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STRIKE-INDUCED CHEMOSENSORY SEARCHING, KLEPTOPARASITISM, AND THE POSSIBILITY OF CHEMICAL CRYPSIS IN RATTLESNAKES

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STRIKE-INDUCED CHEMOSENSORY SEARCHING, KLEPTOPARASITISM, AND THE POSSIBILITY OF CHEMICAL CRYPSIS IN RATTLESNAKES

by

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DISSERTATION

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The University of Texas at El Paso
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Abstract

Predator-prey interactions shape the natural histories of both species as each tries to adapt and counter-adapt to the tactics of the other. This important evolutionary dynamic is crucial for ecosystem formation and stability. Predation is a fundamental aspect of life for most organisms, and many venomous reptiles, particularly ambush-foraging viperids, have evolved a prey-acquisition strategy that is highly effective in immobilizing prey, while minimizing possible counterattacks. Best studied in rattlesnakes, this remarkable behavioral sequence is known as strike-induced chemosensory searching (SICS). Throughout decades of research, the body of SICS literature on venomous reptiles has become fairly robust, particularly in rattlesnakes. However, until now, there has never been a comprehensive review of this topic. In Chapter 1, I explore and discuss key results from decades of SICS research, which has mainly been conducted on rattlesnakes. I also provide a taxonomic overview of SICS in other species, and consolidate all known papers providing experimental tests of SICS into a convenient table. I organize the review topically, and also provide a summary section that provides forward-looking advice for future experimental work. During SICS, rattlesnakes partially rely on venom cues associated with prey trails, and a chemical search image of struck prey, to facilitate relocation of the carcass. However, rattlesnakes are also known to scavenge carcasses, although their propensity for such behavior remains unknown. In Chapter 2, I used captive rattlesnakes to conduct behavioral experiments to determine if rattlesnakes were more likely to locate and consume mouse carcasses if they had been envenomated by another snake. Such behavior would constitute an act of prey theft, known as kleptoparasitism. Results indicated that venom cues are not important to scavenging rattlesnakes, and that the striking of prey is necessary to facilitate efficient trailing behavior. Thus, kleptoparasitism might be an uncommon event in the wild, and scavenging behavior in rattlesnakes is difficult to generalize. Normally, however, rattlesnakes are ambush predators, and most species are small mammal specialists, mostly preying on rodents. Many rodent species have evolved numerous anti-predator defense mechanisms, and one such defense is detection and avoidance of predators via olfactory cues. However, it is likely that ambush-foraging viperids are not easily detected via chemoreception, and complete scent-suppression might be widespread in these snakes. This scent-suppression ability is known as chemical crypsis. Using more captive behavioral experiments in Chapter 3, I tested the ability of prairie voles to detect olfactory cues from two ambush-foraging viperid species and three active-foraging colubrid species. Vole behavioral responses, which were used as a proxy for stress indicators, were quantified during each treatment. The results did not reveal any significant differences in behavioral responses among treatments, rendering my assessment of chemical crypsis in rattlesnakes inconclusive. Voles likely were able to detect the snake scents, but individual responses to the odors were highly variable. Reasons for this response variation are discussed.

Table of Contents

List of Tables

Chapter 2

Chapter 3

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 1: Introduction

Rattlesnakes are cryptic predators that are difficult to find, largely because of a sedentary lifestyle partially spent waiting in ambush for prey to wander by (Reinert et al. 1984; Clark 2016). As a consequence, there remains much to learn about these secretive reptiles. Rattlesnakes are important ecosystem predators, often representing the highest levels in trophic webs (Beaupre and Douglas 2009). Therefore, declines in their population numbers can have deleterious effects upon lower trophic levels, including uncontrolled prey populations, many of which comprised of “pest” species to humans (Beaupre and Douglas 2009:2). Given their understudied nature and importance in ecosystem function, combined with their negative public perception (Seigel and Mullin 2009), continued research into rattlesnake life history traits is crucial, especially concerning predator-prey dynamics (Nowak et al. 2008).

Relationships between predators and prey have evolved over time to shape the natural history of both species, as each tries to stay one step ahead of the other (Crawley 1992; Dieckmann et al. 1995; Marrow et al. 1996). Predation is a fundamental aspect of life for most organisms, and this important evolutionary dynamic is crucial for ecosystem formation and stability (van Baalen and Sabelis 1993; Cressman and Garay 2009). Generally, predators employ two basic modes of prey-acquisition: mobile pursuit (active-foragers) and sit-and-wait (ambush-foragers) (Schoener 1971). Squamate reptiles (snakes and lizards) display both active and ambush strategies, and chemoreception is especially important for prey detection (Burghardt 1970; Vitt et al. 2003; Baeckens et al. 2017).

Many venomous reptiles, particularly ambush-foraging viperids, have evolved a prey-acquisition strategy that is highly effective in immobilizing prey, while minimizing possible counterattacks. Best studied in rattlesnakes, this remarkable behavioral sequence is known as strike-induced chemosensory searching (SICS) (Chiszar et al. 1977; Chiszar et al. 1982a; Chiszar et al. 1983a). During SICS, rattlesnakes follow trails left by envenomated prey, and their trailing ability is further augmented by the formation of a chemical search image (CSI) of struck prey, a neural memory that helps guide the snake to the matching prey item (Chiszar et al. 1982b; Melcer and Chiszar 1989a). SICS is present in many other squamate taxa other than Viperidae, and Chapter 2 provides an in-depth and comprehensive review of this behavior in reptiles.

As an alternative foraging strategy, rattlesnakes will sometimes scavenge carrion, and seem highly attracted to putrescent carcasses, although the extent to which this behavior occurs in the wild is unresolved (Gillingham and Baker 1981; DeVault and Krochmal 2002; Clark 2016). Scavenging by snakes in the wild confers numerous benefits, and species that use chemoreception to locate prey might be more inclined to scavenge than more visually oriented snakes (DeVault and Krochmal 2002). In addition to scavenging for food, animals will also steal food from one another. This theft of another individual's food is known as kleptoparasitism (Rothschild and Clay 1952; Brockmann and Barnard 1979). Such thievery occurs in a wide range of taxa, including reptiles, and kleptoparasites engage in this behavior to capitalize from the efforts expended by another individual to procure food (Iyengar 2008).

Rattlesnakes strongly prefer envenomated prey over non-envenomated prey (Chiszar et al. 1999a; Chiszar et al. 2008). Consequently, rattlesnakes could act as kleptoparasites if they detect envenomated prey in the wild. Since rattlesnakes quickly strike and release prey, and relocate them later for consumption, such a scenario could occur in the wild if a snake consumes a dead prey item that has been envenomated by a different snake. In Chapter 3, I investigated rattlesnakes' propensity to scavenge, and if envenomated carcasses were preferred over non-envenomated carcasses, thus influencing the likelihood that an individual might scavenge.

Commonly referred to as an evolutionary arms race, the dynamic between predators and prey constantly changes as antagonistic coevolution produces adaptations and counter-adaptations to each other (Brodie and Brodie 1999). With few exceptions, rattlesnakes mainly eat small mammals and lizards (Klauber 1982). As primitive viperids began to increasingly specialize on rodents as prey, they developed defensive countermeasures to rodent attacks, including increased armor in the form of heavier scalation, more lethal, faster acting venoms, and a quick strike-and-release attack pattern (Chiszar et al. 1983a). This voluntary release allowed prey to flee a short distance before succumbing to the venom, and over time, viperids honed their trailing skills to relocate them (Chiszar et al. 1983a).

In response, different rodent species have developed many anti-predator defenses against rattlesnakes, including numerous types of vocal calls/alarms, group mobbing, foot drumming, sand kicking, tail flagging, distance awareness, jump-back displays, evasive maneuvers, and toxin resistance (Tamura 1989; Blumstein 2007; Barbour and Clark 2012a; Clark et al. 2012; Putman and Clark 2014; Clark et al. 2016a; Arbuckle et al. 2017; Whitford et al. 2017; Whitford et al. 2019). Additionally, rodents can also detect and avoid predators based on olfactory cues (Richardson 1942; Hennessy and Owings 1978; Randall and Stevens 1987; Jędrzejewski and Jędrzejewska 1990; Ylönen et al. 1992; Jędrzejewski et al. 1993; Nolte et al. 1994; Randall et al. 1995; Parsons and Bondrup-Nielsen 1996; Herman and Valone 2000; Dielenberg and McGregor 2001; Orrock 2010; Staples 2010; Bedoya-Pérez et al. 2019).

However, some predators do not exude integumentary odors. Chemical crypsis is the ability of an animal to suppress its own scent, rendering it odorless (Longhurst et al. 1979). The only terrestrial vertebrate for which this ability has been verified is the puff adder (*Bitis arietans*), members of Viperidae that are related to rattlesnakes (Miller et al. 2015). A crucial component of the ambush strategy is the ability to remain visually hidden (visual crypsis) from predators while waiting for prey to come within striking range, and viperids have accomplished this by evolving camouflage (Klauber 1982; Shine and Li-Xin 2002; Spinner et al. 2013; Singh and Alexander 2017; Harmel et al. 2020). However, when ambushers can be detected by predators via olfaction, thus nullifying the advantage gained by visual crypsis, they become compromised.

By lowering their metabolism, thus releasing less odorous metabolites, puff adders are chemically cryptic to predators (Miller et al. 2015). This ability might be widespread among *Bitis*, and among ambushers in general (Warner 2009; Miller et al. 2015). Chapter 4 is focused on my attempts to elucidate if rattlesnakes are also capable of chemical crypsis, by testing for differences in prairie vole (*Microtus ochrogaster*) behavioral responses to different snake scents.

1.1 Specific aims

(1) Examine and review the existing literature about strike-induced chemosensory searching (SICS) in reptiles

(2) Determine the ability of rattlesnakes to detect and ingest conspecific-envenomated, heterospecific-envenomated, and non-envenomated prey when they themselves have not struck prey

(3) Test for chemical crypsis in rattlesnakes by quantifying the behavioral responses of prairie voles to the scents of both ambush- and active-foraging snakes

Chapter 2: Strike-induced chemosensory searching in reptiles: A review[1]

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2.1 Abstract

Chemosensory searching in squamates with specialized tongue-vomeronasal systems is well documented. By tongue-flicking, these reptiles gather important chemical cues from their environment to guide their feeding behavior. Strike-induced chemosensory searching (SICS) is a specific expression of chemosensory reception that is central to the predatory strategy used by venomous reptiles that strike, release, and relocate their prey. This complex behavioral process is comprised of multiple sequential steps and has been mainly studied in viperids, particularly rattlesnakes. Although this phenomenon has been extensively researched, there is no comprehensive review of the SICS literature. Here, we provide such a review, centered on the idea that SICS is a result of suppression, and then enhancement, of chemosensory searching that serves as a key element of the ambush hunting strategy that most viperid snakes use to consume large and well-defended prey. SICS is also present in other venomous and nonvenomous taxa, and we include a taxonomic categorization of SICS studies in our review. We summarize the key findings discovered during decades of research into this remarkable feeding behavior and highlight areas where our knowledge remains incomplete in an effort to foster further research that will increase our understanding of reptilian feeding ecology.

2.2 Introduction

Viperids, like all snakes, are obligate carnivores, and arguably the most universal feature of their hunting behavior is a reliance on venom. All viperids that hunt large prey inject venom to kill it, and this reliance on venom is associated with a suite of related physiological and behavioral traits that has facilitated the evolutionary success of this group (Greene 1992). One of these traits is the process termed strike-induced chemosensory searching, or SICS. This specialized form of chemosensory searching is a critical aspect of the overall phenotype that allows viperids to kill and ingest prey items that are not only well defended with teeth and claws, but also can be larger than the snake itself. Although general reviews of snake and viperid feeding and hunting behaviors are available (Cundall and Greene 2000; Kardong and Smith 2002; Clark 2016), as are reviews of squamate chemosensory systems (Halpern 1988, 1992; Schwenk 1995), the extensive and diverse literature that focuses specifically on SICS has not previously been reviewed. This monograph is our attempt to not only summarize the major findings from this work, but to synthesize that information in a manner that will be conducive to continued experimental analyses of squamate hunting behavior.

2.3 Squamate chemosensory systems

Snakes and other squamate reptiles tongue-flick to gather chemical information from their surroundings (Burghardt 1970; Halpern 1983, 1992). The long, slender, bifurcated tongue is specially adapted to deliver this information directly to the vomeronasal organ, which is a large chemoreceptor positioned above the roof of the mouth (Halpern and Kubie 1983, 1984; Halpern 1992). The vomeronasal organ was originally described by Ludvig Jacobson (1813), and is also known as the Jacobson’s organ. This cartilaginously enclosed organ is separate from the nasal cavity, and connects to the latter’s base via a duct (Keverne 1999). The vomeronasal organ relays stimuli to the accessory olfactory bulb of the central nervous system, which then processes the information and elicits an appropriate behavioral response (Halpern 1983; Halpern and Kubie 1984; Halpern 1988, 1992). Tongue-flicking is observed in snakes, amphisbaenians, and lizards and facilitates discernment of numerous important chemical cues from predator, prey, and conspecifics (Gove 1979; Halpern and Kubie 1983; Schwenk 1994; Cooper 2007). In snakes, the vomeronasal organ facilitates prey identification, courtship, and aggregation (Halpern 1983). Bertmar (1981) and Eisthen (1992) posited that the vomeronasal organ first arose in amphibians. However, whereas Bertmar (1981) hypothesized that the emergence of this chemoreceptory system was an adaptation to terrestrial life, Eisthen (1992) disagreed, noting that the development of the vomeronasal organ began at the aquatic larval stage. More recent studies have supported an aquatic origin of the vomeronasal organ (Eisthen 2000; Jermakowicz et al. 2004). Regardless of aquatic or terrestrial origin, the vomeronasal organ seems to be ancestral in tetrapods and was secondarily lost in some taxa.

The vomeronasal organ and the tongue comprise the accessory olfactory system, which is one of three major chemosensory systems possessed by squamates, the other two being gustation and the main olfactory system (Lohman and Smeets 1993; Schwenk 1995). The accessory olfactory system has received the most attention in squamates, perhaps because of the visible nature of the tongue-flick. According to what eventually became known as the Cowles and Phelan hypothesis (Cowles and Phelan 1958), olfaction plays an independent, secondary role to the accessory olfactory system in squamate reptiles that have both. Olfaction is used by the individual to obtain volatile scent molecules from the air, which subsequently triggers the accessory olfactory system to activate and detect nonvolatile molecules in the vicinity, ultimately allowing the individual to gather higher-quality information about its surroundings and respond appropriately. This sequential discrimination was demonstrated experimentally in garter snakes (*Thamnophis sirtalis*) (Zuri and Halpern 2003). The prioritization of the accessory olfactory system over the main olfactory system was originally thought to occur only in snakes, until subsequent experiments also verified this hierarchy in at least some lizards (Schwenk 1995).

Vomerolfaction via the accessory olfactory system often involves trailing behavior, especially while searching for prey or mates (Schwenk 1994, 1995). Tongue-flicking and searching movements (repeated cycles of rapid side to side and forward movements of the head) can occur independently of each other, but when an individual displays both actions simultaneously, it constitutes trailing behavior (Cooper 1994a, 2003). Proficient trailing is seen in those taxa with deeply bifurcated tongues (for a review of squamate tongue morphology, see Schwenk [1995]): snakes, amphisbaenians, and anguiomorph lizards. Taxa with less bifurcated tongues do not exhibit extensive trailing behavior (Schwenk 1994). SICS is essentially a specialized form of trailing behavior employed after attacking prey that has then either escaped or been intentionally released.

The confluence of tongue morphology, trailing behavior, and SICS was investigated by Parker et al. (2008), who used SICS to evaluate the hypothesis that snakes use both tines of their bifurcated tongues to detect the edges of chemical trails (tropotaxis, sensu Schwenk 1994). Tropotaxis would facilitate efficient trailing in snakes by allowing them to delineate the boundaries of the trail before them. However, behavioral assays on snakes that had one of their vomeronasal nerves severed indicated no disruption in trailing ability, leading Parker et al. (2008) to conclude that the tongue is a singular, not paired, sensory receptor that evaluates stimulus strength through subsequent, rather than simultaneous, comparisons. Parker et al. (2008) suggested that lingual bifurcation in snakes serves to increase chemosensory detection area, and that trailing is instead guided by chemical cue concentration (i.e., on vs. off the trail).

2.4 Historical overview of SICS research

The late David Chiszar is by far the most influential researcher in the SICS arena. Chiszar et al. (1977) first coined the term SICS while studying rattlesnakes, and conducted much of the initial experimental investigations in this area. SICS is characterized as a stereotyped behavior whereby the individual searches for prey after initially striking (biting), envenomating, and releasing it. This behavior is broadly present in, and primarily associated with, Viperidae (Chiszar et al. 1982c). Among other venomous taxa, SICS has also been observed in Elapidae (Chiszar et al. 1983b; Shine and Covacevich 1983; O'Connell et al. 1985), Helodermatidae (Cooper et al. 1994; Cooper and Arnett 1995), Varanidae (Cooper 1989a, 1993a; Garrett et al. 1996), and Colubridae (Cooper et al. 1989; Cooper 1992a; Burghardt and Chmura 1993). Additionally, many nonvenomous squamates also display SICS or behavior similar to SICS (Cooper 1991a, 1994a). Since SICS is a key element of the ambush foraging strategy employed by most viperids, and could be considered obligate for many of these species, they have provided a model study system that has produced the bulk of important SICS discoveries. Consequently, although we review the SICS literature across different taxonomic groups (Table 2.1), many of the conceptual and functional details of SICS come from studies conducted on a few *Crotalus* species.

Generally, reptile foraging behaviors have been classified as either ambush (sit-and-wait) or active (Schoener 1971; Huey and Pianka 1981; Mushinsky 1987; Cooper 1995a), although Regal (1978) recognized a third mode—cruise hunting, during which the animal moves very slowly in search of prey. Although most taxa can probably exhibit elements of any of these foraging modes under particular circumstances, many species can be accurately characterized as being either mainly ambush or mainly active hunters. Typically, ambush hunters prey on mobile prey, while active hunters prey on sedentary animals (Huey and Pianka 1981; Kuo et al. 2019). SICS is found within each of these foraging modes, but it is a critical behavior for ambush hunters who use venom to immobilize large or dangerous prey that they do not hold on to after striking.

In venomous snakes (which can be ambush or active hunters), Cooper et al. (1994) described the strike-release-trail sequence as consisting of five steps: 1) After striking and envenomation, prey is voluntarily released (to avoid possible retaliatory attack), or involuntarily released (i.e., prey struggles free). 2) After prey release, an extended period of inactivity ensues, presumably to allow time for the venom to incapacitate and kill the prey. 3) Following inactivity, a post-strike elevation in tongue-flick rate occurs. 4) To locate the scent trail left by the envenomated prey, the snake begins moving its head in side-to-side searching movements while simultaneously maintaining the elevated post-strike tongue-flicking rate. 5) Scent-trailing ensues to relocate the prey carcass. Different researchers have classified the sequential phases of SICS differently, and we have provided our own depiction of the SICS behavioral sequence in Figure 2.1.

In rattlesnakes, Chiszar et al. (1978) categorized the steps of a hunting sequence involving SICS as: 1) detection of prey, 2) the strike, 3) chemosensory searching, 4) relocation of prey, 5) location of the prey’s head, and 6) consumption of prey, head first. Chiszar et al. (1978) noted that 2, 3, and 4 rarely occur out of sequence because 2 is a prerequisite for 3. Reoccurrence of 2 is inhibited by the occurrence of 2 and/or 3, increasing the likelihood of 4. Once 4 occurs, 5 and 6 are likely to follow, since at this point the snake will be in physical contact with the carcass. Under this classification scheme, SICS is not synonymous with trailing (Chiszar et al. 1983a), but rather, trailing is a component of SICS.

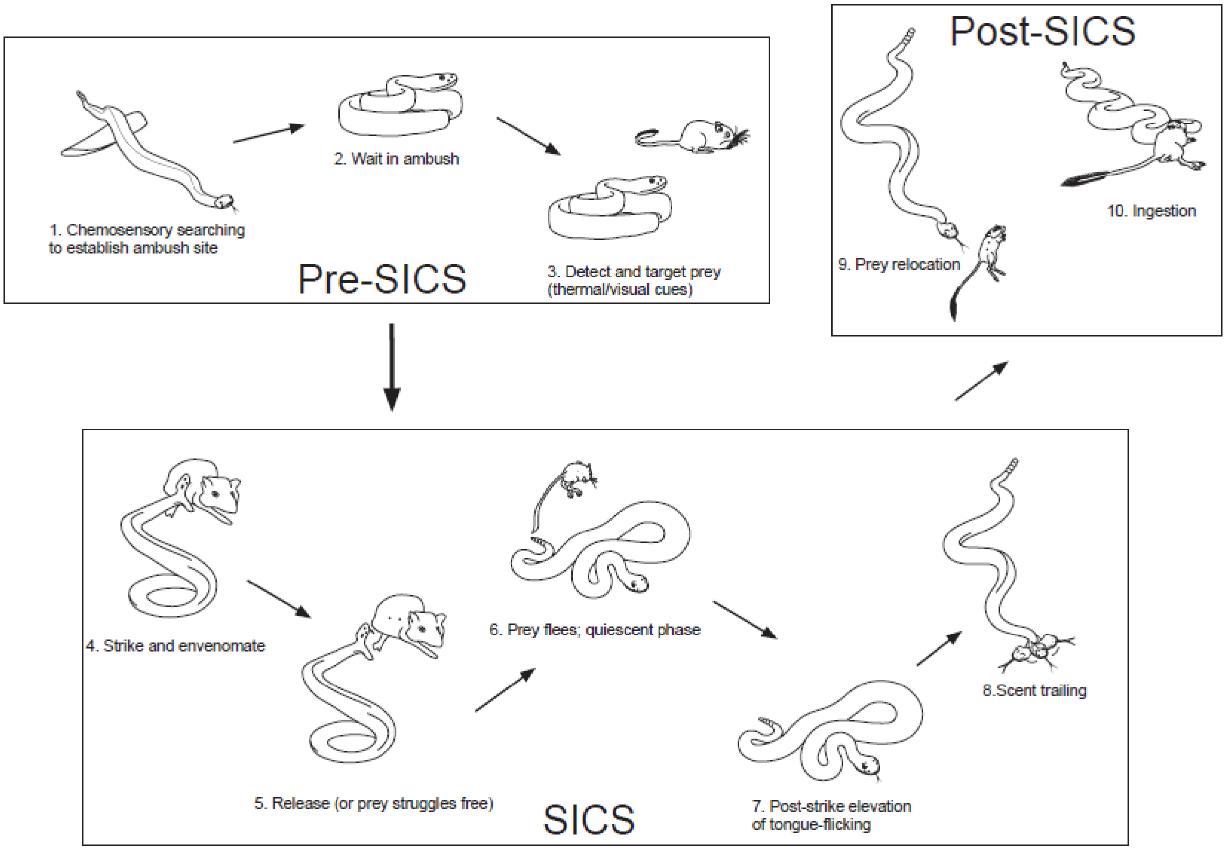


Figure 2.1: The general behavioral sequence associated with strike-induced chemosensory searching (SICS) of viperid snakes. Prior to SICS, viperids search for a suitable ambush position, and then await the arrival of prey. During SICS, the prey is rapidly struck, envenomated, and released. After remaining quiescent while the venom incapacitates the prey, the snake will begin enhanced tongue-flicking while moving its head in rapid side-to-side motions to locate the chemical trail left by the prey. If the prey carcass is successfully located, the snake begins ingesting it, almost always head-first.

