand and sawdust. Pieces of plywood and branches were provided as basking sites and shelter. General illumination was provided by Vita-lights. A single 75 watt heat lamp per cage permitted thermoregulation. To insure maximum activity during the testing period, the lizards were phase shifted from a natural photoperiod to L:D 12:12 with the light cycle from 900 to 1900 hours. The lizards were acclimated to these conditions for at least two weeks prior to testing. Lizards were fed daily on a diet of crickets, cockroaches and meal worms. Water was provided ad lib. in petri dishes, and the terraria were sprayed daily.

The test arenas were provided with a plexiglass shelter, a petri dish, a transparent plastic cylinder, and a sand substrate. The petri dish, containing water, was placed near the plexiglass at one end of the arena, and the cylinder was placed at the other end. Testing took place in an environmental chamber with a light cycle of 12:12, an ambient temperature of 28°C, and relative humidity of about 74%. The lizards were acclimated to the experimental conditions for two days prior to testing. On the second day of the acclimation period the test arenas were placed behind one-way glass through which all subsequent observations were made. Testing took place on the third day between 0900 and 1100, from June 18 through July 24, 1983.
Individual lizards were tested once with one of six possible combinations of two visual and three chemical stimuli. The visual stimuli were a cockroach sealed in a transparent plastic cylinder or an empty cylinder (visual control). The chemical stimuli were: 1. a one centimeter long piece of white pipe cleaner dipped in distilled water, 2. a one centimeter long piece of white pipe cleaner dipped in a cockroach extract (hereafter called extract, prepared after Henderson, et al., 1983, see below), and 3. a dead cockroach (killed by freezing before presentation). All chemical stimuli were handled with forceps to avoid human contamination. Lizards were assigned one of the above treatments using a random number table. The control and extract stimuli were presented "blind" by having someone other than the observer place them in vials labeled "A" and "B". The observer was informed which vial contained the extract and which the control after termination of the experiment.

The cockroach extract was prepared by immersing three grams of live cockroaches in ten milliliters of distilled water heated to 60°C, and gently swirling the flask for two minutes. The resulting fluid was then centrifuged for ten minutes at 2500 rpms (1250 gs) and the supernatant was removed and frozen until use.
During testing, all stimuli were introduced into the arena near the plastic cylinder. The chemical stimuli and control were dropped into the arena with a pair of forceps. The visual stimuli was then lowered on a fine piece of string on top of the chemical stimuli. Each lizard was then observed for at least three minutes (orientation period). If the lizard failed to respond within the three minutes, the test was terminated. A response was defined as movement to within one centimeter of the test cylinder. If the lizard responded to the visual stimulus, the visual stimulus was pulled slowly from the arena, and the lizard observed for an additional five minutes (response period). The potential observation time for each lizard was a maximum of eight minutes. Observations made during testing were the number of tongue flicks during one minute intervals, whether or not the lizard moved to within one centimeter of the test cylinder, the time of response to the visual stimulus, and attacks on the chemical stimuli.

**Statistical Analyses**

Data of Experiments I-II and the orientation period of Experiment III were non-normally distributed. Therefore, non-parametric Kruskal-Wallis tests were used to determine differences among treatments, Wilcoxon 2-sample tests were
used to determine differences between treatments, and Chi-
square tests were used to determine differences among
response variables of Experiment III. The RTF data from the
response period of Experiment III were normally distributed.
Therefore, 2-way ANOVAs were used to determine differences
among chemical treatments, and Duncans multiple range tests
were used to determine differences between treatments.
Analyses were performed using the SAS software package (Ray,
1982).

RESULTS

**Experiment I**

The level of arousal of all lizards prior to testing
was similar across treatments (Table 7). There were no
significant differences in the baseline tongue flicks among
treatments ($X^2=3.35$, df=3, $P>0.05$, Kruskal-Wallis test).
Moreover, variation among lizards for all of the six
response variables was not significant (Table 8). Thus,
individual lizards responded similarly within all
treatments. There were significant differences among
treatments to four response variables: RTF, bumps, lunges,
and orientation time., RTF increased in the sequence:
control, chemical, visual, visual/chemical (Table 9). Although there was a significant treatment effect ($X^2=14.38$, df=3, $P<0.05$, Kruskal-Wallis test), differences between neighboring ranks were not significant (Table 10).

There were no bumps or lunges during either the control or chemical treatments (Table 11). The number of bumps or lunges during the visual and visual/chemical treatments did not differ ( $P<0.45$ and $P<0.71$, Wilcoxon 2-sample tests on bumps and lunges respectively).

Five of thirty eight lizards moved to within one centimeter of the test cylinder during the control and chemical treatments (Table 12). In contrast, nineteen of thirty eight did so during the visual and visual/chemical treatments ($X^2=11.94$, df=1, $P<0.05$, Kruskal-Wallis test). However, there were no significant differences among treatments in orientation times for lizards that responded to the test cylinders ($X^2=2.34$, df=3, $P>0.05$, Table 12).

Lizards tended to spend more time at test cylinders during the visual and visual/chemical treatments than during control or chemical treatments ($X^2=7.01$, df=3, $0.05<P<0.10$, Kruskal-Wallis test). The lack of significance in this response variable was due to five lizards that moved to within one centimeter of the test cylinder during the control and chemical treatments but paid no attention it.
Experiment II

Lizards exhibited a greater RTF to the concentrated chemical stimulus than they did to the control (Table 13, $Z=0.54$, df=1, $P<0.05$, Wilcoxon 2-sample test). The level of responsiveness within a treatment was statistically equivalent on the first and second day of testing (control, $t=1.70$, df=4, $P>0.05$, concentrated chemical, $t=1.12$, df=4, $P>0.05$, students t-test) Thus the order of testing had no affect on the response. The response to the concentrated chemical stimulus was not due simply to the presence of a strong odor, as the RTF to the methyl sulfide stimulus was the same as the RTF to the control (Table 10, $X=2.40$, df=1, $P<0.90$, Wilcoxon 2-sample test).

Experiment III

During the orientation period thirty-eight lizards responded to the visual stimulus and only two responded to the visual control stimulus (Table 14, $X^2=55.88$, df=1, $P<0.05$, Chi-square test). The number of lizards responding and the time for orientation to the visual stimulus was independent of the chemical treatment ($X^2=2.45$, df=2, $P>0.05$, and $X^2=4.87$, df=3, $P>0.05$, respectively, Chi-square test). The RTF during the orientation period of the visual
and the visual control treatments were not significant among chemical treatments ($X^2=4.03$, df=2, $P>0.05$, and $X^2=0.67$, df=2, $P>0.05$, respectively, Chi-square tests).

The response period began when the visual stimulus was removed. The response period of the visual control treatment was not analyzed because only two lizards responded during this treatment. The RTF during the response period of the visual treatment was significantly higher than during the orientation period (Table 15).

In contrast to the orientation period, during the response period there were significant differences in RTF among chemical treatments (Table 16, $F=6.00$, df=2, $P<0.05$, 2-way ANOVA). The RTF to the extract was significantly greater than the RTF to the dead cockroach or the control. The RTF to the distilled water control and the dead cockroach stimulus were not significantly different ($P>0.05$, Duncans multiple range test). There were no significant differences among the one minute intervals during the response period ($F=1.95$, df=4, $P>0.05$, 2-way AVOVA), nor was there any one minute interval and chemical treatment interaction ($F=0.26$, df=8, $P>0.05$, 2-way ANOVA).

The lizards attacked the chemical stimuli during the response period of the visual treatment. They did not attack the distilled water control, and there were no
significant differences between the number of lizards that attacked the dead cockroach and the extract ($X^2 = 0.36, \text{df}=1, P>0.05$, Chi-square test) during the visual treatment (Table 16). Two lizards attacked the chemical stimulus during the visual control treatment, one attacked during the extract treatment, and one attacked during the dead cockroach treatment.