Also in rattlesnakes, Kardong and Smith (2002) offered perhaps the most thorough characterization of the SICS sequence, partially adapted from the predatory sequence described in de Cock Buning (1983). They characterized SICS as broad scenes, within which are phases, with some phases comprised of stages. Within the pre-strike scene are placement, alertness, head turning, approach, and preparation phases. The strike scene includes the strike phase, composed of extend, contact, release, and retract stages. The post-strike scene involves reapproach (composed of the quiescence, locate, and trail stages), head searching, and swallowing phases.

As has been apparent from the outset of SICS research, almost all predatory reptiles probably exhibit SICS-like behavior under some circumstances. Lizards that actively search for prey but do not deliberately strike-and-release it can still use SICS to relocate prey that has been inadvertently lost (Cooper et al. 1994). For example, helodermatids are active foragers, specializing on nest eggs and small nestlings (Jones 1983; Beck 2004, 2005), and varanids are typically active or pursuit predators (King and Green 1993; De Lisle 1996; King et al. 2002; Pianka and King 2004), but both of these taxa are known to sometimes switch hunting styles, adopting an ambush strategy when deemed beneficial to do so (Losos and Greene 1988; De Lisle 1996; Pianka and King 2004), and they can employ SICS if prey are lost (Cooper 1989b, 1993a, Cooper et al. 1994, Cooper and Arnett 1995).

In addition to reviewing empirical work, we provide a taxonomic survey of SICS research and review what is known about its evolutionary origins. Our review focuses primarily on how SICS is employed by captive animals in laboratory studies, as field studies of SICS remain sparse. Although some recent field observations (reviewed by Clark [2016]) have helped bolster this dearth of field data, more empirical field studies would contribute greatly to our understanding of the form and function of SICS.

2.5 SICS as a specific form of chemosensory searching

Traditionally, SICS was viewed as a separate phenomenon from chemosensory searching. However, several researchers have concluded that SICS is likely a specialized form of chemosensory searching, a sensory modality that seems foundational to most anguiomorph squamates. As stated by Withgott (1996, p. 778), “Perhaps SICS in pit vipers may be best viewed as an elaborated or ritualized form of a more general ancestral behavioural trait.” I agree with this view, which essentially holds that heightened chemosensory searching driven by the accessory olfactory bulb is likely present in all reptiles that tongue-flick, but SICS represents a specific type of chemosensory searching that is central to the ambush foraging strategy of venomous snakes that prey on relatively large animals capable of retaliation. Numerous studies have established that heightened chemosensory searching in reptiles can be activated by a variety of stimuli, including chemical or visual cues from prey, predators, or conspecifics, as well as changes in environmental conditions. During SICS, as expressed by ambush-hunting snakes, the striking of prey is the stimulus that activates an urgent bout of chemosensory searching. This bout of chemosensory searching is all the more conspicuous because of the stark contrast to pre-strike behavior: ambush foragers largely suppress tongue-flicking after adopting an ambush position, likely because such movements have the potential to alert nearby prey (Gillingham and Clark 1981; Chiszar et al. 1983c). After the strike is delivered, chemosensory searching is reactivated with great intensity and focus until the prey item is recovered or the chemical search image fades.

2.5.1 Cue-induced chemosensory searching

Burghardt and Chmura (1993:119) favored the term “cue-induced chemosensory searching” for the more general phenomenon of snakes responding to new information in their environment with heightened chemosensory searching, such as garter snakes initiating chemosensory searching when prey chemical cues are introduced to their enclosure. A variety of stimuli can activate this heightened state of searching behavior (Cooper et al. 1989; Cooper 1992a; Burghardt and Chmura 1993). Prey odors alone also elicited attack behavior in bull snakes (*Pituophis melanoleucus*), which constrict prey and subsequently display heightened tongue-flicking following attack, presumably in anticipation of swallowing (Chiszar et al. 1980a). Since both striking and constriction release enhanced chemosensory searching, Chiszar et al. (1980a) viewed constriction in nonvenomous snakes as analogous to striking in venomous snakes.

Heightened chemosensory searching, prolonged SICS, elevated tongue-flicking following prey strikes, and trailing behavior have also been confirmed in several lizards, including the Gila Monster (*Heloderma suspectum*) (Cooper et al. 1994; Cooper and Arnett 1995; Garrett et al. 1996). Increased rates of tongue-flicking following strikes and SICS last longer in Gila Monsters (~ 60 min) than in any other lizard studied thus far (Cooper et al. 1994). Chemical cues alone are also sufficient to release attack behavior in Gila Monsters (Cooper 1989a). Helodermatids do not strike-and-release prey, as they are active foraging, opportunistic nest raiders that mainly feed on eggs and live nestlings (Beck 2005). Consequently, Garrett et al. (1996:262) concluded that striking was not essential to searching behavior, and "prey-induced chemosensory searching" was proposed as a more appropriate term than SICS for helodermatid prey-searching behavior.

2.5.2 Comparisons between viperids and other snakes

In contrast to most rattlesnakes, prey chemical cues alone are sufficient to elicit pre-strike tongue-flicking, attack behavior, and chemosensory searching in other species that have been investigated. Garter snakes have received the most attention in this regard (Burghardt 1969, 1970; Chiszar et al. 1976, 1981a). Chiszar et al. (1979) speculated that the differences between garter snakes and rattlesnakes stemmed from dietary preferences, with garter snakes responding more readily to odiferous, innocuous prey (Gillingham and Clark 1981; Chiszar et al. 1983c). Such prey would not be difficult to hold on to after striking, and colubrids seem much more prone to strike and hold prey than viperids (Deufel and Cundall 2006). Visual cues are often sufficient for garter snakes to sustain exploratory tongue-flicking, but chemical cues are necessary to elicit an attack response or other appropriate predatory strategies (Burghardt 1970;

Chiszar et al. 1981a). For example, upon location of earthworm chemosensory cues, garter snakes not only increase their rate of tongue-flicking, but also increase probing movements in the soil around the chemical cues (Gillingham et al. 1990).

The differential responses of garter snakes and viperids to prey odors might also be expected because, as garter snakes are usually active and opportunistic hunters (Gillingham et al. 1990; Rossman et al. 1996; Ernst and Ernst 2003), striking is not a prerequisite for ingestion. As garter snakes and other colubrids lack loreal pits, they are even more reliant on the vomeronasal organ for prey detection than pitvipers, during both the initial attack response and trailing (Wilde 1938; Kubie and Halpern 1979). Rattlesnakes are typically characterized as having two distinct phases of preingestive behavior: 1) a strike guided by visual and thermal sensory modalities, resulting in 2) chemosensory searching, guided by the vomeronasal organ. In garter snakes, only the second phase occurs (Chiszar et al. 1976, 1977). Consequently, it would be expected that prey chemical cues presented to rattlesnakes that have already adopted a coiled position should not elicit increased tongue-flicking rates (Chiszar et al. 1976, 1977). However, as demonstrated by several experimental studies (e.g., Duvall and Chiszar 1990; Roth et al. 1999; Theodoratus and Chiszar 2000; Clark 2004), viperid snakes will respond to the presentation of chemical cues while searching for suitable ambush sites.

Chiszar et al. (1981a) showed that garter snakes and rattlesnakes utilize different cue types (chemical and visual) when alerted to prey, although the usage of such cues was not mutually exclusive for either species. Using *T. radix* and three rattlesnake species (*C. enyo*, *C. viridis*, and *Sistrurus catenatus*), they found that, because of different predatory strategies, the importance of each type of cue is different for both taxa. Rattlesnakes were alerted to prey presence by visual cues and subsequently tongue-flicked to gather chemical information, whereas garter snakes responded to chemical stimuli regardless of the presence of visual cues.

2.6 Emergence and evolution of SICS

Although the primary purpose of this review is to summarize what we know about the form and function of SICS from experimental research, a portion of the SICS literature has also discussed the evolutionary history of the behavior. Therefore, we attempt to summarize the major concepts that have been discussed concerning the evolution of SICS and its current distribution in the squamate phylogeny. However, this discussion is hampered by the emerging view that SICS is not so much a distinct behavioral trait but more a specialized expression of a general behavior, making it very difficult to characterize on an evolutionary timeline. Additionally, caution must be exercised when attempting to place a behavior on a phylogeny. McLaughlin (1989) determined that phylogenies can serve as confounding factors in determining the evolution of foraging behaviors, a conclusion supported a decade later by Perry (1999).

Furthermore, one need not venture far into the world of squamate phylogenetics to find that it is traditionally, and currently, very controversial. Phylogenies are constantly revised, often contradicting one another, making it difficult to elucidate concrete evolutionary relationships and divergence times, let alone behaviors. These phylogenetic revisions are far too numerous to detail here and will likely change multiple times in the future with additional genomic analyses. However, using current consensus estimates, we can attempt to trace the genesis of SICS or at least the underlying anatomical components (venom and highly developed tongue-vomeronasal organ).

The first squamates are thought to have arisen approximately 174–213 mya (Zheng and Wiens 2016). Anguiomorphs (anguids, helodermatids, and varanids) diverged approximately 108–118 mya, with the subsequent divergence of Serpentes occurring approximately 113–131 mya (Zheng and Wiens 2016). Viperids are thought to have diverged from colubrids and elapids (Mallow et al. 2003) at least 30 mya (Greene 1997; Wüster et al. 2008; Alencar et al. 2016; Zaher et al. 2019).

The origin and development of reptile venom has been controversial (Fry et al. 2009). Traditionally, true venom systems are thought to have evolved at least twice during squamate evolutionary history, once in helodermatids and again much later in advanced snakes, with front-fanged venom systems evolving independently in elapids and viperids (Knight and Mindell 1994; Weinstein et al. 2010). However, studies conducted by Fry and Wüster (2004) and Fry et al. (2006) proposed that venom evolved only once in the common ancestor of snakes and lizards, although this hypothesis remains controversial (Hargreaves et al. 2014). Irrespective of when and how venom evolved in reptiles, its extant forms are taxonomically widespread and used for various functions (e.g., prey acquisition, digestion, defense) (Weinstein et al. 2010; Fry et al. 2015).

Different researchers have speculated about the evolutionary origins of SICS within this broader diversification of venomous squamates. Chiszar et al. (1982c) proposed an elapid origin of SICS, before the first viperids emerged, and also speculated that SICS evolved at least 20–70 mya (Chiszar et al. 1983a). Burghardt and Chmura (1993) stated that the evolutionary origins of SICS and elevated rates of tongue-flicking following strikes cannot be determined without extensive phylogenetic analysis. Cooper (1989b) proposed SICS to be homologous in lizards and snakes, a hypothesis that suggests a much older date for the emergence of SICS than suggested by others. Chiszar et al. (1999b) took issue with the notion that viperids inherited SICS directly from their squamate ancestors (Chiszar et al. 1999b:88), designating such an assumption "unreasonable." Chiszar et al. (1999b) contended that instead, protovipers evolving from colubroids developed and honed SICS as an integral element of their hunting strategy, ultimately leading to the extant iterations of the behavior observed today. To reach these conclusions, the authors verified SICS in the Caucasus viper (*V. kaznakovi*) and Wagner's viper (*M. wagneri*), noting that SICS occurred if the vipers struck rodents, but not sans striking, and that the behavior seemed as well developed in true vipers as in rattlesnakes. As further evidence, they asserted that colubrids and lizards cannot sustain SICS past a few minutes, despite evidence to the contrary in multiple previous studies (Cooper 1993a; Cooper et al. 1994; Garrett et al. 1996).

In the view of Cooper (1989b), SICS predates the strike-release-trail strategy, even though it has evolved for enhanced use during this behavior. Because SICS is also found in nonvenomous taxa, Cooper (2003) surmised that it must have evolved independent of venom. Cooper (1994a) pondered whether the elevated rate of tongue-flicking following strikes predates SICS, and considered it doubtful that elevated tongue-flicking without a subsequent searching mode would be effective in prey recovery. Cooper (1994a) also discussed the evolution of advanced chemosensory behaviors in squamates—along with tongue-flicking and SICS, many anguimorphs developed elongated, forked tongues. Specialized scent-trailing might have evolved in varanids and snakes, while a strike-release-trail strategy further developed in viperids and elapids. This strategy likely evolved independently in Viperidae and Elapidae (Burghardt and Chmura 1993)—although as mentioned previously, SICS occurs in many nonvenomous squamates as well. Cooper (1993a, 1994a) postulated that SICS is only present in species that are able to use tongue-flicking to discern prey chemical cues and also that venom and SICS must have both been precursors to the strike-release-trail strategy that relies on SICS. Cooper (1989b, 1994a) speculated that the voluntary release of prey evolved after SICS, because when bitten by a snake, large, dangerous, struggling prey are more likely to escape. Moreover, involuntary release by snakes is still induced by struggling prey (Whitford et al. 2019), so it would make sense that voluntary prey release evolved after specialization on large or dangerous prey (see Cundall and Beaupre [2001]).

The Order Serpentes might have a varanoid ancestor (Cooper 1994b; Cooper et al. 1994; Forstner et al. 1995; Lee 1997). Cooper et al. (1994) noted that varanoids and snakes are the only squamates known to exhibit prolonged SICS (more than two hours in crotalids [Chiszar et al. 1982c, 1985a], and more than two minutes in helodermatids and varanids [Cooper 1993a; Cooper et al. 1994]). Notably, viperids delay the onset of tongue-flicking following strikes, whereas elapids, colubrids, and lizards do not (O'Connell et al. 1985; Cooper et al. 1994). This duration difference might be attributed to the fact that prey would be more likely to escape from nonvenomous, or mildly venomous, lizards (Cooper 1993a) and snakes (Burghardt and Chmura 1993), and could vacate the vicinity more quickly, thus making the immediate commencement of tongue-flicking and searching movements more beneficial. Conversely, prey released by highly venomous species (i.e., rattlesnakes; the absence of a refractory period in elapids is likely a result of a much more active foraging mode) are likely to die within a relatively short distance of the strike location—thus, the snakes can afford to wait while their venom induces death (Cooper 1993a).

Chiszar et al. (1983a) proposed that even the most primitive rodent-eating snakes probably used the strike-and-release hunting strategy, but these snakes had already evolved effective venoms. Therefore, prey probably would not have traveled far before succumbing to envenomation. The authors further surmised that heightened sensitivity to chemosensory cues and keen eyesight could have negated the need for the highly developed trailing component found in some snakes today, especially if the ancestral species were not rodent specialists (like many elapids). As ancestral snakes continued to specialize on rodent prey, the likelihood of sustaining damage during a strike increased, thus resulting in three morphological/behavioral evolutionary trends in SICS: 1) larger, stronger heads with heavier scales for increased protection from rodent prey, and 2) faster acting venoms, which would facilitate 3) a rapid strike-and-release of prey, thus minimizing potential damage taken. This third specialization is the one that led to the addition of the trailing component of SICS because an instantaneous strike-and-release would result in the subsequent fleeing of the rodent. Cooper (1989a, 1994a) concurred with the idea that SICS predates the strike-release-trail hunting strategy.

2.7 Taxonomic survey

Although the majority of experimental studies of SICS have been carried out on crotaline pitvipers, the general sequence of behaviors has also been investigated in a number of other squamate lineages. The methodology has largely followed the original designs pioneered by Chiszar and Radcliffe (1976), Chiszar et al. (1977), Chiszar and Scudder (1980), and Cooper (1989a,b), with some modifications. Some of the early studies of SICS were more anecdotal than experimental, involving only a few (or sometimes one) study subjects, and lacking the statistical rigor or computational analyses that are commonly used in current experimental literature. Although many of these studies still detail important findings that were corroborated in later studies (e.g. Chiszar et al. 1977, 1982b; Smith et al. 2005), we have attempted to highlight cases where it might be beneficial to further corroborate studies with more replication or controls. In order to compare and contrast these findings, the following sections summarize the experimental approaches and general conclusions of these studies across squamates, organized by taxonomic relationship, beginning with those taxa that have received the most experimental attention.

*2.7.1 SICS in Viperidae: Rattlesnakes (***Crotalus** *and* **Sistrurus***)*

SICS has been primarily studied in viperids and most extensively in rattlesnakes. Of the 105 experimental studies of SICS, 58 of them focus on *Crotalus* spp., and 29 of these on *C. viridis,* the Prairie Rattlesnake (Table 2.1). Thus, most of the conceptual and empirical work on SICS has focused on a limited number of species, although it is often assumed that the general SICS patterns exhibited by rattlesnakes apply widely to other ambush-hunting snakes that use venom to immobilize relatively large prey. Although research in other species generally bears this out, our review highlights important taxonomic differences that have been discovered, and we believe that more diverse comparative studies across multiple taxonomic groups are warranted.

2.7.1.1 Initial studies

The first mention of SICS in the literature appears in Chiszar et al. (1977), although Chiszar and Radcliffe (1976) discussed the elevated rate of tongue-flicking following strikes in *Crotalus culminatus, C. enyo,* and *C. vegrandis* and described the trailing component that would eventually come to be known as SICS. However, perhaps the earliest work on SICS was conducted on Old World vipers (Baumann 1927, 1928; Wiedemann 1932). These studies used captive *Vipera aspis* and *V. berus* to determine that trailing behavior was more frequent and efficient in snakes that had struck prey compared to those that had not. In their landmark paper in which the term “SICS” was first used, Chiszar et al. (1977:418) determined that post-strike chemosensory searching “probably” facilitated prey relocation. Furthermore, although using a low sample size of snakes, they determined that prey must be struck in order to elicit an elevated rate of tongue-flicking. After these early papers that investigated SICS were published, our knowledge of this behavior became increasingly refined over time as further experimentation was conducted.

2.7.1.2 SICS as part of a behavioral sequence

SICS is a key component of the behavioral sequence used by many ambush-foraging snakes to hunt prey, the default hunting strategy of most rattlesnakes and other pitvipers. The initial step in this strategy, prior to SICS, is the selection of the ambush location from where the snake will wait for the arrival of prey (for a detailed overview of the numerous decisions a rattlesnake makes during the hunting process, see Clark [2016]). Rattlesnakes can wait coiled for days for prey to come within striking range, and have been observed to modify their surroundings in a manner indicating that they are anticipating a predatory encounter (Greene 2003; Putman and Clark, 2015). Rattlesnakes use chemoreception to help locate ambush sites (Reinert 1984; Duvall et al. 1985, 1990; Clark 2004), and exhibit periodic bouts of tongue-flicking while waiting in ambush that probably help them continually reassess the site (Barbour and Clark 2012b; Clark et al. 2016b). Rattlesnakes exhibit significantly reduced rates of tongue-flicking prior to striking prey, probably because tongue-flicking movements in close proximity to prey might reveal the snake’s presence (Chiszar and Radcliffe 1976; Gillingham and Clark 1981; Chiszar et al. 1983c, Graves and Duvall 1985).

Once a prey item approaches a hunting rattlesnake, vision and thermoception via pit organs are the primary sensory modalities used to guide strikes (Haverly and Kardong 1996). In this study, when either the eyes or the pits were covered, rattlesnakes (*Crotalus oreganus*) were able to rely solely on the other sensory organ, resulting in a nearly unhindered striking performance under captive conditions. However, when both senses were deprived simultaneously, striking performance was greatly diminished. The authors concluded that when visual and infrared cues are diminished or absent (i.e. environmental obstructions), the vomeronasal organ can partially compensate for these losses, though in a limited capacity, to help rattlesnakes deliver a successful strike. Moreover, whereas the vomeronasal organ is essential for post-strike carcass recovery (Graves and Duvall 1985), it might be entirely unimportant to the strike, as its absence did not affect striking performance in experiments conducted by Chiszar and Radcliffe (1976) and Kardong (1992). Hayes and Duvall (1991) and Hayes and Hayes (1993) also demonstrated that chemical cues were nonessential to striking behavior.

Using a rattlesnake (*C. oreganus*) that was born blind, Kardong and Mackessy (1991) also obtained similar results—the blind rattlesnake displayed the same striking ability as normal ones, even accurately targeting the more vulnerable anatomic regions. However, when the pits were blocked, the snake's striking capability was greatly diminished. Although the opportunistic nature of obtaining a congenitally blind snake precluded statistical analyses, this observation is important in illustrating the ability of pit vipers to obtain visual information with their pits alone.

Kardong and Smith (2002) also highlighted the important differences in the usage of the eyes/pits and vomeronasal/olfactory systems during predatory episodes. The eyes and facial pits are used as prey approaches, and ultimately guide the strike, whereas the accessory and main olfactory systems facilitate efficient carcass relocation. Interestingly, whereas the eyes and facial pits compensate one another, the accessory and main olfactory systems do not. This is likely because these two streams of chemosensory receptors do not merge in the central nervous system, making these senses complementary, but not compensatory. This is seen in Kardong

(1992), where the suppresion of the vomeronasal organ resulted in fewer prestrike tongue-flicks and an 80% decline in strikes, even though the main olfactory system was functional. In a similar study using *C. oreganus*, Alving and Kardong (1996) found that severing the vomeronasal nerves caused strikes to decline by 50%, and poststrike trailing was nonexistent. The authors concluded that the vomeronasal organ is crucial in releasing the predatory strike, as well as the guidance of prey relocation efforts, in rattlesnakes.

After striking, snakes either hold on to the prey item, rendering SICS unnecessary, or the prey item is released or struggles free, thus beginning the SICS process. Rattlesnakes generally strike-and-release prey, but there are several exceptions to this pattern. Kardong (1986a) found that larger *C. viridis* were more likely than smaller snakes to hold onto prey (*Mus musculus*). Furthermore, smaller *M. musculus* were held onto more frequently than larger ones, but regardless of body size, all held prey received greater doses of venom than released prey. When *M. musculus* that were held struggled and inflicted damage to the snake, they were quickly released, a finding that fits with recent field evidence that kangaroo rats (*Dipodomys deserti*) forcibly remove Sidewinder Rattlesnakes (*C. cerastes*) by kicking or twisting out of the jaws of the snake (Whitford et al. 2019). The fact that rattlesnakes are more likely to hold onto smaller prey compared to larger prey indicates that the snakes recognize, to some extent, the retaliatory capacity of prey based on body size (Allon and Kochva 1974; Kardong 1986a). Mackessy (1988) discovered an ontogenetic shift in both prey handling and venom chemistry in *C. oreganus*. He found that juveniles more often struck-and-held lizards (*Uta stansburiana*) and neonate mice (species not given, but presumably *M. musculus)*, and began to strike-and-release comparatively more dangerous rodent prey as the snakes attained a larger body size. Additionally, juveniles of this species possess more toxic venom than adults do, practical for inducing faster prey mortality.

The venom of adults, while less toxic, is better suited to facilitate digestion of larger, bulkier prey.

A series of further experimental studies with *C. viridis* provided a broader context for the understanding of when rattlesnakes might or might not release struck prey. In Hayes (1991), *C. viridis* never held struck prey (deer mice, *Peromyscus maniculatus)*, irrespective of snake or prey size, although small snakes gripped deer mice for slightly longer durations before releasing them. Hayes (1991) explained the disparity between the prey-handling behavior of *C. viridis* in his study and *C. oreganus* in Mackessy (1988) with reference to the different dietary habits of these populations. The *C. oreganus* from Mackessy (1988) primarily feed on lizards, whereas the *C. viridis* from Hayes (1991) primarily feed on mice. Lizards are generally not immobilized as quickly by venom, so the cost of releasing them might be greater, as they could presumably travel further distances once released, making relocation more difficult. Additionally, snakes preying primarily on rodents might have to quickly release them in anticipation of counterattacks, as rodents are capable of more damaging counterattacks than lizards.

The tendency to hold less dangerous prey was also observed in Hayes (1992a). Here, it was found that, out of 9 *C. viridis* that struck both birds (*Pooecetes gramineus*) and deer mice (*P. maniculatus*), mice were released 9 of 9 times, whereas birds were released 3 of 9 times. In no instances in which birds were held were they able to inflict retaliatory damage upon the snake. The consistent strike-and-release behavior of *C. viridis* preying on *P. maniculatus* demonstrated in Hayes (1991) was also observed in Hayes (1992b), although the author acknowledged that prey could not be categorized according to body size, as all prey were approximately the same size. Kardong (1986a) also found that, although rattlesnakes were quick to drop held lab mice (*M. musculus*) after incurring damage from them, this was a rare occurrence, as mice were only able to successfully retaliate 6% of the time. However, wild rodents likely have higher rates or retaliation, as in Whitford et al. (2017, 2019). Kardong (1986a) pondered whether the inclination to sometimes hold prey was a result of the snake compensating for a faulty strike (poor fang placement) with extra venom, although the results of Kardong (1986b) showed this not to be the case. In this subsequent study, some snakes struck with only one fang successfully penetrating the body cavity of *M. musculus*. In such instances, prolonged prey death indicated that the successful fang was not able to deliver more venom to compensate for the missed fang. Additionally, when snakes' initial strikes completely missed their targets, they would deliver 1–2 follow-up strikes until successful contact and envenomation were achieved. In no cases were prey held as a compensatory measure for faulty strikes.

In rare field observations of rattlesnake strikes, Cundall and Beaupre (2001) placed a laboratory rat (*Rattus norvegicus*) in close proximity to two different free-ranging *C. horridus*. During each respective predatory episode, both rattlesnakes delivered multiple strikes to the rats, which both violently retaliated in response. When the rats counterattacked by biting the snakes' heads, both snakes began thrashing and jerking movements in an attempt to free themselves from the rats. Eventually both snakes were able to dislodge the rats, which both succumbed to venom and were consumed. Additionally, these field observations demonstrated that the strike kinematics of wild rattlesnakes were similar to those observed in captive rattlesnakes.

Related to these discoveries, Radcliffe et al. (1980) found that prey size was correlated with a hold or release strategy in three rattlesnake species. Larger *M. musculus* were more often released, whereas smaller, comparatively less dangerous ones were more often held. Interestingly, *C. enyo* held on to small prey every time (8/8), whereas *C. durissus* (1/6) and *C. viridis* (2/5) did so more rarely. The authors explained this important ecological implication by hypothesizing that if envenomated rodents were frequently relocated after release, then there would be no need to hold onto small ones. Conversely, if released envenomated rodents were frequently lost (especially small ones), then it would make more sense from a fitness standpoint to hold smaller prey. Therefore, it seems that during their evolutionary history, *C. enyo* underwent stronger selective pressure to hold onto prey. This is probably because *C. enyo* eats mainly centipedes, lizards, and small rodents (Ernst and Ernst 2012), relatively small prey which can be more safely held after envenomation. These general trends in laboratory studies are also found in the more limited field studies (reviewed in Clark 2016): *C. horridus, C. cerastes, C. ruber, C. oreganus,* and *C. scutulatus* will occasionally hold smaller rodents and lizards rather than releasing them, and observations in Whitford et al. (2017, 2019) and Putman et al. (2016) indicate that relatively large or powerful rodents like *D. deserti* and *Otospermophilus beecheyi* often struggle free or actively remove snakes, rather than being released.

If prey are released after envenomation, rattlesnakes then initiate SICS to locate the carcass (Chiszar and Scudder 1980, Chiszar et al. 1992). With notable variation, rattlesnakes typically begin SICS within 5 min of delivering a strike (Hayes 1992b, 1993; Clark 2006a; Putman et al. 2016) and delay the onset of trailing movements longer when larger prey have been struck (Clark 2006a). Moreover, the onset of SICS seems to be independent of the venom quantity injected (Hayes 1992b). Many rattlesnakes are cathemeral (Barbour and Clark 2012b), and field observations (Clark 2006b; Clark et al. 2012; Clark et al. 2016b), along with one laboratory study (O'Connell et al. 1983), indicate that rattlesnakes can conduct SICS equally as well during day or night (O'Connell et al. 1983).

2.7.1.3 SICS and dietary specialization

Larger species of rattlesnakes typically prey on small mammals as adults, whereas many smaller-bodied species are lizard specialists (Campbell and Lamar 2004). Species that eat more rodents might be more efficient than lizard specialists at performing SICS (Chiszar et al. 1986a; Cruz et al. 1987). In these experiments, Chiszar et al. (1986a) and Cruz et al. (1987) found that *Crotalus viridis* (a rodent specialist) maintained SICS after a successful strike regardless of whether or not mouse odors were present, whereas *C. lepidus* and *C. pricei* (lizard specialists) required the constant presence of rodent odors to maintain SICS. It might be that a greater dependence on rodent prey has led to a more persistent trailing strategy in rodent specialists (Chiszar et al. 1986a), whereas lizard specialists must rely on the more primitive requirement of constant chemosensory feedback to successfully facilitate SICS (Cruz et al. 1987). Additionally, for lizard specialists, rodent chemical cues might not elicit strong responses. Dusky Pygmy Rattlesnakes (*Sistrurus miliarius barbouri*) primarily feed on lizards and anurans (Ernst 1992; Roth et al. 1999; Ernst and Ernst 2003, 2012). Holding et al. (2016) used a captive colony of these snakes, composed of individuals fed strict diets of either mice or lizards for over five years, to verify that *S. miliarius barbouri* innately preferred lizard scent. This preference represents a genetic predisposition for lizards, regardless of diet plasticity. Similarly, Saviola et al. (2013a) observed that 11 subadult *C. viridis* reared on a diet of lab mice (*M. musculus*) still responded significantly more to odors from natural prey items than from the mice.

2.7.1.4 Strike-induced inhibition of further strikes

In their initial study of SICS, Chiszar et al. (1977:422) also introduced the term “strike-induced inhibition of further strikes” to describe the process whereby after striking an initial prey item, rattlesnakes will subsequently ignore additional prey that might appear, for up to 20 minutes. They concluded that striking "switches on" the chemosensory searching process (SICS) and simultaneously "switches off" additional striking (Chiszar et al. 1977:418). The logic for this behavior holds that rattlesnakes prioritize relocation of prey they have envenomated over opportunities to envenomate new prey.

Anecdotal evidence for strike-induced inhibition of further strikes was also observed using six *Crotalus viridis*, six *Sistrurus catenatus*, two *C. durissus*, two *C. lepidus*, two *C. vegrandis*, one *C. atrox*, one *C. catalinensis*, one *C. molossus*, one *C. polystictus*, and one *C. willardi* (Chiszar et al. 1978). However, using a similar experimental paradigm, Gillingham and Baker (1981:221) did not find support for strike-induced inhibition of further strikes in *C. atrox*: within two minutes of initially striking a mouse (presumably *Mus musculus*), Western Diamondback Rattlesnakes killed a secondary "interference" mouse 64.3% of the time. The authors concluded that striking a second mouse might be adaptive for rattlesnakes because, in the event of being "distracted" by an additional mouse during the initial chemosensory searching process, it allows the potential for additional prey acquisition, while still affording the snake the opportunity to relocate the original carcass via scavenging once it begins to putrefy.

An explanation of these disparate results might be that rattlesnakes display a high degree of behavioral variation, and individual snakes can have very different responses to a stimulus (Chiszar et al. 1981b; Whitford et al. 2020; M.S. Teshera, R.W. Clark, and E. Greenbaum, personal observations). It might also be the case that strike-induced inhibition of further strikes is more likely in a captive testing environment. Although the majority of field encounters involve a single attack to a single prey item (Clark 2006a; Clark et al. 2012; Putman et al. 2016; Clark et al. 2016b), rattlesnakes will sometimes strike at a single prey item multiple times (as some elapids do, discussed below). In a laboratory study, O'Connell et al. (1982a) observed that, when

C. viridis was presented with two mice (presumably *M. musculus*) in succession, they struck the first mouse only once, but almost always struck second mouse multiple times. It was hypothesized that this behavior occurred because after striking the initial mouse, the snakes had less venom, and thus needed multiple strikes to inject as much venom into the second mouse as the first one, or that multiple strikes to prey might be compensatory behaviors for a poor initial strike (Kardong 1986a). Similarly, Hayes (1992b) found that *C. viridis* appeared to expend less venom in subsequent bites compared to the first bite. Several anecdotal field observations indicate that *C. oreganus* preying on venom-resistant ground squirrels will deliver additional strikes to squirrels that have been partially immobilized but not killed by venom (R.W. Clark, M.A. Barbour, B.J. Putman, personal observations), indicating that rattlesnakes might use additional strikes when needed to kill prey.

During the time between the strike and the commencement of trailing, rattlesnakes are sedentary, termed the quiescent stage by Kardong and Smith (2002). These authors hypothesized that this refractory period allows ample time for discrimination of the chemical trail that matches the prey struck, and the formation of the chemical search image. After this, rattlesnakes will locate the beginning of the chemical trail and start following it. On balance, the field and laboratory evidence suggests that, although rattlesnakes might be less inclined to strike at an additional prey item during the quiescent stage or if they have started SICS, they will still attempt to do so under some circumstances. In any case, the term strike-induced inhibition of further strikes was largely abandoned in the later SICS literature, although a renewed focus on this subset of SICS experimentation would certainly be warranted.

2.7.1.5 SICS and disturbance

Several studies examining the effects of disturbance on SICS behavior of rattlesnakes have shown that SICS can still occur in the face of some disturbances, but responses to these effects can vary between individuals and species. Initial studies investigating the persistence of SICS in the face of disturbance were conducted by Chiszar et al. (1980b, 1981c). Using a sample of 5 and 6 captive snakes, they found that disturbance effects (handling and transporting) prior to striking rodent prey (species not given in either study, but presumably *Mus musculus*) prevented *Crotalus viridis* from performing SICS, but this same pre-strike disturbance had no effect upon *C. enyo*. The authors explained this behavioral difference by noting the calm demeanor of *C. enyo*, a species that rarely responds to provocation. Conversely, *C. viridis* generally seem to adopt a vigorous defensive posture when threatened (Rubio 2010). The authors concluded that because *C. viridis* is easily agitated, the prioritization of defense overrode the chemical search image formed after striking prey and that no chemosensory searching would occur if the defensive state outlasted retention of the chemical search image. However, these studies should be interpreted with some caution, since subjects were tested for SICS for only five min post-strike, whereas SICS can persist for over 24 hours (Smith et al. 2000). Using similar methods to Chiszar et al. (1980b, 1981c) (and with a similarly small sample of *n* = 6 individuals), O'Connell et al. (1981a) used simulated predatory bird eyes as a disturbance in trials that lasted for 25 min post-strike. The authors found that snakes delayed SICS when exposed to the bird eyes, exhibiting defensive postures for several minutes after removal of the threat. After this period, however, snakes resumed SICS. Thus, the general conclusion from these studies is that disturbances might interrupt SICS, but the effect is mostly temporary, with rattlesnakes resuming SICS once they perceive themselves to be safe again.

2.7.1.6 Discrimination of envenomated prey

After they are struck and released, envenomated animals generally move 5–10 m (0–6.77 m in Estep et al. [1981]; 0.25–13.75 m in Putman et al. [2016]; 0.75–27 m in Clark [2016: table 1]) away from the ambush site before succumbing to the venom. To help facilitate efficient trailing, rattlesnakes can discern between envenomated and nonenvenomated prey trails, and can even discriminate individual prey items of the same species from one another (Duvall et al. 1978; Chiszar et al. 1999a, 2008; Saviola and Mackessy 2017). This discrimination helps the snake avoid following a trail left by a different, nonenvenomated prey item, and allows the snake to focus on the chemical trail left by the individual it struck. The brief period of contact when a rattlesnake strikes a mouse is sufficient for acquisition of the chemical information necessary to form a search image, or chemical memory (Chiszar et al. 1980c; Melcer and Chiszar 1989a). Striking is crucial for the formation of this search image, which can be maintained for up to 24 hrs, although image deterioration begins between 60–120 min post-strike (Melcer and Chiszar 1989a; Smith et al. 2000).

But how do rattlesnakes discern chemical prey trails, specifically? Envenomation results in a number of chemical cues rattlesnakes use to discriminate among different scent trails, including individual prey chemical cues (sometimes related to prey diet), change in chemical cues resulting from mechanical damage, and chemical cues in the venom itself. Lavín-Murcio et al. (1993) presented a hierarchical order in which rattlesnakes prioritize different cues: chemical cues associated with venom are prioritized over individual prey chemical cues, which in turn are prioritized over chemical cues associated with mechanical damage (also see Kardong and Smith [2002]: table 1). Additionally, Robinson and Kardong (1991) and Chiszar et al. (1991a) used venomoid rattlesnakes to determine that venom injection was not required for SICS to occur (contraction of the venom gland compressor muscle might be a prerequisite, however). Thus, when venom cues are not available, rattlesnakes might use integumentary cues to track struck prey. Rattlesnakes can sample the concentration of such integumentary cues in the environment, preferring higher concentrations of prey chemical cues over lower ones (Smith et al. 2005). This assessment allows them to determine the identity of each prey trail, and whether or not prey relocation should be attempted (Smith et al. 2005). Additionally, the post-strike orientation of the rattlesnake, which positions its head facing toward the fleeing rodent, also helps ensure that the correct prey trail is chosen (Lee et al. 1988).

However, Lavín-Murcio and Kardong (1995) found that, when presented with venom and integumentary cues separately, rattlesnakes usually will not select either trail. They offered five *Crotalus oreganus* a choice between two different chemical trails inside of a Y-maze. The first trail was made using a live *Mus musculus*, which was subsequently struck by the rattlesnake. The second trail was made using another live mouse injected via syringe with the same snake's venom. This presented the snake with a choice between a chemical trail from an unstruck mouse that they subsequently struck, or a trail between a different mouse that they did not strike but was nonetheless envenomated with its own venom. In 13/15 trials, snakes did not choose either trail. The authors suggested that, when presented with contradictory chemical information, the chemical search image might become distorted, and rattlesnakes simply abandon their search. Rattlesnakes might perceive this distortion as an indication of incomplete envenomation, thus signaling an unsuccessful strike (Lavín-Murcio and Kardong 1995).

The specific chemical cues that rattlesnakes use to discriminate one individual of the same prey species from another remain unknown, but they are at least in part related to the diet of the prey. Melcer and Chiszar (1989a) allowed a small sample size of 6 *C. viridis* to strike live

M. musculus that had been eating food flavored with either cinnamon or cocoa. After envenomation the carcasses were discarded, and the snakes were presented with two nonenvenomated carcasses that had also been feeding on flavored food. Rattlesnakes spent significantly more time investigating and tongue-flicking the carcass that had eaten the same food as the one that was struck, although this preference dissipated after two minutes.

Dietary differences are not fully responsible for individual variation in prey chemical cues, however, because Furry et al. (1991) found that a small sample of 6 *C. viridis* were capable of distinguishing between *Peromyscus maniculatus* littermates that shared the same bedding and were fed the same food. The experimenters even wiped visible urine and feces away from carcass trails, although glandular secretions and dander from *P. maniculatus* were doubtless deposited. The authors suggested that in the split-second strike of a rattlesnake, enough chemical cues unique to the individual struck are obtained by the rattlesnake to allow for individual identification of prey trails, even when those individuals share similarities in genomes and environment.

Chiszar et al. (1990) also determined that chemical cues used to trail individual mice were not related to urine, and came from the integument. The authors speculated that the snakes' indifference to urinary cues could be a response to the fact that desert and prairie rodents urinate infrequently, and therefore these cues are not often available in the environment. Duvall and Chiszar (1990) reached the same conclusion, noting that rodent urine is irrelevant to rattlesnakes, as these cues dissipate quickly in natural settings.

Blood, however, might be relevant to striking behavior in rattlesnakes during SICS. Using 12 *C. viridis*, Chiszar et al. (1993) applied rat (species not given) homogenate—a mixture of integumentary and internal fluid cues—to the snakes' snouts. In the first experiment, six snakes were observed in six conditions: experimenters in these conditions (1) allowed snakes to strike a rat weanling; (2) presented snakes with a rat weanling but did not allow them to strike it; (3) touched the snout of snakes with 26°C and (4) 38°C tap water; (5) touched the snout of snakes with 26°C and (6) 38°C homogenate. The authors found that rattlesnakes increased rates of tongue-flicking when exposed to the homogenate, compared to water controls. However, these levels did not reach those of the baseline of snakes striking prey.

To determine which component of the homogenate was most important to snakes, the authors used another six snakes in a second experiment with three applicator treatments: (1) tap water, (2) blood, and (3) integument. Only exposure to the blood treatment produced increased tongue-flicking rates. The authors concluded that blood is a highly relevant cue obtained during the predatory strike and helps inform the snake of successful envenomation of the target. However, this conclusion is speculative given that there are alternative explanations for why blood might elicit more tongue-flicks than water or integumentary chemicals when applied to the snout with an applicator, and the authors used increased tongue-flick rate, not SICS, as a response variable.

Further casting doubt, Smith and Kardong (2005) found no relevance of blood alone to the trailing component of SICS. Using a Y-maze, the authors allowed 23 *C. oreganus* to follow two different prey trails in four different treatments. All treatments involved a snake striking *M. musculus* and attempting SICS, with an experimental chemical trail in one arm of the Y and a tap water control trail in the other. In the first treatment, the experimental trail was the standard carcass drag of an envenomated mouse. The second treatment was a carcass drag of a non-envenomated mouse, the third was a carcass drag from an unstruck mouse overlain with blood obtained via cardiac puncture from the same mouse, and the fourth was blood alone. Because snakes could follow the experimental trail in all treatments except the blood-only one, the authors concluded that blood alone is not relevant to rattlesnakes for poststrike trailing. The authors reasoned that, whereas blood is biologically significant to snakes, it might not be relevant in poststrike trailing (Smith and Kardong 2005), likely because it is not present in appreciable amounts on the integument of most struck prey.

Although prey-derived chemical cues seem to be central to SICS, they are not actually necessary for eliciting striking behavior. Hayes and Duvall (1991) discovered that *C. virids* readily struck at warm mouse-sized models lacking any animal-borne odors, indicating that visual and thermal images of prey were sufficient to elicit strikes. Hayes and Hayes (1993) also demonstrated that chemical cues are not essential to striking in *C. oreganus*, although snakes did become more sensitive to such cues when deprived of food. Similarly, Chiszar et al. (1991b) were the first to document that *C. viridis* gather chemical information via the fangs as they deliver a strike. In this experiment, 12 rattlesnakes (n = 6 for each treatment) were allowed to strike either euthanized rat weanlings or moistened cotton balls presented in latex condoms. Condoms from both groups were of equal temperature and mass. Care was taken to ensure that no prey cues were present on the outsides of the condoms, although latex cues were present. Descriptive statistics indicated that snakes that struck the condom-enclosed rats exhibited higher rates of tongue-flicking, but typical SICS did not follow, as the tongue-flicks observed were lower than what was normally observed when *C. viridis* strikes a live rodent. Nevertheless, the authors concluded that the difference in tongue-flicking between the treatments was attributable to the transfer of prey chemical cues, via the fangs, to the vomeronasal organ. The authors postulated that the irregular SICS performance exhibited by snakes that struck condom-enclosed rats was because of a lower quantity of chemical information obtained by the snake than would be acquired during a normal strike, or that latex odors might have somehow inhibited normal SICS behavior.

Aside from fang- and lingual-mediated methods, rattlesnakes can also acquire chemical information solely from the vomeronasal organ. In squamates, the vomeronasal organ opens into the roof of the mouth (Bertmar 1981), and it has been demonstrated that the vomeronasal organ in tongueless individuals can still accumulate chemical molecules when in close proximity to stimuli (Halpern and Kubie 1980; Graves and Halpern 1989). Additionally, during a predatory encounter the vomeronasal duct openings contact prey, likely saturating the attacker’s oral cavity with chemical cues; in rattlesnakes and other pitvipers, these cues presumably help facilitate accurate trailing behavior during SICS (Chiszar et al. 1977, 1985b, 1993).

Early SICS research demonstrated that rattlesnakes are also able to distinguish between individuals that they have struck because the venom itself endows the animal with a unique chemical signature (Chiszar et al. 1982b; Lavín-Murcio et al. 1993). More recently, Saviola et al. (2013b:5) even isolated specific venom components that aid in SICS: disintegrin molecules, known as crotatroxin 1 and 2, act as “relocator proteins” that chemically “tag” prey. Disintegrins are seemingly exclusive to viperid venoms (Saviola et al. 2013b), representing a highly adaptive trait that evolved in snakes for which a strike-release-trail predatory strategy is crucial for survival. Free disintegrins are released by another component of rattlesnake venom, metalloproteinases, which are enzymes responsible for tissue destruction resulting from envenomation (Mackessy 2008, Saviola et al. 2013b). Rattlesnake venoms can typically be classified as either type I, characterized by high metalloproteinase concentration and low toxicity, or type II, characterized by low metalloproteinase concentration and high toxicity (Mackessy 2010). Type I venoms contain more disintegrins than type II, which can sometimes contain fewer than 0.1% metalloproteinases (Saviola et al. 2013b). As this work is relatively new and still taxonomically limited, additional research on the role of venom chemistry in facilitating SICS would be highly beneficial.

Rattlesnakes are also capable of using airborne cues to facilitate SICS, though less effectively (Parker and Kardong 2005, 2006, 2017). Although typically secondary, under some conditions airborne cues might become primary (e.g., favorable wind currents could help alert the snake to the location of an envenomated carcass) (Parker and Kardong 2006). In Parker and Kardong (2005), the authors used a Y-maze equipped with fans at both ends to simulate airflow. *C. oreganus* were allowed to strike a mouse (*M. musculus*), and then given a choice between substrate or airborne odors. Whereas rattlesnakes preferred substrate to airborne cues, they nonetheless showed the ability to locate carcasses via airborne odors 83% of the time when paired with a control treatment (no mouse). Again using *C. oreganus* in a Y-maze, Parker and Kardong (2006) found that snakes preferred substrate trails of unstruck *M. musculus* over unscented air. However, no preference was observed between airborne cues of unstruck mice and unscented air, nor between airborne cues of unstruck mice and cues of struck mice. Thus, SICS might rely primarily on substrate trails, but it can also be facilitated with airborne cues (Parker and Kardong 2006). Parker and Kardong (2017) endeavored to determine how *C. oreganus* modified SICS behavior during exposure to different chemical cues— substrate, airborne, and air-deposited (i.e., settled airborne cues)—which the authors suggested represent the range of available environmental cues in the wild. Using the same fan-equipped Y-maze as described above, rattlesnakes underwent various scoring criteria to determine SICS effectiveness when investigating each cue type. Rattlesnakes performed SICS most efficiently when presented with substrate cues, less efficiently when investigating airborne cues, and least efficiently when investigating air-deposited cues. Rattlesnakes backtracked the most in the latter two treatments. This suggests that, as chemical cues become more dilute in the environment, rattlesnakes exhibit plasticity in their SICS behavior to facilitate foraging success (Parker and Kardong 2017).