**DISCUSSION**

The results of Experiment I indicate that the predatory behavior of *Scincella lateralis* is primarily motivated by visual cues. Chemical cues themselves did not significantly increase the response to prey. Responses in the two treatments with a visual stimulus were statistically equivalent regardless of the presence or absence of chemical cues. Thus, the entire predatory repertoire of *Scincella lateralis* was stimulated by visual cues alone. However, a closer look at the RTF suggests that chemical cues may have contributed to the response. There were consistent shifts in mean and median values of RTF, such that each treatment can be ranked control< chemical< visual< visual/chemical. The order of this ranking suggests that additive effects might be present. This further suggests that visual cues
release a RTF response even when chemical cues were absent. A similar situation was encountered by Chiszar et al., (1981) in work with garter snakes.

Lizards exhibited significantly higher RTF to the concentrated stimulus of Experiment II than to the control. Moreover, this response was not due to the mere strength of the prey stimulus, as response to methyl sulfide did not differ from that to the control. Thus, the chemical cues presented in Experiment I were evidently insufficient to elicit a significant increase in RTF above resting levels (the RTF during the control treatment). Loop and Scoville (1972) encountered a similar situation in their work with neonate *Eumeces inexpectatus*. They presented various surface extracts and controls, and found no significant differences in the RTF. In a later study, Burghardt (1973) presented neonate *Eumeces fasciatus* with more concentrated extract than that used by Loop and Scoville and found significant differences in RTF between the extracts and the control.

The response during the orientation period of the third experiment was similar to the response during the first experiment. A visual cue stimulated an increased RTF and orientation to the prey. Judging from the lack of response to the visual control treatment, the associated chemical
cues did not contribute to this response. The chemical stimuli presented during the orientation period had no apparent effect on any of the behaviors observed. Therefore, Experiment III, like Experiment I, demonstrated that visual cues provide the information necessary to complete a predatory episode.

The removal of the visual stimulus in Experiment III simulated prey disappearance after initiation of the predatory attack. Such loss of visual contact with prey item is probably a normal occurrence for ground skinks. The ability to detect prey under such conditions would be particularly advantageous. Lizards exhibited a higher RTF during the response period of Experiment III than during the orientation period for all chemical treatments. Presumably, lizards were using chemosensory search for escaped prey.

The RTF to the extract was significantly greater than to the dead cockroach or the control. The lack of significant differences in RTF between the dead cockroach and the control is curious. The lizards were obviously able to discriminate between the control and dead cockroach stimulus as they bit and ate the dead cockroach, but did not bite the distilled water control. This suggests that at close range the dead cockroach treatment provided sufficient
chemical cues to complete the predatory episode. The greater RTF to the extract than the dead cockroach was probably due to a greater concentration of chemical cues and the ability to detect these cues at a greater distance. There were however, no significant differences between the number of the lizards that attacked the dead cockroach and extract. This implies that the lizards did not differentiate between a normal prey (cockroach) and a pipe cleaner that smelled like a cockroach.

Results of my experiments suggest that Scincella lateralis have alternative pathways of predatory behavior (Figure 5). Active lizards may adopt one of two basic foraging modes; actively foraging or a sit-and-wait foraging (Pianka, 1966). During sit-and-wait foraging a lizard detects prey visually. The lizard exhibits an elevated RTF, orients to the prey, identifies its target and attacks. The primary component of the visual stimulus is movement (Burghardt, 1964, 1970). Chemical cues become important only if visual contact is lost or movement ceases. Therefore, if the prey eludes capture by freezing or moving out of sight, the lizard either switches to the actively foraging mode and searches for it using both vision and chemical senses, or remains in the sit-and-wait mode and waits for other prey to pass by. Thus, chemical cues do not
normally stimulate predatory behavior, but supplement visual cues.

Actively foraging lizards use both vision and chemosensation to detect prey. If the lizard sights a prey item, it will follow the sit-and-wait behavioral sequence. If prey is discovered by chemosensation, attack can be initiated by chemical cues alone. For example, two lizards were actively tongue flicking and moving about the test arena when the test cylinder was introduced. When they moved to within one centimeter of the test cylinder it was removed. The lizards then approached the chemical stimulus and after tongue flicking it several times, attacked.