Although no field-based experiments on the use of airborne cues have been conducted, M.D. Whitford and R.W. Clark (personal observation) recorded a nocturnal strike sequence in the field wherein a Mohave Rattlesnake (*C. scutulatus*) struck and released a Merriam's kangaroo rat (*Dipodomys merriami*), which traveled approximate 10 m before succumbing to venom. Rather than following the circuitous substrate-borne scent trail of the prey, the snake began SICS and moved in a more or less straight line to the carcass, presumably using airborne chemical cues to relocate the prey.

2.7.1.7 Field studies of SICS

SICS in viperids has been studied extensively in a laboratory setting, and much less often in the field. Clark (2016) summarized the available field observations and concluded that, at least some of the time, rattlesnakes have difficulty relocating envenomated prey in field environments. Importantly, laboratory studies show that the decision to trail is made independently of the decision to strike (Chiszar et al. 1991c), which can save a rattlesnake time and energy if a strike is unsuccessful. The cost of engaging in SICS when prey are not immobilized by venom can be substantial, as SICS can persist for several days in a natural setting, with the snakes covering hundreds of square meters in the process (Diller 1990). Rattlesnakes are more likely to fail in relocating struck prey when the latter has developed a physiological immunity to venom, thus enabling such prey to travel further after being struck (Clark 2016).

To date, only a single experimental manipulation demonstrating SICS in a free-ranging snake ($n = 1$) has been recorded (Goode et al. 1990). The authors found that when an Aruba

Island Rattlesnake (*Crotalus unicolor*) struck mice (*Calomys hummelincki*) and a scent trail was available (made by the investigators by dragging the carcass along the ground), it commenced SICS. However, when no scent trail was made following a successful strike, despite displaying increased rates of tongue-flicking and performing local searches within the confines of its cover, the snake did not emerge from its sheltered location. Goode et al. (1990) postulated that while elevated rates of tongue-flicking might be an obligate response to striking prey, a scent trail is needed for the trailing component of SICS to occur. This manipulation was an important observation, and should be built upon with further field experiments that statistically analyze SICS in free-ranging snakes.

In contrast to Goode et al.'s (1990) observation, *C. viridis* has been documented to vacate cover in search of prey, even in the absence of a scent trail, or after recent exposure to simulated predators (O'Connell et al. 1981a; Golan et al. 1982; Chiszar et al. 1986a). Another possibility is, as the decision to trail is made independently of the decision to strike (Chiszar et al. 1991c), perhaps the strike in Goode et al. (1990) was deemed unsuccessful. Rattlesnakes seem able to assess the quality of the strike they deploy and, perhaps, there is central processing that enables revision in the decision-making process leading to trailing behavior. Recent high-speed field recordings of *C. cerastes* and *C. scutulatus* provide direct evidence for this (Whitford et al. 2019; Higham et al. 2017): snakes that struck prey and either missed prey or did not contact prey long enough to envenomate did not exhibit SICS.

In laboratory settings, SICS has been observed to last up to 24 hrs (Smith et al. 2000), but in natural settings it can last much longer (up to several days [Diller 1990; R.W. Clark, personal observation]), with successful relocation of prey less certain compared to simulated captive studies of SICS (Clark 2016). At times, rattlesnakes can experience difficulty in relocating prey even when the animal has not travelled far before becoming immobile. Between two *C. horridus*, one individual took 12 min to relocate a rodent that had traveled 0.75 m, and another took 41 min to find a rodent that had traveled 7 m (Clark 2016). Likewise, *C. scutulatus* will periodically have difficulty locating its primary prey, kangaroo rats (*Dipodomys* spp.). One snake took 43 min to locate a *D. merriami* that had gone 15 m before expiring, another took 21 min to reach a *D. merriami* that had covered 9.5 m, a third took at least 15 h to relocate a *D. merriami* that had traveled 18 m, and others have also been observed to spend several hours before successful relocation of prey (Clark 2016). Part of this occasional inefficiency might be related to the fact that kangaroo rats, because of their saltatory locomotion, presumably leave an intermittent chemical trail. Various authors have speculated that the highly potent neurotoxin present in the venom of most *C. scutulatus* specimens evolved to immobilize prey quickly (Clark 2016).

2.7.1.8 SICS and body condition

Importantly for those keeping captive rattlesnakes, poor husbandry conditions can have negative effects on their behavior, including SICS. Busch et al. (1996) received six abused and neglected *Crotalus oreganus*, and found that the snakes were incapable of performing SICS. However, one year later, though still substandard compared to healthy snakes, their SICS abilities had significantly improved. Thus, rattlesnakes can improve and regain their innate SICS behavior as they recover over time, though it might take years for this process to occur. Fortunately for these six individuals, they regained full SICS capabilities after two years (Chiszar et al. 1999c). This recovery time highlights the importance of full rehabilitation before potential release back into the wild, as these six individuals likely would have perished if released prematurely (Chiszar et al. 1999c).

2.7.2 SICS in Viperidae: **Agkistrodon**

After rattlesnakes, species of the genus *Agkistrodon* are the next most frequent experimental subjects in the SICS literature (Table 2.1). Unlike rattlesnakes, which generally specialize on rodents or lizards, *Agkistrodon* spp. tend to have a more catholic diet (seemingly anything they can swallow), and will employ active hunting and scavenging strategies as well as the traditional viperid ambush hunting. Potential prey include small mammals, snakes, turtles, juvenile alligators, amphibians, fish, birds, bird eggs, arthropods, mollusks, and carrion (Gloyd and Conant 1990; Ernst and Ernst 2012). Different geographic populations of Copperheads (*A. contortrix*) even prefer different prey types (Greenbaum et al. 2003).

Morphologically, *Agkistrodon* share the same general characteristics as their rattlesnake relatives. Both genera are typically comprised of medium- to large-bodied, relatively sedentary snakes that possess heat-sensing facial pits and front-fanged venom delivery systems (Gloyd and Conant 1990; Campbell and Lamar 2004). Also similar to rattlesnakes is the commencement of SICS subsequent to striking and chemically sampling prey (Ernst and Ernst 2012). However, the way SICS is activated in *Agkistrodon* might be more variable than in most rattlesnakes, perhaps because of the former's more varied dietary preferences and hunting modes. Chiszar et al. (1979) performed two experiments that are supportive of this idea, although the trials involved small sample sizes of individual snakes and only descriptive statistics. In the first experiment, the authors used six Cottonmouths (*A. piscivorus*) to demonstrate that the snakes displayed much higher rates of tongue-flicking when exposed to fish mucous than to mouse odors (cue-induced, as opposed to strike-induced, chemosensory searching). Based on these results, they then tested whether striking a rodent would induce SICS in *Agkistrodon*, as it does in rattlesnakes. Using two cantils (*A. bilineatus*), they observed that striking a mouse caused sustained tongue-flicking, leading the authors to conclude that SICS likely occurs in these snakes. SICS was also tentatively confirmed by observations of 2 *A. bilineatus* and 4 *A. piscivorus* by Chiszar et al. (1982c). Although they did not specify when this occurred or detail a specific experiment with sample sizes, the authors wrote that they also exposed rattlesnakes to fish mucous odors, to which the snakes responded as the Cottonmouths did, displaying an increased rate of tongue-flicking to fish mucous but not rodent odors. Because rattlesnakes do not eat fish, the authors were uncertain whether this increased chemosensory exploration was a result of the mucous cues, or simply a response to a novel stimulus. Chiszar et al. (1979) ultimately concluded that *Agkistrodon* detects mucous odors more readily than integumentary ones, and that striking is necessary for the detection of rodent odors. However, the latter conclusion was later refuted by Chiszar et al. (1986b) (see below). Because of the anecdotal nature of some of these studies, an expanded experimental study on the response of *Agkistrodon* spp. to prey odors and SICS experimental paradigms is warranted.

2.7.2.1 Cottonmouths (*Agkistrodon piscivorus*)

Further experimental verification of SICS in *Agkistrodon piscivorous* was conducted by O’Connell et al. (1981b) and Chiszar et al. (1982c). Like rattlesnakes, Cottonmouths seem to assess the retaliatory capacity of prey, as O’Connell et al. (1981b) noted that they were careful to avoid the dorsal spines of fish (*Lepomis macrochirus*) when striking and holding them. Holding fish after striking is likely adaptive because releasing them back into the water would make relocation difficult (O'Connell et al. 1981b). Similarly, Chiszar et al. (1986b) observed that Cottonmouths held fish, whereas they released presumably more dangerous and trackable rodents. However, Ernst and Ernst (2012) noted a Cottonmouth that struck and held a rat, a decision that resulted in the destruction of the snake’s tongue and face.

Chiszar et al. (1985b) found that, as in rattlesnakes, Cottonmouths maintain a chemical search image of prey for at least 70 min after striking. Using 16 Cottonmouths, 8 snakes were allowed to strike a mouse (presumably *M. musculus*), whereas the other 8 snakes were allowed to strike a fish (*Osmerus mordax*). Subsequently, when presented with either a nonenvenomated fish or a nonenvenomated mouse, it was shown that Cottonmouths preferred the same carcass type as the one they struck, a preference likely facilitated by the chemical search image. These search images guide chemosensory searching until the prey item is located and consumed, or, following unsuccessful relocation of prey, the stimulus that initiated the pattern loses its potency (Chiszar et al. 1985b). Moreover, Cottonmouths trail both mice and fish chemical cues equally well (Chiszar et al. 1986b). This perhaps reflects the reputation *Agkistrodon* spp. have for being voracious, opportunistic predators with a tendency to eat anything they can swallow. For example, a Cottonmouth was observed eating a brown water snake (*Nerodia taxispilota*) that was 15 cm longer and 230 g heavier than itself—the Cottonmouth could not move and died the next day (Ernst and Ernst 2012). Another experiment revealed that Cottonmouths will consume at least four mice in 90 min (Kardong 1982).

During the SICS behavioral sequence, *A. piscivorous* seem to differ from rattlesnakes in some respects. While Chiszar et al. (1983a) and Golan et al. (1982) determined that striking prey was a prerequisite of trailing behavior in rattlesnakes, Chiszar et al. (1986b) discovered that Cottonmouths would follow odiferous prey trails regardless of prior striking behavior. The authors hypothesized that, as concluded by Chiszar et al. (1983c), this disparate behavior might occur because if rattlesnakes have not struck prey, but are presented with mouse odors, they remain in an ambush posture waiting for the source of the odor to come within striking range. Chiszar et al. (1986b) ultimately concluded that Cottonmouths are less likely than rattlesnakes to remain in an ambush posture, and that Cottonmouths might have superior chemoreception to rattlesnakes, as they are better able to detect prey trails without striking. However, Cottonmouths display a greater plasticity in their foraging methods than rattlesnakes do, and are known to scavenge dead fish (Lillywhite et al. 2002, 2008). One Cottonmouth was even observed ingesting seaweed that had fish odor on it (Lillywhite et al. 2008). Whereas rattlesnakes are known to occasionally scavenge (Gillingham and Baker 1981), the extent to which they rely on scavenging as a primary food source is uncertain—in the several thousand hours of field observations of rattlesnake activity summarized in Clark (2006a), Clark et al. (2012, 2016b), and Putman and Clark (2016), no observations of scavenging occurred. We find it likely that the general chemoreceptive abilities of *Crotalus* and *Agkistrodon* are similar, but Cottonmouths are simply more attuned to foraging opportunities involving scavenging or active pursuit of prey than rattlesnakes.

Like rattlesnakes, Cottonmouths are more likely to strike-and-release, rather than hold, larger prey (Kardong 1982). In this study, successful retaliatory attacks inflicted by thrashing rodents were low (7%), and unlike rattlesnakes (Kardong 1986a), Cottonmouths did not always release mice that bit them. Whether a Cottonmouth held or released mice had no effect on the latter’s mortality rates, a result different than that observed by Kardong (1986a), in which prey held by rattlesnakes died much more quickly than those that were released. Kardong (1982) also offered up to four mice in close succession to Cottonmouths, and found that they consistently struck and released the first mouse but tended to hold subsequent mice. Kardong (1982) discussed the possibility that the snakes were more likely to hold subsequent mice because of lower venom stores, but because some viperids can deliver at least six successful strikes without significantly depleting their venom stores (Kochva 1960; Allon and Kochva 1974), he concluded this was not the case (but also see Hayes et al. 1992, 2002). Also, like rattlesnakes, Cottonmouths orient their heads in the direction that their struck prey fled, likely to aid in the detection of the visual as well as chemical cues to guide post-strike trailing behavior (Keith et al. 1985).

2.7.2.2 Copperheads (*Agkistrodon contortrix*)

SICS also occurs in Copperheads, and although the general behavioral sequence is similar, this species differs in some notable ways from rattlesnakes and Cottonmouths (Stiles et al. 2002; Greenbaum et al. 2003; Greenbaum 2004; Greenbaum and Jorgensen 2004). Stiles et al. (2002) determined that striking, the presence of a prey chemical trail, and cover (or a retreat site) were all prerequisites for the trailing component of SICS for Copperheads. Furthermore, Copperheads released, rather than held, all struck mice. The authors offered a simple explanation—although more closely related to Cottonmouths than rattlesnakes, a Copperhead's diet contains a higher proportion of rodents than a Cottonmouth's diet does, and therefore, Copperheads are more inclined to strike-and-release prey than Cottonmouths are. Stiles et al. (2002) explained this by stating that SICS is likely an ancestral condition developed prior to the rise of New World vipers, and that at least some aspects of the feeding behavior of Cottonmouths might be derived, as these snakes relied increasingly less on rodents as food over time.

Greenbaum (2004) offered Copperheads from three different populations, each with different dietary preferences, a choice between different prey items (*Mus musculus, Rana pipiens*, *Manduca sexta*) contained in nylon bags. In the first experiment, 30 snakes (9 from Kansas, 13 from Texas, 8 from Louisiana) were each presented with envenomated and nonenvenomated prey. Envenomated mice were innately preferred by all populations, as quantified by tongue-flicking and attempted ingestion, in spite of their dietary differences in nature. However, searching and consumption behaviors were seemingly independent, because mice were always envenomated first, initiating SICS, but nonenvenomated mouse carcasses were not preferred during consumption. This indicates, as described above in rattlesnakes, that envenomated tissue is of greater relevance to Copperheads than integumentary cues. In a subsequent experiment, each snake was allowed to strike a mouse, and then presented with two different nonenvenomated prey species in nylon bags. Copperheads which had struck mice did not preferentially direct tongue-flicks toward nonenvenomated mice and instead tongue-flicked all prey items randomly, indicating that their mouse strike did not seem to predispose them toward integumentary chemical cues from mice. Greenbaum (2004) suggested that Copperheads might not form chemical search images of struck prey in the same way as other crotalines. However, given the differences in methodology between this study and other SICS experiments, direct comparisons are problematic.

In another study of *Agkistrodon contortrix,* Greenbaum et al. (2003) demonstrated that, like rattlesnakes, Copperheads prefer to trail envenomated over nonenvenomated prey. This study also demonstrated that Copperheads even preferred to trail prey injected with more potent venom over prey injected with less potent venom (snakes from Louisiana possessed more potent venom than snakes from Texas, which in turn possessed more potent venom than snakes from Kansas; protein composition was generally similar in all three venoms). This finding indicates that Copperheads (and perhaps other viperids) can detect subtle differences in venom biochemistry and/or its physiological effects; some Copperheads could even distinguish conspecific venoms from those of Cottonmouths and Massasaugas (*Sistrurus catenatus*). It is also possible the venoms differed in disintegrin content (i.e., Saviola et al. 2013b), although we are not aware of any analyses of disintegrins in Copperhead venom. This preference for more lethal venom might be intertwined with the enhanced action of the venom, which presumably will incapacitate prey faster, facilitating a shorter search distance for the snake (Greenbaum et al. 2003).

2.7.3 SICS in Viperidae: Other crotalines

A handful of additional studies have explored the occurrence of SICS in other pitvipers, mostly from the New World (Table 2.1). Chiszar et al. (1989) and Boyer et al. (1995), although using small sample sizes of snakes (*n* = 2–7), verified SICS in juvenile bushmasters (*Lachesis muta*). Although bushmasters are ambush hunters (Campbell and Lamar 2004), in captivity they tend to strike-and-hold prey, presumably because of skin folds around the eyes and pits that might offer more protection from counterattacks (Chiszar et al. 1989). Protective skin folds have also been observed during predatory episodes involving jumping pitvipers (*Atropoides nummifer*). Chiszar and Radcliffe (1989) observed that, when *A. nummifer* held mice (species not given), loose skin would completely cover the pits and partially cover the eyes. The more the prey struggled, the harder the snakes bit down, in which cases the eyes became completely covered. Eyelash vipers (*Bothriechis schlegelii*) and white-lipped pitvipers (*Trimeresurus albolabris*) also have protective skin folds, and both typically hold prey following a strike (Chiszar and Radcliffe 1989), presumably as an adaptation to arboreal hunting, because arboreal prey are less likely to leave continous substrate-borne chemical trails. Therefore, viperids with protective skin folds might attempt to hold prey after striking more often, as the cost of counterattacks are lessened. Species that usually hold prey would presumably still use SICS if prey struggled free or were released.

Several studies indicate that Old World pitvipers also seem to be able to use SICS and distinguish between envenomated and nonenvenomated prey. Chiszar et al. (1992) mentioned an unpublished experiment conducted by Robert Lee, in which this was observed in four Mamushi (*Gloydius blomhoffii*), and Waters et al. (1996) documented SICS in Habu (*Protobothrops flavoviridis*). Waters et al. (1996) noted that Habu likely descended from an arboreal ancestor, becoming secondarily terrestrial in Japan while still retaining certain behavioral and morphological characteristics indicative of an arboreal lifestyle (i.e., lengthy, slender bodies and an occasional propensity to climb trees). Given that arboreal viperids typically hold struck prey (Deufel and Cundall 2006), the authors proposed that Habu re-evolved SICS as an adaptation to life on land.

2.7.4 SICS in Viperidae: Old World vipers

SICS is primarily associated with New World pitvipers, especially rattlesnakes. However, the general behavioral pattern of SICS can be inferred from early reports on the behavior of several Old World vipers (*Vipera aspis, V. berus*) (Baumann 1927, 1928; Wiedemann 1932; Naulleau 1964) that predate the use of SICS terminology. After the first SICS research on rattlesnakes in the late 1970s, some additional research on SICS has been conducted on true vipers, as well (Table 2.1).

Chiszar et al. (1982c) conducted several experiments on SICS in true vipers, and offered an interesting hypothesis. After confirming SICS in vipers from different geographic regions (Macmahon's Vipers (*Eristicophis macmahoni*) from Asia; Armenian Mountain Vipers (*Montivipera raddei*), Ottoman Vipers (*M. xanthina*), Long-Nosed Vipers (*V. ammodytes*), and Latifi's Vipers (*M. latifii*) from Europe; Gaboon Vipers (*Bitis gabonica)* and Puff Adders (*B. arietans*) from Africa), even in genera that typically retain struck prey (*Bitis, Eristicophis*), they concluded that SICS is a paedomorphic retention among *Crotalus*, *Sistrurus*, *Agkistrodon*, and *Vipera.* Their reasoning was based on observations that juvenile *B. gabonica* and *B. arietans* released prey, whereas adults retained prey, a behavior also observed in cobras. However, as they advanced their paedomorphic evolution hypothesis, the authors acknowledged that other hypotheses were also tenable. Notably, the studies of Chiszar and colleagues were conducted with captive snakes. Glaudas et al. (2017) observed adult *B. arietans* in the wild, and found that the decision to hold or release struck prey was based on prey body size. Additionally, one individual seized a small mouse, and upon a retaliatory bite, dropped it, subsequently conducting SICS. Ultimately, Chiszar et al. (1982c) concluded that SICS must be homologous in elapids and viperids because the behavior first appeared in elapid ancestors before they split from viperids.

O'Connell et al. (1982b) documented SICS in captive-born Russell's Vipers (*Daboia russelii*), showing that they exhibited SICS after striking rodents. Therefore, SICS seems to not only be innate in vipers and pitvipers, but the behavior is also apparently undiminished in snakes raised in captivity, as they performed SICS equally as well as wild-caught snakes.

In fascinating sequential studies, Carr et al. (1982) and Chiszar et al. (1983d) documented SICS behavior in a congenitally tongueless *D. russelii.* Observations of this snake indicated that, while efficiency was greatly diminished, the snake was nevertheless able to successfully relocate envenomated prey. The authors concluded that olfactory acquisition and transfer of chemical cues to the vomeronasal organ via nonlingual means (c.f. Chiszar et al. 1991b) was sufficient to guide the snake.

2.7.5 SICS in Other Squamate Reptiles

In most SICS studies involving Viperidae, investigators typically used, at a minimum, a strike versus no-strike presentation of prey to quantify tongue-flicking. As a control, prey would first be presented to the snake in the no-strike condition, during which the snake could direct tongue-flicks toward the prey before it was removed. In the strike condition, prey were presented in the same way, except snakes were allowed to strike them prior to removal. These two conditions allow comparison of pre-strike versus post-strike tongue-flicking.

Typically, viperids suppress chemosensory searching in the presence of prey prior to striking, exhibiting little to no tongue-flicking, most likely as an attempt to maintain crypsis as a component of their ambush hunting strategy. When assessing SICS in taxa other than Viperidae, which are typically active foragers that readily tongue-flick when exposed to prey cues, this prey presentation control is essential in order to disentangle the effects of strike-induced and cue-induced chemosensory searching. Additionally, active foragers (especially lizards) often do not release prey voluntarily, so when prey are bitten investigators must forcibly remove it from the attacking animal’s grasp in order to measure SICS. Consequently, one or more disturbance controls were also added to most of these experiments, to further distinguish SICS from other possible effects. Although active foragers will typically tongue-flick in the presence of prey or prey cues alone, strike-induced and cue-induced chemosensory searching are not mutually exclusive—both behaviors can be displayed depending on the predatory encounter, and both effects can be quantified with the proper experimental controls in place.

2.7.5.1 Elapidae

SICS, or SICS-like behavior, has been verified in many species of cobras and other elapids (Table 2.1). O’Connell et al. (1985) observed SICS in 5 Tiger Snakes (*Notechis scutatus*), 2 Indian Cobras (*Naja naja*), 2 Taipans (*Oxyuranus scutellatus*), and 1 Death Adder (*Acanthophis antarcticus*), and compared their responses to SICS in a viperid (2 Rhinoceros Vipers, *Bitis nasicornis*). Using *Mus musculus* as the prey item, the authors found that elapids showed at least some level of chemosensory searching based on visual cues alone (no striking), whereas striking was necessary to elicit chemosensory searching in *B. nasicornis*. These disparate responses can likely be explained by the different hunting strategies generally employed by elapids and viperids, as the former typically incorporate visual detection of prey with an active hunting mode, whereas the latter typically remain in ambush posture awaiting prey to come within striking range. Chiszar et al. (1983b:58) also found that cobras (11 *N. pallida* and 6 *N. kaouthia*) use both visual and chemosensory cues to detect and reacquire prey. Cobras in this study frequently stood up ("hoodless standing") after striking prey, apparently in an effort to visually detect the prey item in the post-strike environment, thus combining vision and chemosensory-mediated relocation strategies.

Radcliffe et al. (1986) also compared SICS of an elapid (*N. pallida*, *n* = 6) to a viperid (*Crotalus viridis*, *n* = 6). Their results were similar to those of O'Connell et al. (1985) in that both strike and no-strike presentations of rodents elicited chemosensory searching in cobras, whereas rattlesnakes only performed SICS. As such, the authors stated that these taxa should serve as model systems of their respective hunting strategies. They also discussed the belief that viperid ancestors were perhaps cobra-like active hunters, and during the evolutionary process of specializing on rodent prey using an ambush strategy, viperids lost the ancestral pre-strike behaviors seen in extant cobras.

One noteworthy elapid bears particular mention because of its morphological and behavioral similarities to Viperidae. Appearing and behaving more like viperids, Death Adders (*Acanthophis* spp.) are thick-bodied elapid ambush hunters, an apparent case of convergent evolution with Viperidae (Shine 1980; Mirtschin et al. 2017). Although not rodent specialists, these snakes consume a higher proportion of rodent prey than most other elapid species, making their diet convergent with viperids as well (Shine 1980). O'Connell et al. (1985) observed SICS in a single *A. antarcticus* by demonstrating that tongue-flicking increased after striking *M. musculus* (it should be noted, however, that the finding for the single *A. antarcticus* was pooled with that of four other elapids, *n* = 2 *N. naja* and *n* = 2 *O. scutellatus*), although it remains unknown if the extent of such behavior is analogous to that known in viperids such as rattlesnakes. Presumably, one would expect death adders to possess robust SICS—although, these snakes tend to hold rather than release prey (Mirtschin et al. 2017). SICS has also been confirmed in Eastern Green Mambas (*Dendroaspis angusticeps*). Chiszar et al. (1994) found that both juvenile and adult mambas would strike and release prey, with adults exhibiting much higher tongue-flick rates following strikes (matching the highest rates observed in rattlesnakes) than juveniles. Also of note is that juveniles briefly held prey for 1–2 s before the release.

Semi-oceanic sea kraits (Laticaudinae) are likely not the first venomous reptiles that come to mind when considering SICS. Nonetheless, these marine snakes exhibit SICS-like behavior. Radcliffe and Chiszar (1980) observed the feeding behavior of Yellow-Lipped Sea Kraits (*Laticauda colubrina*), which are eel specialists (Pernetta 1977; Mirtschin et al. 2017). All *L. colubrina* immediately struck and released eels upon first contact. After this, the kraits moved a short distance away and became motionless. At times, dying eels bumped into the kraits as they swam about. This almost always resulted in the kraits retreating further away from the eels.

Eel mortality occurred after a mean of 16 min, yet kraits waited an additional mean of 8 min before approaching and rapidly consuming the carcasses. Tongue-flicking was high pre-strike, but significantly reduced immediately post-strike. However, elevated tongue-flicking occurred until 11–20 min post-strike, as the kraits began chemosensory searching to relocate the struck eels. Thus, striking seems to inhibit further snake activity, including striking, with a delayed increase in the rate of tongue- flicking—the same general pattern observed in terrestrial ambush-foraging viperids (Chiszar and Scudder 1980; Chiszar et al. 1983a). Ultimately, it seems that some sea snakes and sea kraits are capable of implementing their own aquatic variations of SICS.

Additional observations show this same basic pattern. Klemmer (1967) observed the feeding behavior of two captive Black-Banded Sea Kraits (*L. laticaudata*), which are also eel specialists (Mirtschin et al. 2017). The kraits refused to eat various small fish offered to them, but, following the introduction of a European eel (*Anguilla anguilla*), they readily began chemosensory searching, subsequently striking and releasing the prey upon first contact. During the next ten minutes, the author could not provoke additional responses from the krait. Upon cessation of movement from the eel, the krait swallowed it head-first.

McCosker's (1975) description of the feeding behavior of *L. laticaudata* is very similar. Unlike many elapids, most hydrophiids (subfamily Hydrophiinae) and laticaudids (subfamily Laticaudinae) do not seem as visually oriented when hunting, instead using olfaction and water currents to locate, identify, and strike prey (Heatwole 1999). Thus, as has been discussed previously in terrestrial venomous snakes, perhaps the specialization upon dangerous prey was a driving evolutionary force that dictated the development of SICS in marine snakes as well.

2.7.5.2 Colubridae

Within Colubridae, garter snakes (*Thamnophis* spp.) have been studied the most extensively (Cooper et al. 1989; Cooper 1992a; Burghardt and Chmura 1993; also, see "Comparisons Between Viperids and Other Snakes", above). SICS-like behavior has also been confirmed in Corn Snakes (*Pantherophis guttatus*), Black Rat Snakes (*P. obsoletus*), and Bull Snakes (*Pituophis melanoleucus*) (Chiszar et al. 1980a; Cooper et al. 1989; Withgott 1996). In most of these experiments, snakes increased their rate of tongue-flicking after striking at or constricting prey (*Mus musculus*, *Notemigonus crysoleucas*), or being exposed to prey chemical cues (*Gambusia affinis*, *Lumbricus terrestris*).

In Cooper et al. (1989), *P. guttatus* were allowed to strike *M. musculus*, but the mice were pulled away before they could be constricted. Disturbance controls were used to account for this, and prey presentation controls were used to distinguish SICS from chemosensory searching. In a third experiment, snakes were allowed to strike and ingest a mouse. Tongue-flicking increased after striking prey, but was highest post-ingestion. In this same study, similar experiments were conducted using *T. sirtalis* and *N. crysoleucas*. Snakes also displayed elevated tongue-flicking following strikes, but interestingly, tongue-flicks did not increase post-ingestion. The authors suggested that this difference in post-ingestion tongue-flicking observed between the two snake species might be a result of disparate foraging strategies. Constrictors (*P. guttatus*) often release prey prior to swallowing, and can sometimes lose contact with them (especially if multiple prey are being constricted during a single predatory episode), necessitating tongue-flicking for prey relocation. Nonconstrictors (*T. sirtalis*) are more likely to retain their grasp on prey while swallowing, rendering them less likely to be lost. Using prey presentation and disturbance controls, Cooper (1992a) showed that ingestively naïve *T. radix* neonates displayed increased rates of tongue-flicking and searching movements after striking *N. crysoleucas*. Burghardt and Chmura (1993) also used ingestively naïve neonatal *T. sirtalis* to show that snakes emitted a higher number of tongue-flicks in response to aqueous *L. terrestris* extract than to water.

Using constricting snakes, Chiszar et al. (1980a) and Withgott (1996) did not explicitly test for SICS, instead observing a post-attack and post-ingestion increase in tongue-flicking during predatory encounters. Chiszar et al. (1980a) used four *P. melanoleucus* to demonstrate that the snakes exhibited an increased rate of tongue-flicking after constricting a mouse (presumably *M. musculus*). Post-constriction tongue-flicking was higher than that observed during the baseline period, but it must be noted that a prey presentation control was not used. Post-ingestion and post-constriction tongue-flicks were similar, and the authors suggested that this is an adaptation for detecting additional prey, as constrictors can encounter several prey per predatory episode. Withgott (1996) observed increased tongue-flicking in *P. obsoletus* after ingesting *M. musculus*, which he termed post-prandial chemosensory searching. Tongue-flicking during post-prandial chemosensory searching was higher than that observed during the attack sequence, and Withgott determined that this behavior might be analogous to SICS.

2.7.5.3 Pythonidae

Only a single relevant study has been conducted on boid or pythonid snakes. Cooper (1991a) found that Ball Pythons (*Python regius*) exhibited an elevated rate of tongue-flicking after they bit mice (presumably *M. musculus*) and concluded that they would be capable of SICS. Cooper (1991a) also discussed the hypotheses that snakes evolved from either varanoid or scleroglossan lizards, and stated that if either hypothesis is true, then SICS is likely plesiomorphic in snakes.

2.7.5.4 Helodermatidae

Although not strike-and-release ambush foragers, Gila Monsters are capable of SICS and possess bifurcated tongues, highly sensitive vomeronasal organs, and excellent trail-following abilities (Cooper et al. 1994; Cooper and Arnett 1995; Garrett et al. 1996). Since Gila Monsters do not voluntarily release prey, bitten *Mus musculus* were forcibly removed from the lizards' mouths in all experiments. Tongue-flicking was much higher after Gila Monsters bit prey, and lizards displayed proficient trailing abilities. Cooper and Arnett (1995) attributed these results to foraging mode. Ambush foraging lizards are not likely to display SICS because they do not tongue-flick to recognize or locate prey or ambush sites (Cooper 1989b,c, 1995a). Conversely, active-foraging lizards like Gila Monsters tongue-flick to find and trail food (Cooper 1989b, 1990). The authors suggested that the duration of SICS is directly linked to the specialized forked tongues (highly evolved for chemoreception) and more complex vomeronasal organs (containing higher amounts of sensory cells) characteristic of Serpentes and Varanoidea (Schwenk 1988, 1994).

2.7.5.5 Varanidae

The monogeneric family Varanidae contains the monitor lizards (*Varanus* spp.), which are far-ranging active foragers (Pianka and King 2004). Cooper (1989b) was the first to document SICS in a varanid, using 7 Savannah Monitors (*V. exanthematicus*), by demonstrating that mean tongue-flicking rates were greater after striking *Mus musculus*. The author postulated that SICS would be adaptive in these lizards as a tool to help relocate dropped or escaped prey. Cooper further suggested that SICS might be basal in snakes and lizards, having evolved before the strike-release-trail-strategy as a means to recover lost prey rather than convergently evolving in viperids and elapids. Both Savannah and Gould’s Monitors (*V. gouldii*) can exhibit and sustain elevated rates of tongue-flicking and SICS for at least 20–30 min (Cooper 1993a; Garrett et al., 1996), which can perhaps be taken as a rough estimation of the extent of this ability in monitors as a whole. Lizards in this study again displayed higher tongue-flicking rates after biting *M. musculus*. In Cooper (1993a), some individuals ceased tongue-flicking only to resume this behavior several minutes later, prompting the author to suggest that this could be a strategy to relocate escaped prey that have reemerged from hiding. In the same experiment, the trailing component of SICS did not last as long as the post-strike elevation in tongue-flicking, and while not quantified, locomotion was clearly associated with this increased tongue-flicking. Monitor lizards moved about while swinging their heads laterally and tongue-flicking, and these head swinging movements were also observed in all SICS studies on snakes. These same searching movements were also observed in Bengal Monitors (Auffenberg, 1984), suggesting SICS might be widespread in *Varanus*, although the trail-following abilities of these lizards were unknown at the time (Cooper 1993a).

In fact, monitors are adept at following prey trails. Garrett et al. (1996) used 8 *V. gouldii* to find that they could trail and recover *M. musculus* carcasses in nearly every instance. Ultimately, the authors determined that biting prey, distinguishing prey at a distance, or simply the presence of prey chemical trails, can all induce chemosensory searching in these lizards. Moreover, chemical cues, in the absence of biting prey, are enough to elicit this behavior. Likewise, Komodo dragons (*V. komodoensis*) are also expert trailers, and can locate prey via airborne (up to 11 km away) or terrestrial means (Auffenberg, 1981; Burghardt et al., 2002). In Lederer (1942), dragons following chemical trails rarely deviated from them by more than 1 m.

2.7.5.6 Anguidae

SICS was observed in the anguid lizards *Barisia imbricata* and *Elgaria coerulea* (Ballinger et al. 1992; Cooper 1995b). After prey (crickets and grasshoppers) were bitten and forcibly released, both species exhibited elevated rates of tongue-flicking (although Ballinger et al. [1992] used only descriptive statistics to observe a single *B. imbricata*), and *E. coerulea* also displayed concomitant searching movements. Both experiments concluded that SICS was ancestral in squamates. Furthermore, Cooper (1995b) discussed that if SICS was prolonged in Anguidae (as it is in Helodermatidae and Varanidae), then this long duration likely arose in the common ancestor of Anguimorpha. However, since SICS was found to be brief in Anguidae, Cooper (1995a) suggested that prolonged SICS originated in a common ancestor of varanids, snakes, and helodermatids (assuming a shared ancestry among those taxa—a relationship that has been brought into question by more recent molecular phylogenies [Figueroa et al. 2016; Zheng and Wiens 2016]).

2.7.5.7 Eublepharidae

DePerno and Cooper (1996) and Cooper et al. (1996) investigated SICS in *Eublepharis macularius*. In Cooper et al. (1996), geckos bit live crickets (*Acheta domesticus*), which were then experimentally removed. Geckos subsequently increased tongue-flicking and displayed labial licking (chemosensory sampling) before beginning searching movements. Although DePerno and Cooper (1996) did not investigate SICS *per se*, they found that geckos increased tongue-flicking and displayed labial licking after their mouths were forcibly swabbed with an applicator soaked in distilled water containing cricket cues. In contrast to the pattern typically displayed by other lizard taxa that use SICS, the geckos used in Cooper et al. (1996) delayed their searching movements, prompting the authors to conclude that SICS is much less pronounced in *E. macularius* than it is in other lizard families such as Helodermatidae and Varanidae.

2.7.5.8 Gerrhosauridae

Gerrhosaurus nigrolineatus exhibited increased rates of tongue-flicking and searching movements after biting neonatal house mice (Cooper 1992b). The author stated that SICS is likely widespread in active foraging lizards that use vomerolfaction for prey capture, but not in ambush foragers (for lizard families in which SICS is absent, see Cooper [1994a: table 1]), which do not use chemoreception for prey acquisition.

2.7.5.9 Iguanidae

Though unconfirmed experimentally, SICS might occur in the Desert Iguana (*Dipsosaurus dorsalis*), an herbivorous forager (Cooper and Alberts 1993). The authors induced iguanas to bite a carrot slice, which was subsequently removed from their mouths. Elevated rates of tongue-flicking, and possibly SICS, were observed. The authors explained that increased tongue-flicking and SICS could be adaptive in herbivores because it might allow for continued assessment of dropped plant material and also might facilitate location of nearby vegetation.

2.7.5.10 Lacertidae

After biting and being forced to release crickets, *Podarcis muralis* exhibited increased rates of tongue-flicking and SICS, behaviors likely widespread in insectivorous lizards (Cooper 1991b). These behaviors were only expressed for a short period of time (0–22 tongue-flicks per min, observed over 10 min), which can likely be explained in at least two ways. First, injured insects are unlikely to be relocated, because they do not leave suitable prey trails to follow. Second, mobile, actively foraging lizards typically investigate a given area for prey only briefly before moving on to the next area.

2.7.5.11 Scincidae

Broad-Headed Skinks (*Eumeces laticeps*) were allowed to bite neonatal mice and exhibited increased tongue-flicking and SICS upon forced removal (Cooper 1992c). As in Cooper (1991b), these behaviors were brief, supporting the hypothesis that increased tongue-flicking and SICS are only expressed for a short time in active-foraging predators that primarily eat insects and other invertebrates, as prey is unlikely to be recovered if lost. Conversely, SICS lasts longer in varanids (Cooper 1993a). Assuming snakes are descended from a varanoid, Cooper (1992c) hypothesized that the highly specialized SICS seen in snakes is a more complex and developed form of the ancestral condition in lizards.

2.7.5.12 Teiidae

SICS was tested in the teiid lizards *Aspidoscelis sexlineatus* (*n* = 8) and *Tupinambis teguixin* (*n* = 10) (Ballinger et al. 1992; Cooper 1993b). The lizards displayed increased tongue-flicking and SICS after biting and being forced to release prey (crickets, grasshoppers, or mice). Furthermore, Cooper (1993b) discussed the theory that SICS is an adaptation based on foraging mode among lizards; SICS should only be adaptive in active foragers that tongue-flick to find prey and not ambush foragers that do not use such means for prey detection.

2.8 Summary/future directions

Summarizing across the SICS literature, we can codify some general patterns that have been repeatedly documented:

1) SICS or SICS-like behavior is probably expressed under some conditions by almost every squamate reptile with a well-developed chemical sense, but it is highly stereotyped and central to the feeding strategy of venomous snakes that consume relatively large prey.
2) The SICS-associated behavioral sequence in viperids can be categorized into five steps—a) the strike and release of prey, b) a refractory period, c) elevated rates of tongue-flicking, d) the commencement of locomotion while tongue-flicking, e) following of chemical trail until the prey item is recovered or the behavior pattern is terminated. The SICS-associated sequence in squamates other than viperids is similar, except that prey are unlikely to be released voluntarily, and there is no refractory period (with some exceptions in elapids), with searching commencing immediately after the strike.

3) Multiple chemical cues are integrated to discriminate among different prey trails, but venomous snakes generally prioritize cues from envenomation over individual prey odors, which in turn are prioritized over odors related to mechanical damage from fangs.
4) Snakes seem to recognize the capacity for their prey to retaliate, which influences whether they release or hold prey following the strike.
5) Chemosensory searching and SICS are innate in neonates and juveniles.
6) Even in viperids the taxonomic representation of detailed SICS experimentation is limited—a large portion of the studies examining nuances and variability in this behavioral sequence have been conducted on one species, *Crotalus viridis.*
7) Although more experiments in field settings are sorely needed, the limited observations to date indicate that, in comparison to captive subjects, free-ranging snakes are probably more persistent in their searching efforts and more variable in how they integrate visual, olfactory, and vomeronasal chemical cues to locate envenomated carcasses.

The body of literature on SICS is robust. By our count, 105 research papers have experimentally confirmed that some form of this behavior occurs in 70 different species (Table 2.1). Most of these are pitvipers, which is due in part to the early pioneers of this work being located in North America, but also reflects the fact that SICS is most refined in those species that rely on it as a critical step in the strike-and-release hunting strategy that ultimately allows them to kill large and well-defended prey with minimal retaliation. Despite this extensive body of work, new and surprising details of the SICS behavioral sequence continue to emerge, such as the recent work identifying specific venom components that act as "relocator proteins" and facilitate the tracking of struck prey (Saviola et al. 2013b:6).

Within Viperidae, further SICS experimentation is warranted in species outside of *Crotalus* and *Agkistrodon*. Research on species with different foraging strategies (e.g., arboreal bird specialists, semi-aquatic fish specialists) would be particularly beneficial, as these species are likely to express interesting variation in SICS. Broader phylogenetic diversity in SICS studies is also needed. For example, it would be useful to have more experimental data on Azemiopinae, the third, monogeneric subfamily contained within Viperidae, comprised of *Azemiops feae* and *A. kharini.* Although they are slender, likely semi-fossorial (and thus perhaps not inclined to ambush prey) and have been noted to strike-and-hold prey, Fea's Vipers are also apparently rodent specialists, refusing lizards and amphibians in captivity (Kardong 1986c; Mallow et al. 2003; Phelps 2010).

SICS should also continue to be examined further in elapids that envenomate and then release prey, as relatively few studies have been conducted on this family. Although the presence of SICS has been verified in *Oxyuranus* (O'Connell et al. 1985), additional testing would doubtless prove beneficial, since taipans are rodent specialists that use a strike-and-release strategy (Shine and Covacevich 1983). Although SICS has been confirmed in several elapid species, it has not been formally investigated in any new world coral snakes (*Micruroides* and *Micrurus* spp.). Coral snakes only rarely prey on rodents, and they do not voluntarily release them after striking (Greene 1984; Roze 1996), perhaps rendering them an unlikely candidate for SICS behavior. However, coral snakes use chemoreception in their active search for prey, they can also detect and follow prey trails via tongue-flicking (Greene 1984; Roze 1996), and they might employ SICS following the involuntary release of prey. In support of this notion, Greene (1984) noted two observations of Eastern Coral Snakes (*M. fulvius*) that seized a Five-Lined Skink (*Plestiodon fasciatus*) and then released it as the lizard began thrashing. One skink was immediately recaptured and eaten, and the other crawled away and hid under a piece of bark. This skink was subsequently relocated by the coral snake and consumed, probably via SICS.

Garter snakes are the only venomous colubrids hitherto tested for SICS, and Cooper (1992) believes that this behavior is prevalent in all species of *Thamnophis*. Considering the large number of venomous species in this family (Minton 1990; Weinstein et al. 2011), it seems highly plausible that additional species are capable of some form of SICS-like behavior. Further testing in additional colubrid species should be conducted.

Additional SICS experiments on venomous lizards and other squamates would be beneficial for establishing a broader evolutionary context for this behavior. The heightened chemosensory abilities of anguiomorphs are well documented, and the comparative dearth of SICS studies outside Viperidae makes other anguiomorphs particularly enticing for further experimentation.

Finally, as noted above, more experimental work on SICS should be undertaken using free-ranging snakes, snakes housed in semi-natural enclosures, or snakes striking prey species other than mice. SICS has been observed repeatedly in free-ranging individuals (summarized in Clark 2016), but Goode et al. (1990) remains the only experimental manipulation carried out in a field setting to study SICS. The available field observations show that SICS is probably even more robust under natural conditions, perhaps because free-ranging snakes are typically food-limited and more motivated to relocate a prey item following an envenomation.

The lack of field studies underscores another shortcoming of the SICS literature—for the most part, the prey in this predator-prey interaction has been treated as a static entity that always leaves a continuous chemical trail on a homogenous substrate. Although these factors are necessary for standardizing experimental conditions in a controlled environment, they are not ecologically realistic. The mammalian prey consumed by free-ranging snakes have evolved many antipredator defenses towards snakes, including pursuit-deterrent signaling (Owings and Coss 2008, Barbour and Clark 2012b), harassment (Randall 1993, Whitford et al. 2017, Clark et al. 2016a), venom resistance (Biardi 2008), and active removal of fangs from their bodies during bite attempts (Whitford et al. 2019). Venom resistance and fang removal are particularly relevant for SICS, as these factors reduce venom efficacy and can greatly increase the distance prey travel post-envenomation, even to the point where snakes are unable to recover envenomated prey despite investing hours in post-strike searching. Our current understanding of SICS and viperid predatory behavior is that snakes can adjust their striking and envenomation behaviors based on prey size and species, and then make exceedingly fine-scale differentiation of prey chemical trails following the strike. Future studies could determine if factors other than species and individual identity could be assessed via chemosensory investigation following strikes, such as prey mobility or degree of incapacitation.

The early research on SICS often treated this behavioral sequence as an independent behavior from chemosensory searching. However, our view (and that of many other researchers in the field) is that SICS is simply a heightened expression of general chemosensory searching activated in a specific circumstance. SICS is clearly an integral aspect of the foraging behavior of many squamate reptiles, and thus its expression is also integral to the trophic systems and ecosystems in which these species play a role. For new investigators making initial forays into the behavioral ecology of squamates, SICS has the added benefit of being supported by an extremely robust empirical body of work, and it is our hope that this review will facilitate new investigations by providing an overview of the relevant findings to date. Every new investigation into SICS enables us to fill important gaps in knowledge, leading to a more comprehensive understanding of this remarkable behavior. It is therefore incumbent upon herpetologists to continue investigating this important and fascinating aspect of reptilian natural history.

Table 2.1: Reptile families and species (V = Venomous; NV = Nonvenomous) known to exhibit SICS or SICS-like behavior.