The predatory behavior of ground skinks is similar to that of crotalid snakes. Visual cues stimulate tongue flicking in both groups (Chiszar et al., 1981). Both use visual cues to initiate a predatory episode, to identify prey, and to direct their predatory attack (crotalids also use thermal cues). The predatory repertoires differ somewhat after the attack. If the prey escapes they search for it using both visual and chemical cues. In contrast, crotalids trail the wounded prey using vomeronasal olfaction and upon discovery ingest the prey (Golan et al., 1981). In general, crotalids also follow the pathways diagramed in Figure 5. However, the actively foraging mode is generally associated
with extreme hunger in crotalids (Chiszar et al., 1981) and if the initial strike fails, the subsequent behavior of crotalids is unknown.
LITERATURE CITED


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Table 1. Ascalobotan and autarchoglossan lizards utilized in interspecific and intraspecific comparisons. The adult (N=18) and juvenile (N=28) specimens of *Scincella lateralis* represent a complete ontogenetic series. *Sceloporus undulatus* is represented by three adult and five juvenile specimens.

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<th>Autarchoglossans</th>
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<td></td>
<td><strong>Anguidae</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ophisaurus ventralis</em></td>
<td>2</td>
</tr>
</tbody>
</table>
Table 2. The relationship between vomeronasal measurements (Y) and head width (X) for *Scincella lateralis*.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Regression equation</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (VOL)</td>
<td>Y = 0.1679 + 0.0746 X</td>
<td>0.87</td>
</tr>
<tr>
<td>Height (VOH)</td>
<td>Y = 0.0949 + 0.0531 X</td>
<td>0.73</td>
</tr>
<tr>
<td>Capsule length (VOC)</td>
<td>Y = 0.2675 + 0.0738 X</td>
<td>0.78</td>
</tr>
<tr>
<td>Epithelium thickness (VOE)</td>
<td>Y = 0.1400 + 0.0128 X</td>
<td>0.09</td>
</tr>
</tbody>
</table>
Table 3. The relationship between the thickness of the vomeronasal epithelium (VOE, Y) and the vomeronasal capsule length (VOC, X) for *Sceloporus undulatus* and *Scincella lateralis*.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Regression equation</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. undulatus</em></td>
<td>8</td>
<td>Y = 0.057 + 0.1128 X</td>
<td>.01</td>
</tr>
<tr>
<td><em>S. lateralis</em></td>
<td>47</td>
<td>Y = 0.1464 + 0.0734 X</td>
<td>.27</td>
</tr>
</tbody>
</table>
Table 4. The mean residual values calculated from the common regression equation \(Y = 0.1398 + 0.0749X\) for the relationship between vomeronasal sensory epithelium thickness \(Y\) and vomeronasal capsule length \(X\) for all species utilized in this study. Lines connect means that are not significantly different (Wilcoxon 2-sample tests, \(P<.05\)).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Group</th>
<th>Mean Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ophisaurus ventrals</td>
<td>2</td>
<td>Autarchoglossa</td>
<td>0.0393</td>
</tr>
<tr>
<td>Hemidactylus turcicus</td>
<td>4</td>
<td>Ascalobota</td>
<td>0.0115</td>
</tr>
<tr>
<td>Scincella lateralis</td>
<td>47</td>
<td>Autarchoglossa</td>
<td>0.0072</td>
</tr>
<tr>
<td>Eumeces</td>
<td>6</td>
<td>Autarchoglossa</td>
<td>-0.0047</td>
</tr>
<tr>
<td>Xantusia vigilis</td>
<td>3</td>
<td>Ascalobota</td>
<td>-0.0054</td>
</tr>
<tr>
<td>Sceloporus undulatus</td>
<td>8</td>
<td>Ascalobota</td>
<td>-0.0490</td>
</tr>
</tbody>
</table>
Table 5. Measures of response by *Scincella lateralis* during the visual and chemical treatments of Experiments I-III.

1. Orientation time (OT) = the time (seconds) from when the test cylinder was introduced until the lizard moved to within one centimeter of the cylinder.

2. Time spent at the cylinder (AT) = the amount of time (seconds) the lizard spent within one centimeter of the test cylinder.

3. Base line tongue flicks (BTF) = the total number of tongue flicks during the five minute period just prior to the introduction of the test cylinder.