Taxon	Primary foraging mode	Venomous	References
Anguidae			
Barisia imbricata	Active	NV	Ballinger et al. 1992
Elgaria coerulea	Active	NV	Cooper 1995b
Colubridae			
Pantherophis guttatus	Active	NV	Cooper et al. 1989
P. obsoletus	Active	NV	Withgott 1996
Pituophis melanoleucus	Active	NV	Chiszar et al. 1980a
Thamnophis radix	Active	V	Cooper 1992a
T. sirtalis	Active	V	Cooper et al. 1989; Burghardt and Chmura 1993
Elapidae			
Acanthophis antarcticus	Ambush	V	O'Connell et al. 1985
Dendroaspis angusticeps	Active	V	Chiszar et al. 1994
Laticauda	Active	V	Radcliffe and Chiszar 1980

colubrina			
L. laticaudata	Active	V	Klemmer 1967
Naja kaouthia	Active	V	Chiszar et al. 1983b
N. naja	Active	V	O'Connell et al. 1985
N. pallida	Active	V	Chiszar et al. 1983b; Radcliffe et al. 1984; Radcliffe et al. 1986
Notechis scutatus	Active	V	O'Connell et al. 1985
Oxyuranus microlepidotus	Active	V	Shine and Covacevich 1983
O. scutellatus	Active	V	Shine and Covacevich 1983; O'Connell et al. 1985
Eublepharidae			
Eublepharis macularius	Active	NV	DePerno and Cooper 1996; Cooper et al. 1996
Gerrhosauridae			
Gerrhosaurus nigrolineatus	Active	NV	Cooper 1992b
Helodermatidae			
Heloderma suspectum	Active	V	Cooper et al. 1994; Cooper and Arnett 1995; Garrett et al. 1996
Iguanidae			
Dipsosaurus dorsalis[a]	Neither (herbivore)	NV	Cooper and Alberts 1993
Lacertidae			
Podarcis muralis	Active	NV	Cooper 1991b
Pythonidae			

Python regius	Both	NV	Cooper 1991a
Scincidae			
Plestiodon laticeps	Active	NV	Cooper 1992c
Teiidae			
Aspidoscelis sexlineatus	Active	NV	Ballinger et al. 1992
Tupinambis teguixin	Active	NV	Cooper 1993b
Varanidae			
Varanus bengalensis	Active[b]	?	Auffenberg 1984
V. exanthematicus	Active[b]	?	Cooper 1989b; Cooper 1993a
V. gouldii	Active[b]	?	Garrett et al. 1996
Viperidae			
Agkistrodon bilineatus	Both	V	Chiszar et al. 1979; Chiszar et al. 1982c
A. contortrix	Both	V	Stiles et al. 2002; Greenbaum et al. 2003; Greenbaum 2004; Greenbaum and Jorgensen 2004
A. piscivorus	Both	V	O'Connell et al. 1981b; Chiszar et al. 1982c; Chiszar et al. 1985b; Chiszar et al. 1986b; Chiszar et al. 1991b
Bitis arietans	Ambush	V	Chiszar et al. 1982c
B. gabonica	Ambush	V	Chiszar et al. 1982c
B. nasicornis	Ambush	V	O'Connell et al. 1985
Crotalus	Ambush	V	Chiszar et al. 1982c; Chiszar et al. 1991b

adamanteus			
C. atrox	Ambush	V	Chiszar et al. 1977; Chiszar et al. 1978; Duvall et al. 1978; Gillingham and Baker 1981; Chiszar et al. 1985a; Chiszar et al. 1999a; Chiszar et al. 2008; Saviola et al. 2013b
C. catalinensis	?	V	Chiszar et al. 1978
C. concolor	Ambush	V	Saviola and Mackessy 2017
C. culminatus	Ambush	V	Chiszar and Radcliffe 1976
C. durissus	Ambush	V	Chiszar et al. 1978; Duvall et al. 1978; Duvall et al. 1980; Chiszar et al. 1982c; Scudder et al. 1983; Chiszar et al. 1985a
C. enyo	Ambush	V	Chiszar and Radcliffe 1976; Chiszar et al. 1977; Chiszar et al. 1978; Duvall et al. 1978; Chiszar et al. 1980b; Chiszar et al. 1982c
C. horridus	Ambush	V	Chiszar et al. 1982c; Chiszar et al. 1985a; Clark 2006a; Clark 2006b
C. lepidus	Ambush	V	Chiszar et al. 1977; Chiszar et al. 1978; Duvall et al. 1978; Chiszar et al. 1983a; Chiszar et al. 1986a
C. lutosus	Ambush	V	Diller 1990; Chiszar et al. 1991b
C. mitchellii	Ambush	V	Duvall et al. 1978
C. molossus	Ambush	V	Chiszar et al. 1978; Chiszar et al. 1982c
C. oreganus	Ambush	V	Kardong 1986a; Robinson and Kardong 1991; Lavín-Murcio et al. 1993; Lavín-Murcio and Kardong 1995; Haverly and Kardong 1996; Busch et al. 1996; Chiszar et al. 1999c; Smith et al. 2000; Parker and Kardong 2005; Smith and Kardong 2005; Smith et al. 2005; Parker and

			Kardong 2006; Parker et al. 2008; Putman et al. 2016; Parker and Kardong 2017
C. polystictus	Ambush	V	Chiszar et al. 1977; Chiszar et al. 1978
C. pricei	Ambush	V	Duvall et al. 1978; Chiszar et al. 1982c; Cruz et al. 1987
C. pyrrhus	Ambush	V	Chiszar et al. 1991b
C. scutulatus	Ambush	V	Chiszar et al. 1982c
C. triseriatus	Ambush	V	Duvall et al. 1978; Chiszar et al. 1982c; Chiszar et al. 1983a
C. unicolor	Ambush	V	O'Connell et al. 1982b; Chiszar et al. 1985a; Goode et al. 1990
C. vegrandis	Ambush	V	Chiszar and Radcliffe 1976; Chiszar et al. 1977; Chiszar et al. 1978; O'Connell et al. 1982b; Chiszar et al. 1985a
C. viridis	Ambush	V	Chiszar et al. 1978; Duvall et al. 1978; Duvall et al. 1980; Chiszar et al. 1981c; O'Connell et al. 1981a; Chiszar et al. 1982a; Chiszar et al. 1982b; Chiszar et al. 1982c; Golan et al. 1982; O'Connell et al. 1982a; O'Connell et al. 1982c; Chiszar et al. 1983c; O'Connell et al. 1983; Scudder et al. 1983; Chiszar et al. 1986a; Radcliffe et al. 1986; Cruz et al. 1987; Lee et al. 1988; Melcer and Chiszar 1989a; Melcer and Chiszar 1989b; Duvall and Chiszar 1990; Chiszar et al. 1990; Hayes and Duvall 1991; Chiszar et al. 1991a; Chiszar et al. 1991c; Furry et al. 1991; Hayes 1993; Chiszar et al. 1993; Chiszar et al. 2008
C. willardi	Ambush	V	Chiszar et al. 1977; Chiszar et al. 1978; Duvall et al. 1978
Daboia russelii	Both	V	Carr et al. 1982; O'Connell et al. 1982b; Chiszar et al.

			1983d
Eristicophis macmahoni	Ambush	V	Chiszar et al. 1982c
Lachesis muta	Ambush	V	Chiszar et al. 1989, Boyer et al. 1995
Montivipera latifii	Data deficient; likely ambush	V	Chiszar et al. 1982c
M. raddei	Data deficient; likely ambush	V	Chiszar et al. 1982c
M. wagneri	Data deficient; likely ambush	V	Chiszar et al. 1999b
M. xanthina	Data deficient; likely ambush	V	Chiszar et al. 1982c
Protobothrops flavoviridis	Ambush	V	Waters et al. 1996
Sistrurus catenatus	Ambush	V	Chiszar et al. 1978; Duvall et al. 1978
Vipera ammodytes	Ambush	V	Chiszar et al. 1982c
V. aspis	Ambush	V	Baumann 1927; Baumann 1928; Naulleau 1964
V. berus	Ambush	V	Wiedemann 1932
V. kaznakovi	Ambush	V	Chiszar et al. 1999b

[a] SICS might occur.

[b] Varanids are primarily active foragers, but can employ multiple foraging strategies (Losos and Greene 1988; De Lisle 1996; Pianka and King 2004).

2.7.5.12 Acknowledgments

Honor and respect compel us to pay tribute to the pioneers of SICS research, the investigators whose early contributions helped shape and define what is currently known about this behavior. This review, along with other contemporary works about SICS, would not be possible without the extensive and impressive collective body of work of D. Chiszar, K. Kardong, and W. Cooper. We thank E. Greenbaum for his thoughtful and helpful feedback on the first draft, and we thank V. Clark for her editorial suggestions on a more finalized draft. We are very grateful to N. Kordbacheh for her wonderful artwork depicted in Figure 2.1. We also thank W. Hayes and an anonymous reviewer for detailed and thorough comments and suggestions that greatly improved this manuscript.

Chapter 3: Kleptoparasitism and scavenging behavior in rattlesnakes

3.1 Abstract

Most viperids are ambush predators that primarily use venom to subdue prey, using a strike-release-trail hunting strategy whereby snakes use the unique scent of envenomated prey to locate carcasses they have bitten and released. In addition to killing prey, rattlesnakes (like most carnivores) will also opportunistically scavenge carrion. This scavenging strategy likely includes the occasional consumption of carcasses killed by other snakes (i.e., kleptoparisitism). In areas with high densities of other pitvipers, utilizing the unique scent of animals envenomated by other snakes might be a viable alternative foraging strategy. I evaluated this possibility experimentally using a series of captive behavioral experiments on prairie rattlesnakes (*Crotalus viridis*) to determine whether conspecific or heterospecific (*C. scutulatus*, *C. ornatus*) envenomation cues might increase the likelihood of kleptoparasitism. Rattlesnakes did not prefer envenomated prey over nonenvenomated prey, nor did they prefer venom cues of one species over another. Although they did frequently scavenge carcasses, in the absence of striking, snakes generally located carcasses using random searching movements instead of scent trails. Additionally, the amount of time rattlesnakes spent investigating carcass trails did not differ significantly among treatments, suggesting that striking, and the resultant formation of a chemical search image of prey, is more crucial to trailing behavior than venom cues. Moreover, a high degree of behavioral variation among individuals was observed, suggesting that scavenging and kleptoparasitism in rattlesnakes is more complex than previously realized, making generalizations about this behavior challenging.

3.2 Introduction

Most carnivores are also opportunistic scavengers (Britton and Morton 1994; DeVault et al. 2003). This is likely because predators that are already adapted to consume the dead carcasses of their prey will readily do so, when given the opportunity, even if they did not kill the animal they are consuming. Some species go beyond opportunistic scavenging, and specialize on consuming animals killed by others, either through actively chasing away the predators that made the kill, or scavenging carcasses that have been abandoned (or not yet discovered) (Wilmers et al. 2003; Trinkel and Kastberger 2005; Allen et al. 2015). Predators that regularly consume prey killed by others are known as kleptoparasites, a form of parasitism that involves the stealing of food resources from other individuals (Brockmann and Barnard 1979; Gorman et al. 1998). Kleptoparasitism has been documented as an opportunistic, but important, foraging strategy in a wide range of species (reviewed in Iyengar, 2008: table 1).

All snakes are obligate carnivores, and most viperid snakes are reliant on their venom for killing prey (Klauber 1982). By combining a cryptic ambush attack strategy with a rapid envenomating strike, these predators can consume relatively large and active vertebrates—rodents, lizards, fish, rabbits, and other small vertebrates are common in the diets of large viperid snakes (Campbell and Lamar 2004; Ernst and Ernst 2012). Although the majority of these prey seem to be killed via ambush-hunting behavior, vipers also use alternate foraging strategies, including scavenging, nest-raiding, and active searching (Funderburg 1968; Patten and Banta 1980; Lillywhite 1982; Dornburg and Weaver 2009; Platt and Rainwater 2011; Groen et al. 2020). Indeed, in some populations, scavenging or alternative feeding tactics are the dominant method of obtaining food (Lillywhite et al. 2002, 2008; Lillywhite and McCleary 2008).

However, a long history of behavioral analyses on the process by which ambush-hunting vipers obtain prey through their strike-and-release hunting strategy indicates that striking and injecting venom is an important, often necessary, step in triggering the active search for prey carcasses (reviewed in Teshera and Clark, in press). David Chiszar and others (Chiszar et al.

1977, 1978, 1982a; Stiles et al. 2002) found repeatedly in different experiments with captive rattlesnakes that most individuals would not respond to chemical cues from potential prey with searching behavior unless they had first struck and envenomated something. Thus, although viperids can (and do) scavenge carcasses they have not killed themselves, it is still unclear if scavenging is an important mechanism of obtaining food for most species, or a relatively rare occurrence.

Because their normal hunting strategy involves locating and swallowing a carcass, perhaps incidentally encountered carcasses are also readily consumed by vipers. Several other authors have also noted the potentially overlooked importance of scavenging (Gillingham and Baker 1981; DeVault and Krochmal 2002) and also pointed out that the strike-and-release strategy employed by most ambush-hunting viperids might predispose them to scavenging. Although it is clear that viperids can scavenge, more systematic studies are needed to examine how important this mode of foraging might be, and under what conditions it is employed.

Other aspects of the life history of viperids indicate that kleptoparasitism is a potentially viable foraging strategy for this group. Because viperids are low-energy specialists, a given prey resource base can support populations that reach much higher densities than most predators of vertebrates. Some island populations can reach 160 (Martins et al. 2019) to 200 (Shine et al. 2002) vipers per hectare. High densities of ambush-hunting snakes that strike and release prey could lead to the frequent occurrence of a snake exposed to the chemical trail left by the envenomated prey of a different individual, creating an opportunity for kleptoparisitism.

Although viperid snakes are known to scavenge, to my knowledge, despite the clear potential for kleptoparasitism using envenomation cues, no previous studies have investigated the possibility that doing so is an important foraging technique for viperid snakes. The kleptoparasitism hypothesis makes testable predictions with respect to how snakes will respond to scent trails from different carcasses. If kleptoparasitism via conspecific envenomation is an important foraging strategy, snakes should be more responsive to scent trails from carcasses that have been envenomated by other snakes than to scent trails from carcasses that have not been envenomated. Previous studies have documented that striking and envenomating prey releases heightened chemosensory searching compared to conditions when rattlesnakes have not struck prey (Chiszar and Scudder 1980; Chiszar et al. 1982b; Melcer and Chiszar 1989; Lavín-Murcio et al. 1993; Smith et al. 2000). However, such studies have not compared the behaviors of snakes responding to envenomated and non-envenomed carcass trails in a context conducive to testing the kleptoparasitism hypothesis, such as allowing snakes to respond over a more prolonged time period in a large testing arena. I sought to address this gap in knowledge by experimentally evaluating the responses of a wide-ranging rattlesnake species (*Crotalus viridis*) to scent trails from carcasses envenomated by a conspecific. Further, in order to evaluate the role of species-specificity, I also included treatments where prey items were envenomated by congeners with different venom types.

3.3 Methods

All snakes were long-term captives housed at The University of Texas at El Paso (UTEP), maintained at 24–27° C with a 12:12 L:D cycle. I examined the behavioral response of 20 *C.viridis*, and also used 8 *C. scutulatus* and 5 *C. ornatus* when experimentally envenomating mice. One *C. viridis* was collected from Nebraska, whereas all other snakes were collected from western Texas and southern New Mexico. Snakes were housed individually in either custom plastic enclosures with plexiglass windows (66.7 cm x 24.8 cm x 24.8 cm) or 50 qt clear plastic tubs (67.8 cm x 40.1 cm x 27.4 cm), all containing newspaper for substrate. Each snake was fed a mouse once per month, and had access to water ad libitum.

All *C. viridis* were subject to four treatments (n = 80 total trials), each of which exposed the snake to scent trails from a different type of freshly killed mouse carcass (*Mus musculus*). In Treatment 1 (V), mice were envenomated by a conspecific (*C. viridis*). In Treatment 2 (S), mice were envenomated by a closely related heterospecific (*C. scutulatus*). In Treatment 3 (O), mice were envenomated by a more distantly related heterospecific (*C. ornatus*). In Treatment 4 (C), as a control, mice were euthanized (no envenomation) via cervical dislocation.

Two snakes were involved in each experiment, a test subject (*C. viridis*), and a striking snake used to envenomate test mice (either *C. viridis, C. ornatus,* or *C. scutulatus*). Testing took place in a 1.4 m x 1.7 m x 1.2 m plywood observation arena, lined with clean butcher paper for each trial. The arena was also cleaned with a chemical deodorizer in between trials (Chemspec Kill Odor, Burlington, WA) to eliminate any residual chemical cues.

I ran all experiments at the same time of day to help standardize trials. At 17:00 h (1 hour prior to the onset of scotophase), test snakes were placed inside the arena, underneath a bucket in one of two randomly selected (SW or SE) corners and left in place for a one-hour acclimation period. A plastic bin, for placement of the forthcoming mouse carcass, was also placed against the center of the N wall at this time, with the bin opening facing the wall. At ~17:45 h a set of four cameras (Amcrest 3-megapixel 8ch network POE video security system (NVR kit), Houston, TX) began recording snake behaviors during experiments. At ~17:50 h, a mouse was offered to the striking snake via tongs, inside its own enclosure.

After the mouse was envenomated, it was euthanized via cervical dislocation if still alive after 5 s. After the envenomation process, a scent trail was made by dragging the mouse carcass along the arena floor, following techniques used in similar studies (Lavín-Murcio et al. 1993; Lavín-Murcio and Kardong 1995; Smith et al. 2000, 2005). This trail started 30 cm in front of the inverted bucket housing the test subject, extended straight out, and then curved around the distal side of the bin, then into the bin, ending with the carcass being placed inside the bin so it was not visible to the test subject. During the envenomation/carcass trail process, concealment underneath the bucket ensured that the test subject was isolated from obvious visual, thermal, and olfactory cues.

Each experimental trial began at 18:00 h, at which time the timed lights in the room turned off (i.e., the onset of scotophase). The bucket concealing the test snake was then lifted and the experimenter vacated the room to allow the camera system to record the snake behavior while it was undisturbed. I used the video recordings to quantify time to latency of contact with the carcass and time to begin consumption, to the nearest second. I also recorded the total time spent chemosensory searching (tongue-flicking) in the arena, and the proportion of that searching time that was spent investigating the carcass trails. To quantify this, I approximated 10 cm away from the carcass trail on either side, and when the test snake’s tongue began chemosensory searching inside of this area without leaving it for 3 s, I noted a shift in behavioral state from general chemosensory searching to trail following. When the test snake’s tongue was outside the 20 cm trail area for longer than 3 s, I recorded a shift from trail following back to general chemosensory searching. However, I was only able to record chemosensory searching when snakes were away from darkened corners and walls of the arena—thus time spent wall-following or resting in corners was counted as a separate behavioral state. I used the point at which snakes moved their heads past the edges of the bin as the time of carcass encounter, as the carcass was then in direct proximity to the snake.

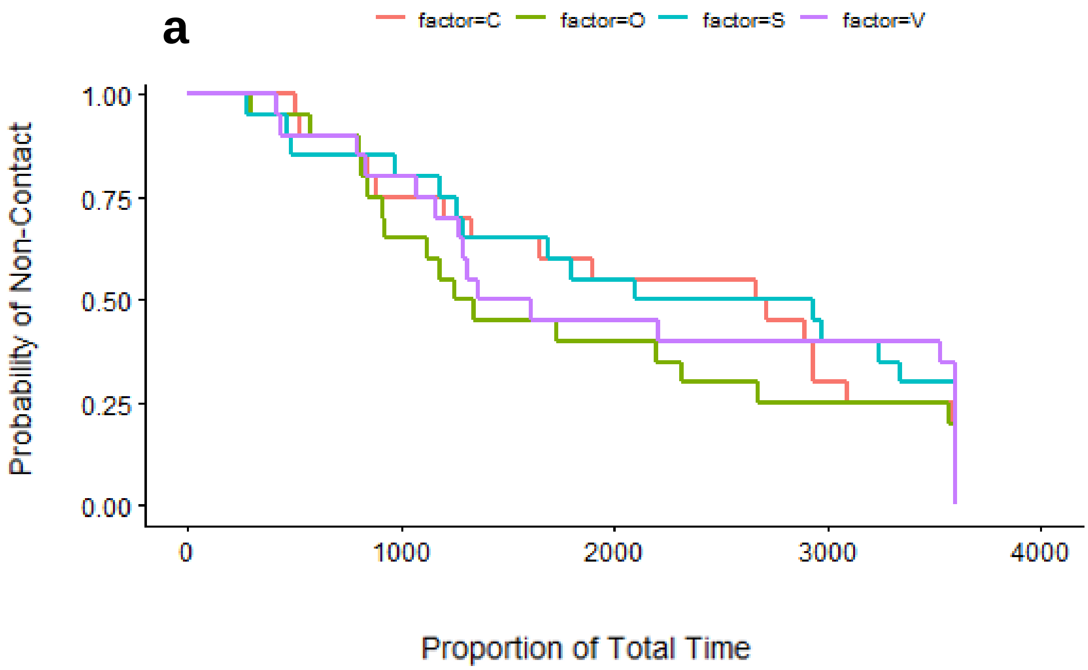
After the test snake ingested the carcass, it was returned to its cage. If the snake did not ingest the mouse within 60 min, the trial was terminated, with both the carcass and the snake returned to the latter's enclosure. An exception to this occurred if a snake made initial contact with the carcass very near the end of, but still within the 60 min time limit, and then began to consume it, thus exceeding the time limit. In such cases, the snake was allowed to consume the carcass, since the initial contact was made within 60 min. Snakes were fed inclusive of experimental feedings during trials every 34 ± 2 days. The experimental order in which each test snake was chosen, the treatment it received, and which snake struck the carcass, were all determined by random selection.

I used Kaplan-Meier survival analysis to compare time to carcass location and consumption across treatments. The results of the estimated survival function were interpreted to compare the risk of each snake making contact with and consuming the carcasses at particular time points. Marginal and conditional measures of the variance components for the fixed (treatment) and random (snake ID) are reported as pseudo-R^2 measures. This quantifies the relative contributions of the treatment and snake variability to the overall differences in response. Assessment of the time to both contact and consume carcasses was performed using Cox Proportional Hazards models with a random effect controlling for snake heterogeneity. Comparisons at individual time points indicated when treatment groups differed. These comparisons were controlled for multiplicity using a Tukey error rate adjustment. Statistical analyses were performed using R statistical software (R Core Team 2020), version 3.4.1.

I also tested whether there were significant differences among treatments in both general chemosensory searching and time spent investigating carcass trails. Mixed effect models were employed to assess the effect of treatment on the time spent searching or investigating while controlling for the heterogeneity contributed by individual rattlesnakes (i.e., rattlesnake disposition). The responses were log-transformed for both outcomes due to the skewed right tail. These were an appropriate mode of analysis since the random effect partitioned the random error into two parts, one that is snake-specific and another that accumulates other sources of error. Furthermore, the right-skewed response of time required a transformation to stabilize the variance and make data close to normal. All analyses were performed in R (R Core Team 2020) and made use of the included lme4 package.

3.4 Results

I observed a high degree of behavioral variation between individuals, and even between different trials from the same individual (Table 3.1). Overall, snakes ingested carcasses in the majority of trials across all treatments; 13/20 (65%) snakes ingested the carcass in the treatment with conspecific envenomation, 10/20 (50%) in the *C. scutulatus* envenomation, and 12/20 (60%) in both the *C. ornatus* envenomation and control treatments. Survival analysis indicated there was no difference in time to contact or ingest prey between the four treatments (Figure 3.1). This non-significant difference is also reflected in the very similar latencies across treatment groups for carcass contact and consumption time (Figure 3.2).


a
factor=C
factor=O
factor=S
factor=V
Probability of Non-Contact
1.00
0.75
0.50
0.25
0.00
0
1000
2000
3000
4000
Proportion of Total Time

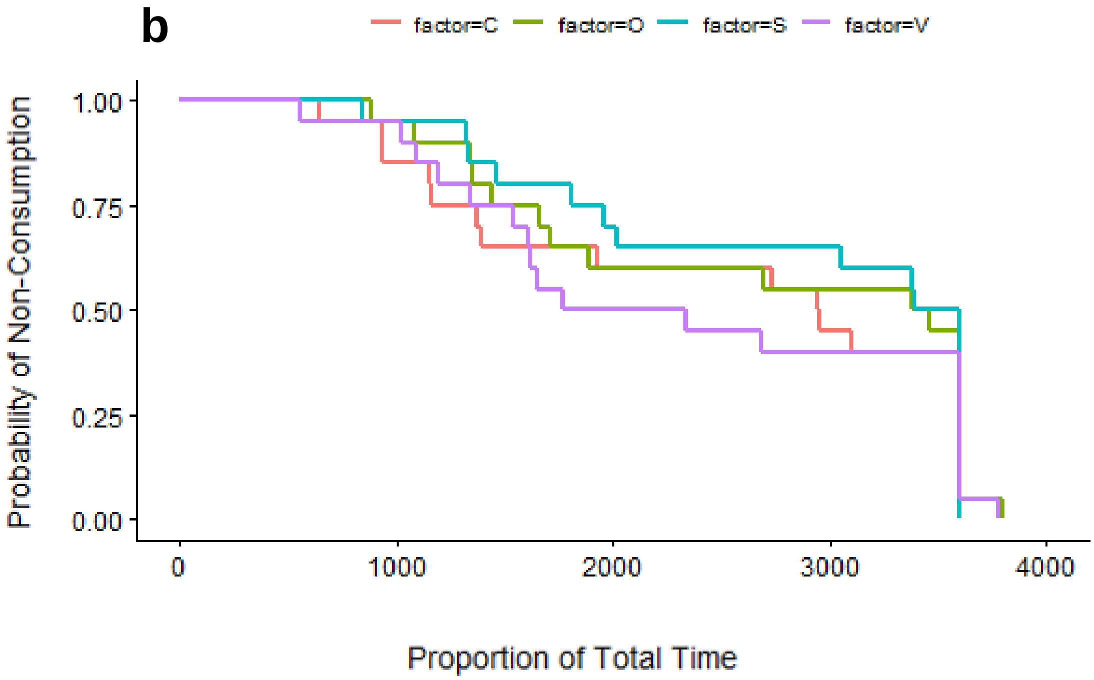
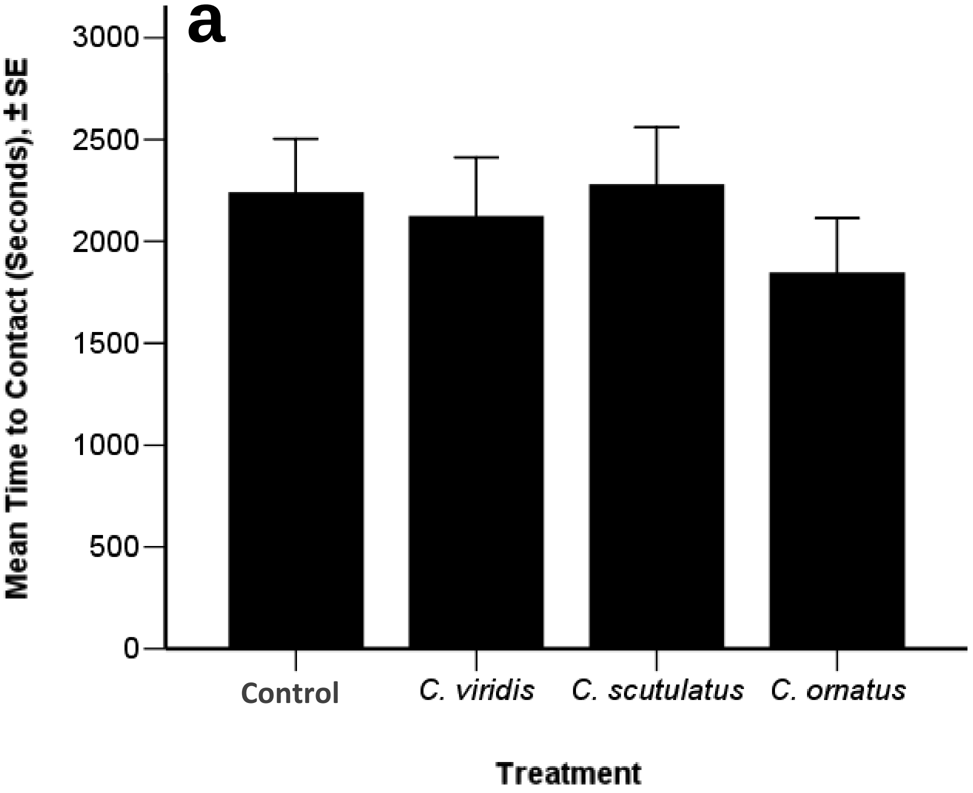

b
factor=C
factor=O
factor=S
factor=V
Probability of Non-Consumption
1.00
0.75
0.50
0.25
0.00
0
1000
2000
3000
4000
Proportion of Total Time

Figure 3.1: Survival Analysis depicting probability of contact with carcass (a) and consumption of carcass (b) over time. For the factors, C = control, O = *C. ornatus*, S = *C. scutulatus*, and V = *C. viridis*.

There were also no significant differences among treatments regarding both the amount of time rattlesnakes spent chemosensory searching and the time spent investigating carcass trails, respectively. Mean times ± SD spent chemosensory searching can be seen in Table 3.1.

The incidence of consumption of the carcass was assessed for snake-to-snake variability using a generalized mixed model with a logit link and a random effect modeling snake effects. Overall, the snake-to-snake differences account for at least 54.4% of the observed variability, whereas the effect due to the treatment only accounts for 1.8% of variation.

Similarly, for times spent both general chemosensory searching and carcass trail investigation, snake behavioral plasticity generally contributed heavily to the overall variability seen in the results. Snake heterogeneity accounted for 19% of the variation in the responses observed for the time spent general chemosensory searching. Snake heterogeneity accounted for 22% of the variation in the responses observed for the time spent investigating carcass trails. The models indicated an effect due to the treatment once snake variation is controlled, indicating the presence of differences in response.


a
Mean Time to Contact (Seconds), ± SE
3000
2500
2000
1500
1000
500
0
Control
C. viridis
C. scutulatus
C. ornatus
Treatment

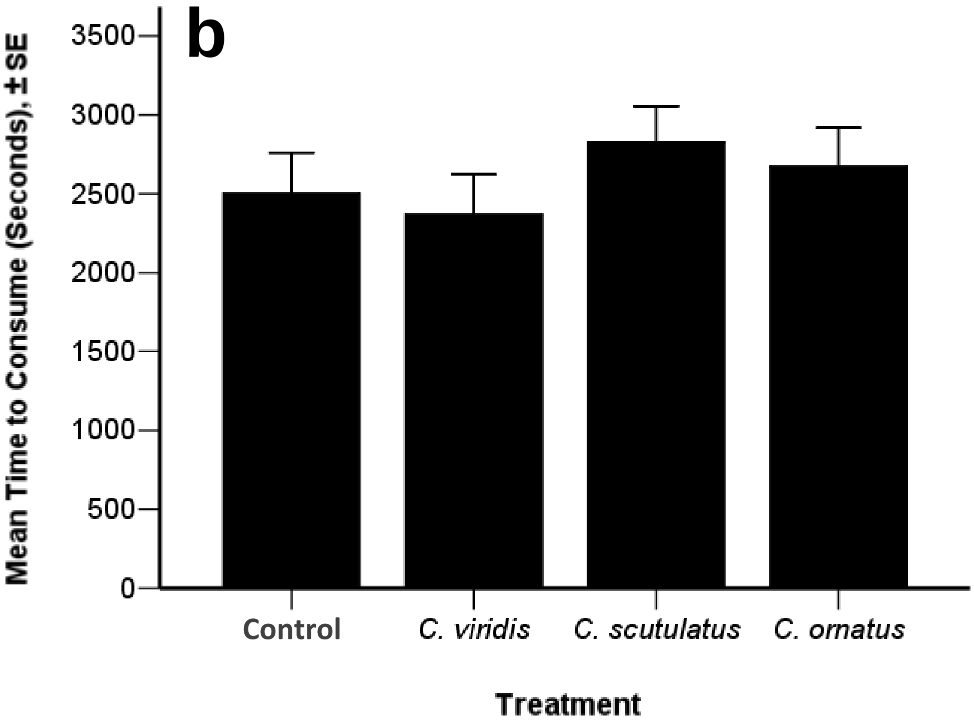

b
Mean Time to Consume (Seconds), ± SE
3500
3000
2500
2000
1500
1000
500
0
Control
C. viridis
C. scutulatus
C. ornatus
Treatment

Figure 3.2: Mean ± SE time for rattlesnake to contact (a) and consume (b) mouse carcass.

Table 3.1: Mean ± SD seconds spent chemosensory searching inside the arena, and time spent investigating carcass trails. Shaded cells indicate trials in which the mouse carcass was consumed. For Snake ID, MV = male *viridis*; FV = female *viridis*.

Snake ID	**Time Spent Investigating Carcass Trail**				**Time Spent Chemosensory Searching**			
	Treatment							
	V	S	O	C	V	S	O	C
MV-1	0.00	0.00	0.00	0.00	0.00	713.5	607.72	0.00
MV-2	0.00	87.28	146.59	0.00	8.12	306.47	594.46	0.00
MV-3	0.00	0.00	58.03	0.00	0.00	252.81	201.16	176.86
MV-4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MV-5	0.00	1510.43	279.78	165.02	6.03	1629.31	412.64	251.78
MV-6	794.57	0.00	385.09	0.00	1516.65	0.00	439.54	0.00
MV-7	0.00	0.00	14.09	154.58	0.00	50.15	24.66	371.23
MV-9	34.07	59.62	74.18	20.15	260.34	246.57	493.53	97.29
MV-10	292.68	149.76	0.00	0.00	319.94	296.51	0.00	97.19
MV-11	208.05	436.93	134.98	0.00	474.22	551.5	232.61	0.00
MV-13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MV-14	0.00	0.00	0.00	202.75	5.53	107.09	21.28	310.41
MV-15	0.00	0.00	72.31	70.98	0.00	0.00	163.0	383.2
FV-2	0.00	0.00	0.00	0.00	24.56	79.24	53.21	0.00
FV-3	230.13	262.15	0.00	196.5	611.25	440.75	0.00	377.83
FV-4	0.00	0.00	203.76	0.00	0.00	0.00	339.63	0.00
FV-5	5.94	67.34	101.79	151.08	25.66	158.41	317.49	451.09
FV-7	0.00	0.00	0.00	0.00	0.00	0.00	26.87	0.00
FV-8	82.88	0.00	0.00	0.00	318.64	59.37	15.34	9.44
FV-9	19.74	41.9	25.16	78.08	41.78	693.79	377.74	241.5
Total	1668.06	2615.41	1495.76	1039.14	3612.72	5585.47	4320.88	2767.82
Mean	83.4	130.77	74.79	51.96	180.64	279.27	216.04	138.39
SD	189.54	343.27	107.9	76.51	364.26	393.3	215.34	164.83

3.5 Discussion

My results do not provide support for a major role of envenomation by conspecifics in locating and ingesting carcasses opportunistically (kleptoparasitism). Although there was substantial inter-individual variation, there were no behavioral patterns that were different between the four treatments. However, most snakes scavenged carcasses: 7 of the 20 individuals scavenged carcasses in all 4 treatments, 3 never scavenged, and the other 10 scavenged carcasses during some of the treatments (but not in any pattern with respect to envenomation status). Because the large majority (17/20) of the snakes scavenged carcasses in at least some treatments, my general conclusion is that rattlesnakes will opportunistically consume carcasses they did not kill, but, despite the fact that they are very good at identifying and following prey chemical cues after striking prey themselves, they do not seem to use those envenomation cues as a mechanism to facilitate kleptoparasitism.

However, a few individuals in the experiment exhibited clear trail following, wherein they moved consistently along the scent trail left by the dragged carcass while tongue-flicking. This behavior seemed random with respect to whether the carcass was envenomated or not. Although these results reinforce the finding repeatedly documented in the SICS literature that heightened attraction to envenomated mice only occurs consistently for individuals that have very recently struck and envenomated a prey item (Chiszar and Scudder 1980; Melcer and Chiszar 1989; Smith et al. 2000; Stiles et al. 2002), they also indicate that chemosensory prey searching and trailing can occur in the absence of striking, probably as an extension of a general chemosensory awareness of the environment maintained by snakes. Although not quantified, when snakes were observed in the middle of the arena (away from the walls and corners) they maintained a near-constant rate of tongue flicking. Even snakes hiding in ambush regularly exhibit "chemosensory probing," wherein they occasionally extend the head and upper body outside the coil in various directions while tongue-flicking (Barbour and Clark 2012:481).

Outside of striking prey, the other main factor that seems to be involved in heightened chemosensory searching for prey is hunger. Chiszar et al. (1981) found that food-deprived rattlesnakes exhibit higher rates of tongue-flicking in response to prey chemical cues, and postulated that this hunger-induced response is what leads to scavenging behavior in rattlesnakes. Similarly, Hayes and Hayes (1993) also demonstrated that rattlesnakes become more responsive to prey stimuli, especially chemical cues, with increased food deprivation (Hayes and Hayes 1993). Duvall et al. (1978) and Golan et al. (1982) found that nonstarved rattlesnakes are unlikely to trail and consume prey.

Hunger is also a plausible explanation for the differences found in this study compared to Gillingham and Baker (1981), who found that captive *C. atrox* would ignore freshly killed carcasses, but would actively seek out and ingest euthanized carcasses of various stages of putrefaction. The snakes used by Gillingham and Baker (1981) were not food-deprived, and were put through their experimental trials one week apart, whereas the snakes in the current study were deprived of food for four weeks prior to testing. The fact that my snakes did not prefer envenomated carcasses over nonenvenomated carcasses indicates that putrescence and hunger, rather than venom, are the driving factors in rattlesnake scavenging behavior.

Thus, my conclusion from this study is that kleptoparasitism might be an uncommon event in the wild, although in at least one species (*Crotalus atrox*) the more a carcass putrefies the greater the odds it might occur (Gillingham and Baker 1981). If putrid odors emanating from decaying carcasses reach the snake, this likely represents a very different chemical stimulus than venom or integumentary cues, and the snake likely associates such odors with flesh that is already in the process of decomposing. Perhaps putrescent odors indicate to the snake that an easily digestible meal within a relatively close proximity can be obtained with minimal risk and effort.

Diller (1990) observed a *C. lutosus* performing SICS for several days, before successfully locating and consuming a mountain cottontail (*Sylvilagus nuttallii*), leading to the inference that rattlesnake scavenging episodes are actually successful conclusions of prolonged searches in which struck prey are finally relocated. Whether this is frequently the case or not is unknown, but kleptoparasitism events are more frequent in areas with high predator densities, lengthy handling times, and/or low prey densities (Ruxton and Moody 1997; Whiting and Greeff 1997; Triplet et al. 1999; Cooper Jr. and Pérez-Mellado 2003). Therefore, in areas with high densities of rattlesnakes or low densities of rodents, kleptoparasitism via chemical cues associated with putrefaction could still be a viable foraging strategy. Although I did not find evidence for a specialized kleptoparasitic foraging strategy in rattlesnakes, this study has some important limitations to consider. I conducted experiments with just one species (*Crotalus viridis*) in a captive context. It is possible that kleptoparasitism via strike-induced chemical cues occurs more readily in free-ranging snakes, or in other viperid species that are more attuned to scavenging opportunities.

Chapter 4: Responses of prairie voles to different snake scents, and the possibility of chemical crypsis in rattlesnakes

4.1 Abstract

Most rattlesnake species are small mammal specialists, mostly preying upon rodents. Many rodent species have evolved numerous anti-predator defense mechanisms, and one such defense is detection and avoidance of predators via olfactory cues. However, it is likely that ambush-foraging viperids are not easily detected via chemoreception because of their cryptic habits, and there is evidence that at least one viperid species might be chemically cryptic compared to other snakes. However, it is currently unknown how widespread chemical crypsis might be as a hunting adaptation in viperid snakes, and a wider array of species needs to be tested to make more general taxonomic inferences. Using a series of captive behavioral experiments, I tested the ability of prairie voles (a rodent commonly consumed by both viperid and non-viperid snakes) to detect olfactory cues from two ambush-foraging viperid species and three active-foraging colubrid species. Vole behavioral responses, which were used as a proxy for stress indicators, were quantified during each treatment. The results did not reveal any significant differences in behavioral responses among treatments, rendering my hypothesis of chemical crypsis in rattlesnakes unsupported. Voles likely were able to detect the snake scents, but individual responses to the odors were highly variable. Reasons for this response variation are discussed.

4.2 Introduction

Crypsis is the ability of organisms to avoid detection by others (Endler 1978, 1981, 1988). This concealment strategy can be used by predators to hunt prey, or by prey to avoid predators (Ruxton et al. 2018). Although primarily studied in a visual context, animals can employ crypsis by a variety of means (Ruxton 2009, 2011). One such method of concealment is chemical crypsis, the ability of an organism to conceal itself from olfactory detection (Endler 1981; von Beeren et al. 2012). Suppressing scent cues, or chemical crypsis, has been investigated far less than visual or auditory crypsis, even though chemical senses are a primary sensory modality in many non-human species (Longhurst et al. 1979; Resetarits and Binckley 2013; Brooker et al. 2015; Satoi and Iwasa 2019). Ambush-hunters especially could benefit from chemical crypsis. Because they rely on an immobile ambush posture for their predatory strategy, they already are not easily heard or seen, but almost no experimental work has examined if they also are somehow able to suppress their scent.

At least one viperid, the puff adder (*Bitis arietans*), is capable of masking its own scent, and such an ability might be widespread in Viperidae (Miller et al. 2015). Known as chemical crypsis, this ability is more commonly found in insects, fish, and birds (Longhurst et al. 1979; Ruxton 2009). The puff adder is the only documented terrestrial vertebrate that is capable of chemical crypsis, and it uses this ability as an anti-predator defense as it waits for prey (Miller et al. 2015). Chemical crypsis in these vipers occurs when they lower their metabolism, which suppresses the release of odorous metabolites, rendering them chemically concealed from predators (Miller et al. 2015). However, it is unclear if puff adders lower their metabolism to become chemically cryptic, or if they do so to conserve energy, with chemical crypsis a concomitant byproduct. Chemical crypsis has only been studied in one snake species, and in one context (remaining cryptic from predators). My study attempts to expand on this by examining the potential for chemical crypsis in multiple species of snakes in a different context (remaining cryptic from prey).

Like puff adders, rattlesnakes (*Crotalus* spp.) are members of Viperidae, and share similar morphology and life history traits with puff adders. Both are large, low-energy ambush-hunters that use cryptic coloration (visual crypsis) for concealment as they wait to ambush small rodents, their preferred prey (Mallow et al. 2003; Campbell and Lamar 2004; Phelps 2010). Because of this behavioral convergence, rattlesnakes might also exhibit chemical crypsis to avoid detection by potential prey and/or predators.

I used two ambush-foraging rattlesnakes (*C. scutulatus* and *C. viridis*) and three nonvenomous active-foraging colubrids (*Arizona elegans*, *Pantherophis emoryi*, and *Pituophis catenifer*) as scent donors, and prairie voles (*Microtus ochrogaster*) as scent detectors. I used both types of foragers because some ambush-foragers exhibit lower metabolic rates than active-foragers (Ruben 1976; Secor and Diamond 1998; Lourdais et al. 2014). Therefore, by comparison, active-foragers should produce more metabolites than ambush-foragers. Prarie voles were chosen as scent detectors because they are sympatric in some parts of their distribution with all snakes used in this study, except *C. scutulatus*, and therefore should constitute natural prey items (Stalling 1990; Ernst and Ernst 2012).

Past studies of the ambush-hunting behavior of rattlesnakes indicated that they typically select sites to hide that are used by multiple potential prey items (Clark 2006b, 2016). However, rattlesnakes almost always abandon a given hunting location after envenomating prey at that site, and instead move to a new location to hunt. Clark (2016) speculated that this was because of the site becoming chemically contaminated by the very same chemosensory cues given off by envenomated prey that the snakes themselves use to locate carcasses. If these cues are obvious enough for snakes to use them, they might also be detectable by small mammals and other animals preyed upon by snakes.

In the current study, I used timed, recorded behavioral trials to compare the responses of prairie voles to scent from viperids and colubrids. I hypothesized that voles would be more likely to recognize colubrid scents than viperid scents due to the latter being chemically cryptic. I quantified vole grooming, locomotion, and jumping in response to snake scents, because these behaviors can serve as proxies for stress in voles exposed to predator odors (Perrot-Sinal et al. 2000; Borowski and Owadowska 2010; Hegab et al. 2014a; Hegab et al. 2014b). If rattlesnake olfactory cues could not be detected, it would indicate that they are chemically cryptic.

4.3 Methods

All snakes (n = 7 *C. scutulatus*; n = 10 *C. viridis*; n = 2 *A. elegans*; n = 2 *P. emoryi;* n = 2 *P. catenifer*) were collected from western Texas and southern New Mexico, and housed at the University of Texas at El Paso (UTEP). The room was maintained at 24°–27° C with a 12:12 L:D cycle, and all snakes were fed thawed mice once per month, and had free access to water. Individuals were housed in either adjoined cat litter tubs with plexiglass windows (66.7 cm x 24.8 cm x 24.8 cm) or 50 qt plastic tubs (67.8 cm x 40.1 cm x 27.4 cm), all of which contained newspaper for substrate. Voles (n = 72) were long-term captives reared in laboratory conditions at UTEP. They were previously weaned into same-sex sibling pairs and housed in polysulfonate mouse cages (19.05 cm x 29.21 cm x 12.7 cm) provisioned with pine chip bedding, and maintained under 14:10 L:D cycle. High-fiber rabbit diet was placed in cage-top feeding troughs and provided ad lib. Water was also provided ad lib in glass water bottles located on the cage tops.

All experiments were recorded using two cameras (Amcrest 3-megapixel 8ch network POE video security system (NVR kit), Houston, TX). Two voles were used per experimental trial. Approximately 24 hrs prior to each experiment, scent from two different snakes was collected by removing the substrate and all contents from the snake’s individual enclosure, and lining the bottom with clean butcher paper. After 24 hrs of the snake lying atop this paper, each one was cut and taped inside of two different chambers (41.9 cm x 33.0 cm x 31.1 cm storage containers). These chambers were covered with white construction paper on three of four sides and the lid, in order to eliminate any external stimuli that might influence the voles' behavior. After the snake-scented papers were taped into each chamber, they both were placed, back-to-back, inside of a 1.4 m x 1.7 m x 1.2 m plywood arena, with the uncovered side of each chamber facing one of two cameras (Figure 4.1). Two voles in individual cages were placed in an adjacent room ~ 1 hr before the start of each trial.