4. Rate of tongue flicking (RTF) = the total number of tongue flicks during the five minute test period.

5. Bumps (B) = a closed mouth touch of the test cylinder.

6. Lunge (L) = an open mouth attack upon the test cylinder.
Table 6. The standardized rotation order used in Experiment I (see text for details).

<table>
<thead>
<tr>
<th>Lizard No.</th>
<th>Sequence of test stimuli</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>1 2 3 4</td>
</tr>
<tr>
<td>2.</td>
<td>2 3 4 1</td>
</tr>
<tr>
<td>3.</td>
<td>3 4 1 2</td>
</tr>
<tr>
<td>4.</td>
<td>4 1 2 3</td>
</tr>
<tr>
<td></td>
<td>etc.</td>
</tr>
</tbody>
</table>
Table 7. The rate of tongue flicking by *Scincella lateralis* during the five minute interval prior to the presentation of the stimulus (baseline tongue flicks of Experiment I). Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Median</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4</td>
<td>10.7 (2.85)</td>
</tr>
<tr>
<td>Chemical</td>
<td>6</td>
<td>8.2 (2.01)</td>
</tr>
<tr>
<td>Visual</td>
<td>2</td>
<td>5.0 (1.26)</td>
</tr>
<tr>
<td>Visual/chemical</td>
<td>1</td>
<td>5.4 (1.82)</td>
</tr>
</tbody>
</table>
Table 8. The results of Kruskall-Wallis tests\(^1\) on the variation in response among *Scincella lateralis* to the four treatments of Experiment I.

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Chi-square</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base Line Tongue Flicks</td>
<td>11.11</td>
<td>0.88</td>
</tr>
<tr>
<td>Rate of Tongue Flicking</td>
<td>13.41</td>
<td>0.76</td>
</tr>
<tr>
<td>Time spent at the Cylinder</td>
<td>16.13</td>
<td>0.58</td>
</tr>
<tr>
<td>Orientation Time</td>
<td>14.65</td>
<td>0.68</td>
</tr>
<tr>
<td>Bumps</td>
<td>16.97</td>
<td>0.52</td>
</tr>
<tr>
<td>Lunges</td>
<td>15.34</td>
<td>0.64</td>
</tr>
</tbody>
</table>

1. All statistical tests had eighteen degrees of freedom.
Table 9. The rate of tongue flicking during the five minute test period by *Scincella lateralis* to the four treatments of Experiment I. Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Median</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>8</td>
<td>10.4 (2.24)</td>
</tr>
<tr>
<td>Chemical</td>
<td>13</td>
<td>14.4 (2.89)</td>
</tr>
<tr>
<td>Visual</td>
<td>20</td>
<td>22.2 (3.98)</td>
</tr>
<tr>
<td>Visual/chemical</td>
<td>27</td>
<td>27.1 (3.88)</td>
</tr>
</tbody>
</table>
Table 10. Pairwise comparisons of the rate of tongue flicking to the four treatments of Experiment I by *Scincella lateralis* (Wilcoxon 2-sample tests, with one degree of freedom).

<table>
<thead>
<tr>
<th>Treatments Compared</th>
<th>Z</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control vs Chemical</td>
<td>-0.63</td>
<td>0.52</td>
</tr>
<tr>
<td>Chemical vs Visual</td>
<td>-1.39</td>
<td>0.16</td>
</tr>
<tr>
<td>Visual vs Visual/Chemical</td>
<td>-1.08</td>
<td>0.27</td>
</tr>
<tr>
<td>Control vs Visual</td>
<td>-2.49</td>
<td>0.01</td>
</tr>
<tr>
<td>Chemical vs Visual/Chemical</td>
<td>-2.56</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table 11. The number of bumps and lunges by *Scincella lateralis* to the four treatments of Experiment I. Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Lunges</th>
<th></th>
<th>Bumps</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean</td>
<td>Median</td>
<td>Mean</td>
</tr>
<tr>
<td>Control</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chemical</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Visual</td>
<td>0</td>
<td>1.4 (0.87)</td>
<td>0</td>
<td>3.5 (1.49)</td>
</tr>
<tr>
<td>Visual/chemical</td>
<td>0</td>
<td>0.7 (0.40)</td>
<td>0</td>
<td>1.7 (0.74)</td>
</tr>
</tbody>
</table>
Table 12. The number of *Scincella lateralis* that responded by moving to within one centimeter of the test cylinder during the four treatments of Experiment I, and the time for that response to occur (seconds). Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N responded</th>
<th>Median</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>2</td>
<td>152</td>
<td>152.5 (92.50)</td>
</tr>
<tr>
<td>Chemical</td>
<td>3</td>
<td>156</td>
<td>170.0 (18.15)</td>
</tr>
<tr>
<td>Visual</td>
<td>10</td>
<td>50</td>
<td>98.5 (29.50)</td>
</tr>
<tr>
<td>Visual/chemical</td>
<td>9</td>
<td>132</td>
<td>138.7 (27.45)</td>
</tr>
</tbody>
</table>

1. N= 19 for each treatment.
Table 13. The rate of tongue flicking during the five minute test period by *Scincella lateralis* to the three treatments of Experiment II. Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Median</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Concentrated chemical</td>
<td>10</td>
<td>20</td>
<td>18.4 (4.24)</td>
</tr>
<tr>
<td>Methyl sulfide</td>
<td>18</td>
<td>2</td>
<td>4.1 (1.52)</td>
</tr>
<tr>
<td>Control</td>
<td>18</td>
<td>3</td>
<td>4.4 (1.37)</td>
</tr>
</tbody>
</table>
Table 14. The general response of *Scincella lateralis* to the visual and chemical treatments during the orientation period of Experiment III. Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number Tested</th>
<th>Mean Number RTF&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Responding&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Mean time to Orientation&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vision Control</td>
<td>14</td>
<td>.5 (.38)</td>
<td>13</td>
<td>62.3 (13.78)</td>
</tr>
<tr>
<td>Extract</td>
<td>16</td>
<td>1.5 (.46)</td>
<td>13</td>
<td>110.7 (18.41)</td>
</tr>
<tr>
<td>Dead cockroach</td>
<td>17</td>
<td>1.2 (.44)</td>
<td>12</td>
<td>65.0 (14.22)</td>
</tr>
<tr>
<td>Vision control</td>
<td>15</td>
<td>.7 (.34)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Extract</td>
<td>15</td>
<td>1.1 (.47)</td>
<td>1</td>
<td>&lt;30.0</td>
</tr>
<tr>
<td>Dead cockroach</td>
<td>15</td>
<td>.7 (.40)</td>
<td>1</td>
<td>&lt;30.0</td>
</tr>
</tbody>
</table>

1. The rate of tongue flicking was calculated as the number of tongue flicks per one minute interval prior to response.
2. The response criterion was movement to within one centimeter of the test cylinder during the first three minutes of the test.
3. The mean orientation time (seconds) is the time from test cylinder introduction until movement to within one centimeter of the test cylinder.
Table 15. The rate of tongue flicking by *Scincella lateralis* that responded to the visual stimulus in the first, second, and third minute intervals during the orientation period of Experiment III, and the rate of tongue flicking during the following response period. Means are followed by one standard error. Statistical differences between the orientation period and the following response period were tested with students t-tests, all tests were significant P<0.05.

<table>
<thead>
<tr>
<th>Interval</th>
<th>Orientation period</th>
<th>Response period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (Median)</td>
<td>Mean/ Min.</td>
</tr>
<tr>
<td>1</td>
<td>0.9 (0.55)</td>
<td>4.4 (0.81)</td>
</tr>
<tr>
<td>2</td>
<td>0.3 (0.25)</td>
<td>4.6 (1.06)</td>
</tr>
<tr>
<td>3</td>
<td>1.5 (0.37)</td>
<td>4.7 (1.3)</td>
</tr>
</tbody>
</table>

1. Test statistic of the students t-test.
Table 16. The rate of tongue flicking (RTF) to the chemical stimuli by *Scincella lateralis* in the response period during the visual treatment of Experiment III. Means are followed by one standard error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Mean RTF</th>
<th>N attacked¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>13</td>
<td>4.2 (0.63)</td>
<td>0</td>
</tr>
<tr>
<td>Extract</td>
<td>13</td>
<td>6.7 (1.09)</td>
<td>8</td>
</tr>
<tr>
<td>Dead roach</td>
<td>12</td>
<td>4.1 (0.57)</td>
<td>7</td>
</tr>
</tbody>
</table>

¹. The number of lizards that either bit or ate the chemical stimulus.
Figure 1. Sagittal section of the vomeronasal organ of Scincella lateralis depicting the measurements taken. Vomeronasal capsule length (VOC), vomeronasal organ length (VOL), vomeronasal sensory epithelium thickness (VOE), and vomeronasal capsule height (VOH).
Figure 2. A sagittal section of the snout of Scincella lateralis depicting the vomeronasal system. Key to lettering: aob accessory olfactory bulb, cnc cartilaginous nasal capsule, 1 lumen, mb mushroom body, ob olfactory bulb, ose nasal olfactory sensory epithelium, pm premaxilla, sm septomaxilla, to tongue, vo vomer, voe vomeronasal sensory epithelium, von vomeronasal nerve.
Figure 3. Sagittal sections of the vomeronasal organs *Scincella lateralis* (1), *Eumeces inexpectatus* (2), *Ophisaurus ventralis* (3), *Sceloporus undulatus* (4), *Hemidactylus turcicus* (5), and *Xantusia vigilis* (6). Photographs depict typical vomeronasal sections. Arrows point anteriorly. See Figure 2 for specific tissue and organ identification. Scale: 18 mm=0.400 mm.
Figure 4. The relationship between vomeronasal sensory epithelium thickness and vomeronasal capsule length for the autarchoglossans: Scincella lateralis (○), Eumeces fasciatus, E. ineffectus (□), and Ophisaurus ventralis (△), and the ascidobots: Sceloporus undulatus (●), Hemidactylus turcicus (▲), and Xantusia vigilis (■). A common regression line is plotted for all species (VOE = 0.1398 + 0.0749 VOC). Numbers within circles indicate repeated identical observations.
Figure 5. A flow diagram of the alternate pathways of predatory behavior by the skink, *Scincella lateralis*. 
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A qualitative and quantitative comparison of the vomeronasal organ was made of the autarchoglossan lizards: *Scincella lateralis*, *Eumeces fasciatus*, *Eumeces inexpectatus*, and *Ophisaurus ventralis*, and the ascalobotans: *Sceloporus undulatus*, *Hemidactylus turcicus*, and *Xantusia vigilis*. As judged by the thickness of the vomeronasal sensory epithelium the vomeronasal organ was most highly developed in *Ophisaurus ventralis* and least developed in *Sceloporus undulatus*.

A comparison of the relationship between the vomeronasal sensory epithelium thickness and vomeronasal capsule length of autarchoglossans and ascalobotans supports the hypothesis that the vomeronasal organs of autarchoglossans are larger than ascalobotans. However, a comparison of mean residuals for the species utilized in this study indicate that the relative size of the vomeronasal organ may be related to ecology as well as systematic relationships. Lizards that are secretive, fossorial, nocturnal or crepuscular have a tendency to have relatively well developed vomeronasal
organs as measured by the thickness of the vomeronasal sensory epithelium, and lizards that are diurnal, visually oriented, and aboreal generally have smaller, less developed vomeronasal organs.

*Scincella lateralis* responds to both visual and chemical cues of prey. A visual stimulus is associated with an increased rate of tongue flicking, orientation to the prey, and attack behavior. Chemical cues are unimportant when the visual cue (movement) is present. When prey are non-moving or dead, chemical cues enable the lizard to distinguish potential prey from inanimate objects.

Vision and the chemical senses interact in a complex way to form the predatory repertoire of *Scincella lateralis*. Lizards may adopt one of two basic foraging strategies; an active foraging strategy or a sit-and-wait strategy. Lizards in the active foraging mode use both visual and chemical cues to detect moving or non-moving prey. A lizard in the sit-and-wait mode uses vision to detect prey movement. However, if the prey eludes capture after a lizard in the sit-and-wait mode begins its predatory attack, chemical cues may be used to track or identify the prey.