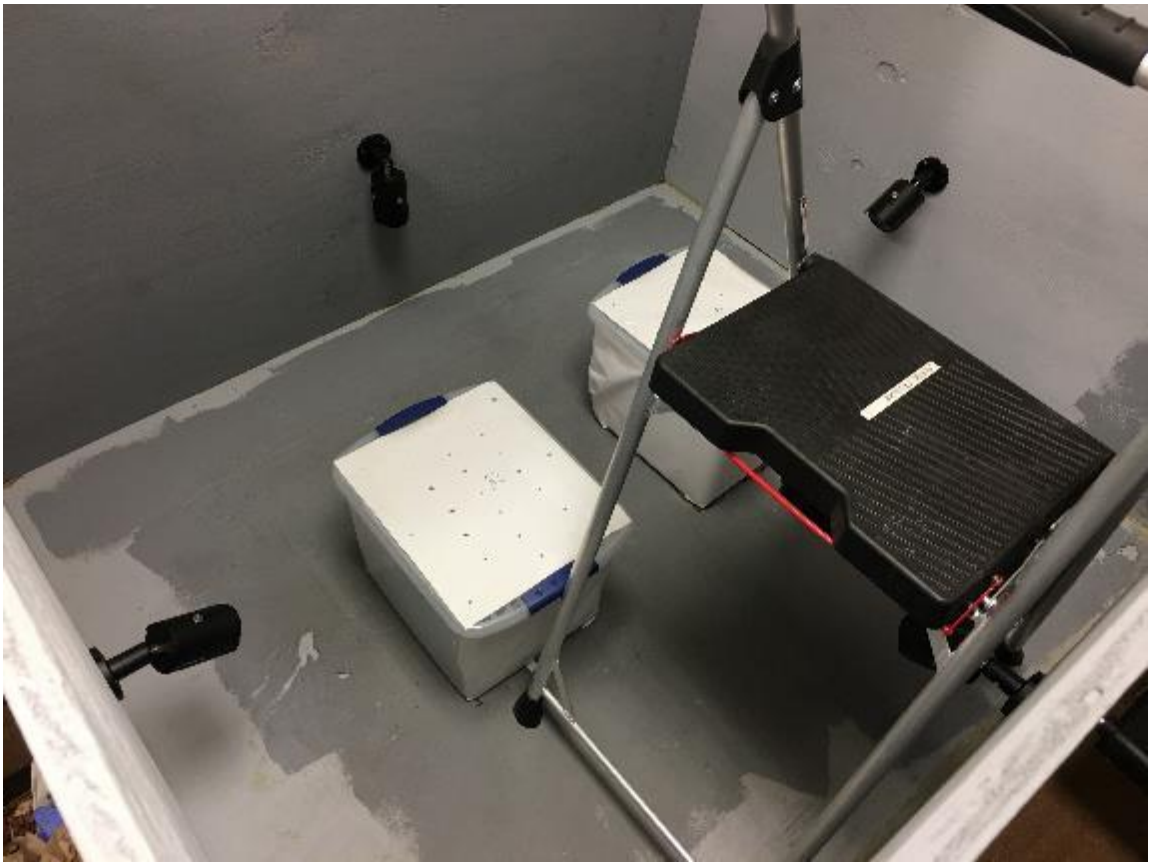


Figure 4.1: Each bin contains one vole. All sides are covered with white butcher paper to prevent possible distraction of the voles. The only uncovered opening is facing toward one of the two cameras (only the left and right cameras are operational).

After placement of the two chambers, cameras were turned on and began recording. Then, each vole was scooped into small containers and transferred to the chambers. Each vole was placed inside of a chamber, to which lids were subsequently affixed, and the researcher exited the room and closed the door. Vole behaviors were quantified for 10 min, and after each trial, voles were euthanized (the brains were preserved for use in future neurological studies). The chambers were then cleaned three times using a chemical deodorizer (Chemspec Kill Odor, Burlington, WA), to eliminate residual chemical cues. Behaviors were quantified using Behavioral Observation Research Interactive Software (BORIS) version 7.9.7 (Friard and Gamba 2016). One-way ANOVAS were used for statistical analysis, and was performed using R statistical software, version 3.4.1.

4.4 Results

I observed a high degree of behavioral variation among individual voles for all treatments (Figure 4.2). Vole behaviors were quantified as follows:

4.4.1 Grooming

Grooming time ranged from 2.1—85.9 s for *C. scutulatus* scent; 3.7—78.2 s for *C. viridis* scent; 4.0—34.2 s for *A. elegans* scent; 1.4—92.4 s for *P. emoryi* scent; 0.0—60.9 s for *P. catenifer* scent; and 1.6—75.8 s for the control. The longest grooming time was observed in response to *C. scutulatus* scent (mean ± SE; 30.7 ± 6.5) and the shortest in response to *A. elegans* scent (15.4 ± 7.8) (Table 1). The variation in the mean grooming time was not statistically significant (ANOVA, F = 0.9, p = 0.49).

4.4.2 Locomotion

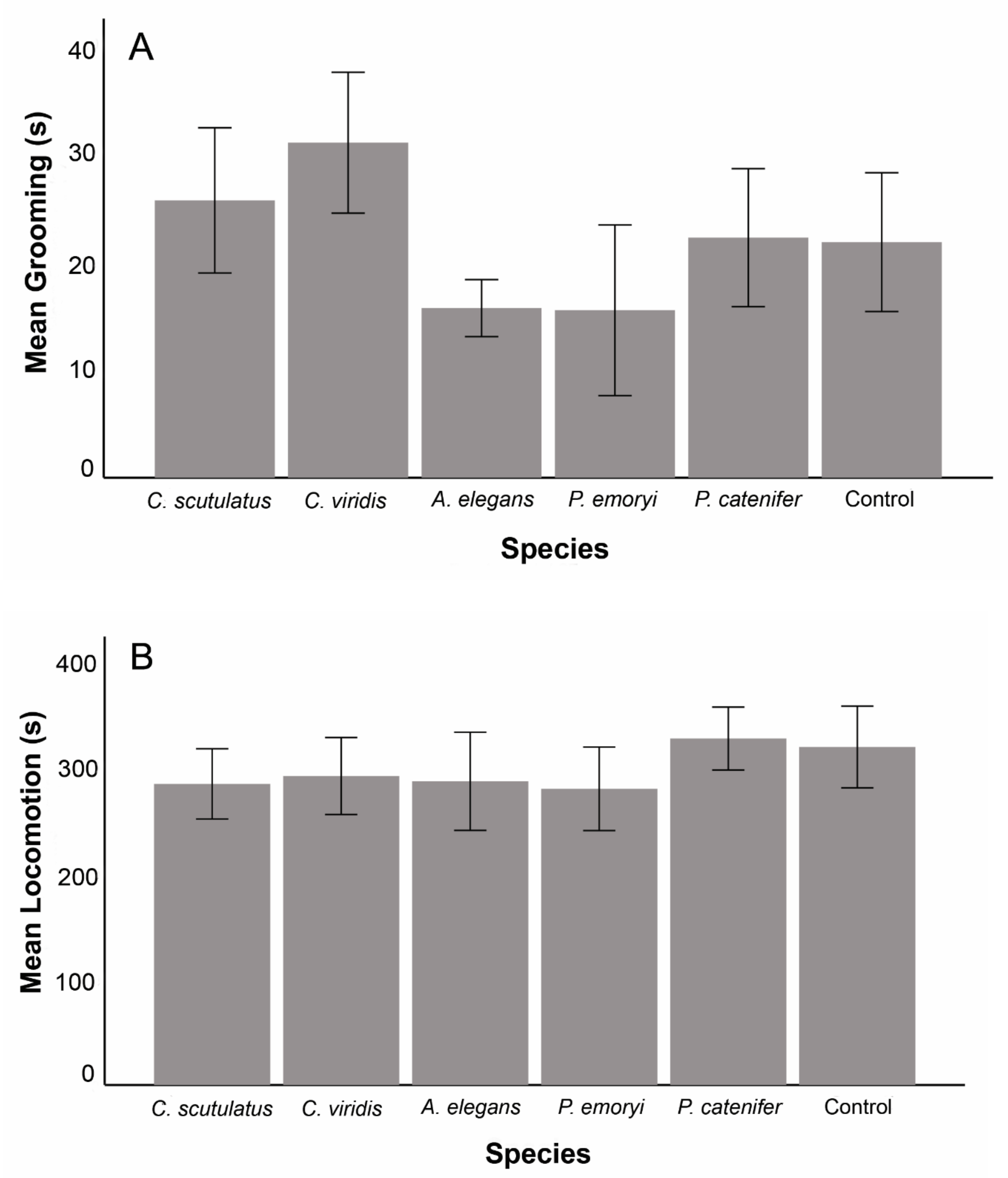
Locomotion time ranged from 72.5—497.7 s for *C. scutulatus* scent; 2.1—525.5 s for *C. viridis* scent; 143.9—547.2 s for *A. elegans* scent; 153.9—552.8 s for *P. emoryi* scent; 171.8—476.0 s for *P. catenifer* scent; and 173.9—543.7 s for the control. The longest locomotion time was recorded in response to *P. emoryi* scent (mean ± SE; 325.3 ± 29.6) and the shortest in voles exposed to *A. elegans* scent (278.1 ± 39.2) (Table 1). There was no significant difference in mean locomotion time among treatments (ANOVA, F = 0.27, p = 0.93).

4.4.3 Jumping

Jumps ranged from 0.0—58.5 for *C. scutulatus* scent; 0.0—191.8 for *C. viridis* scent; 0.0—32.5 for *A. elegans* scent; 0.0—15.0 for *P. emoryi* scent; 0.0—27.8 for *P. catenifer* scent; and 0.0—53.8 for the control. I observed the highest number of jumps in voles under the *C. scutulatus* scent treatment (mean ± SE; 18.4 ± 13.5) and the lowest in voles under the *A. elegans* scent treatment (4.8 ± 1.6). The variation in the mean number of jumps among treatments was not statistically significant (ANOVA, F = 0.53, p = 0.75).

4.5 Discussion

Voles displayed a high degree of variation when responding to the same treatment. Voles are known to exhibit such individual variation in response to predator odors (Sullivan et al. 1988), and Phelps and Young (2003:573) discussed a “surprising” level of variation in the *M. ochrogaster* forebrain structure. Response variability can depend on age and sex (Jędrzejewski and Jędrzejewska 1990; Perrot-Sinal et al. 1996; Perrot-Sinal et al. 2000; Mazza et al. 2018), but the voles in the current study were all adult males, approximately 60–100 days old. Therefore, I consider below other factors that might explain the results observed in this study.


A
Mean Grooming (s)
0
10
20
30
40
C. scutulatus
C. viridis
A. elegans
P. emoryi
P. catenifer
Control
Species
B
Mean Locomotion (s)
0
100
200
300
400
C. scutulatus
C. viridis
A. elegans
P. emoryi
P. catenifer
Control
Species

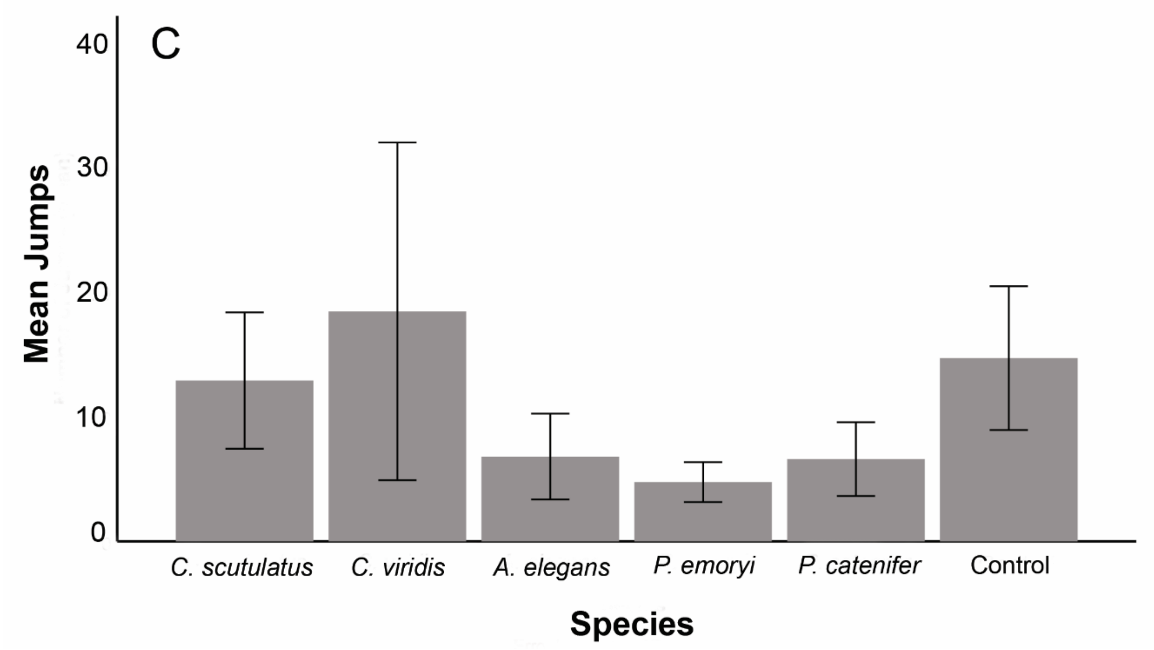


Figure 4.2: Mean ± SE grooming (A), locomotion (B), and jumps (C) displayed by prairie voles in response to different snake scents. Error bars: +/- 1 SE.

Conducting studies that attempt to measure the responses of small mammals to predator odors can be challenging. Apfelbach et al. (2005: Table 2) listed 33 published studies where the prey species (13 of which were vole species) displayed little or no response to predator odors. A universal problem in studies that assess prey fear responses to olfactory predator cues is the panoply of study designs, context, and interpretation of results (Parsons et al. 2018). Thus, deciphering my results was not an easy task.

One possibility is that voles were not as concerned with snake scents as they might have been with other predator scents. Whereas *A. elegans*, *P. emoryi*, and *P. catenifer* are all sympatric with *M. ochrogaster*, none are vole specialists (Degenhardt et al. 1996; Tennant 1998). Therefore, if *M. ochrogaster* has limited contact with these snakes, there might be little benefit in avoiding them. Or, if naïve to some degree to these odors, *M. ochrogaster* might have been uncertain how best to respond to them. Banks and Dickman (2007) discussed three levels of naiveté in prey responsiveness to novel predators. First, such predators are not perceived as a risk, and prey do not exhibit anti-predator responses as a result. Second, prey perceive predators as risks, but employ the wrong behavioral response. Third, the prey fully recognizes the predator, employs the proper anti-predatory response, but is overmatched by the predator. However, the idea that snake odors of sympatric species are novel to *M. ochrogaster* is problematic. After all, if prey fail to adapt to evolutionary predators, one might expect that the former would be at risk of extinction. Therefore, *M. ochrogaster* should be able to assess snake scents of sympatric species as threatening. Given the experimental design of the current study, assessment of these levels as they relate to voles' responses would be inappropriate, but they are still key points to consider when analyzing the results.

Although *M. ochrogaster* face predation from other snakes as well (Martin 1956; Madison 1978; Getz et al. 1990), many small predators from the family Mustelidae (e.g. weasels, stoats, mink, etc.) are vole specialists (Hanski et al. 1993; Koskela et al. 1996; Parsons and Bondrup-Nielsen 1996; Ylönen et al. 2003). Voles exhibit different behaviors in response to different predators (Jędrzejewski et al. 1993; Hegab et al. 2014b). Thus, it might be tempting to conclude that *M. ochrogaster* are perhaps more sensitive to mustelid odors than snake odors. This same idea was demonstrated in laboratory rats (*Rattus norvegicus domestica*), which displayed increased anxiety and defensive behaviors toward cat (*Felis catus*) odor, but not fox (species not given) odor (McGregor et al. 2002).

However, experiments quantifying the avoidance response of voles to mustelid odor have produced mixed results. In some experiments, voles were found to be averse to mustelid odor, whereas in others, they exhibited little-to-no response to the same odors (Kats and Dill 1998; Apfelbach et al. 2005). Numerous factors might explain these disparate results, and why they are sometimes negative; attempts at such explanations are difficult and complex (Apfelbach et al. 2005). For example, strong aversive responses by prey to predator odors should occur when the two species have co-evolved over a lengthy period of time, but prey can also exhibit aversive responses, thought to be innate, to novel predator scent (Stoddart 1980a; Apfelbach et al. 2005). An explanation for this detection might be that some prey consider different predator odors variations of one another, at least in the case of urine and fecal odors, and thus elicit an avoidance response (Stoddart 1980b; Dickman and Doncaster 1984). In other studies, prey did not respond to predator odors, regardless of whether or not the predator species used was natural or novel (Apfelbach et al. 2005). It seems that the specific pairing of predator and prey species, as well as context of odor exposure, is crucial for interpretation of results (Dickman 1992; Apfelbach et al. 2005; Bleicher et al. 2018).

Bleicher et al. (2018) cautioned that human researchers tend to misjudge the perceptual and neural responses an animal might have to an odor. The authors provide two examples of this. We might expect that prey, in the presence of predator scents, will display one or more alarm behaviors, for fear of the predator. Instead, we underestimate the idea that perhaps the prey is aware of the scent and is unconcerned, because 1) whereas there was once a predator in the vicinity, it is not there now, and the animal can continue its normal behavior as it pleases, and 2) the animal assesses risks vs. rewards of continuing to occupy a given area, choosing to exploit resources that competitors might avoid, and remaining in the area until the predator returns. The second alternative is impossible to apply to my results, since the voles were in relatively small chambers. The first alternative, however, is intriguing. Perhaps *M. ochrogaster* in the current study were well aware of, and attuned to (i.e., the odors were not novel), all or some of the snake odors; while possibly alarmed upon initial contact, they might have quickly determined that there was an absence of imminent danger. After realizing that no actual snakes were present, they did not consider the residual odors alarming, and continued to explore the chamber as they would in the absence of any odor. Thus, predator odors, at least in some cases (and using this experimental protocol), appear to be ineffectual in acting as proxies for the actual presence of predators (Blanchard et al. 2003).

Experimental protocol considerations raise the possibility is that the concentration of the snake odors was insufficiently strong enough to be detected. For example, Takahashi et al. (2005) demonstrated that rats (species not given, presumably *Rattus norvegicus domestica*) exhibited elevated fear responses when exposed to higher amounts of cat (species not given, presumably *Felis catus*) odors. In other cases, the type of predator odor, rather than the concentration, might be the effect that produces a defensive response in prey; exposure of prey to urine, feces, and skin/fur can all elicit different responses (Blanchard et al. 2003; Apfelbach et al. 2005). Therefore, as discussed above, the context of predator odor presentation to prey is crucial to the design of these experiments (Blanchard et al. 2001; Blanchard et al. 2003; Apfelbach et al. 2005; Bleicher et al. 2018; Parsons et al. 2018).

Ultimately, prey can respond to predator odors by three complementary catalysts: chemical, neurobiological, and contextual (proximity and vulnerability) (Parsons et al. 2018). This creates an incredibly complex framework of overlapping factors that determine how an odor is perceived, and how the recipient of such olfactory signals should respond. Despite this, and the difficulties in interpreting the disparate results and logic of prior studies, I posit the following most plausible explanations for the results of the current study:

1. The concentration of the snake odors was too weak to be detected by *M. ochrogaster*. Assuming voles were able to detect the scents, the following four possibilities seem most likely.
2. Voles might have been relatively unconcerned with the different snake scents, perhaps because they were somewhat novel, as *M. ochrogaster* are not primary prey of any of the species. Consequently, voles did not perceive any benefit from avoiding (and thus displaying increased defensive behavior) the scents.
3. Voles did not know the best way to respond to the snake odors within the chambers, perhaps because of difficulty in interpreting, processing, and responding to the stimuli.
4. Voles, while cognizant of some or all of the snake scents, did not feel threatened because no snakes were with them in the chamber.
5. This experiment might have been conducted in an inappropriate environmental context; perhaps under different experimental parameters (e.g., different prey species, different size/type of chamber) prey would have responded differently to the snake scents.
6. Another possibility is that being reared in captivity affected the behavior of *M. ochrogaster*. Some studies have shown that the faculties of lab-reared animals are reduced compared to their wild counterparts (Kihslinger et al. 2006; Burns et al. 2009; Feenders et al. 2011). However, the voles used in this study were only 3rd generation animals, so they might not have been as affected given this relatively short amount of time in captivity.

Since no significant differences were observed in the results of this study, I am unable to determine if rattlesnakes are capable of chemical crypsis. However, assuming snake odor concentrations were sufficient, I suggest the following two possibilities: 1) Perhaps *M. ochrogaster* detected active predator scent and did not respond as expected, for any of the reasons stated above. This possibility would explain why there was no significant difference between the active predator scent and control. Furthermore, rattlesnake scent was not detected, rendering the response to this scent by *M. ochrogaster* statistically similar to the other treatments. In this scenario, rattlesnakes are thus chemically cryptic. 2) Rattlesnake odor was detected, but as stated above, *M. ochrogaster* did not respond as expected, for the numerous possible reasons previously discussed, rendering the responses to all three treatments statistically similar. In this scenario, rattlesnakes are not chemically cryptic.

Moving forward, one primary suggestion for improvement of this experimental design is to substitute different prey species for *M. ochrogaster*. Using prey that face heavier predation pressure from both rattlesnakes and nonvenomous species should ensure that any snake scent presented to the prey should not be novel. Other considerations include modifications/substitutions to any number of factors that might facilitate an “ideal” experimental setup (i.e. size/type of chamber, type of predator odor presented, combination of predator and prey species used). Keeping such variables in mind, the single most important one to consider is context, to create the most appropriate and realistic environment possible. Using the previously mentioned framework put forth by Parsons et al. (2018) should help alleviate this perpetual problem. Perhaps the most important change that could be implemented to this or any similar study is to expose live, hidden predators, rather than predator odors, to prey. Live predators elicit an entirely different prey response than predator odors, which are too often presented in an inappropriate environmental context (Bleicher et al. 2018).

Chapter 5: Conclusion

5.1 Strike-induced chemosensory searching in reptiles

Strike-induced chemosensory searching (SICS) has a very robust experimental literature, but until now, there has never been a comprehensive review of this topic. In this manuscript, I explored and discussed key results from decades of SICS research, which has mainly been conducted on rattlesnakes. I also provided a taxonomic overview of SICS in other species, and consolidated all known papers providing experimental tests of SICS into a convenient table. SICS has traditionally been viewed as an independent behavioral phenomenon. However, the narrative of the document posits that all reptiles that tongue-flick are capable of intensified chemosensory searching, which is unlocked by some type of stimulus (visual or olfactory prey cues, pheromones from potential mates, location of abundant water sources, etc.). It can be any stimulus that causes heightened interest in a snake. In viperids, and especially rattlesnakes, that stimulus is the striking of prey, which activates urgent and focused searching movements to relocate that prey for ingestion. I organized the review topically, and provided a summary section that provides forward-looking advice for future experimental work.

5.2 Rattlesnakes as kleptoparasites

Rattlesnakes' ecological role as scavengers in the wild is poorly understood. How often might rattlesnakes scavenge carrion? Given their preference for envenomated prey, are rattlesnakes more likely to scavenge when venom cues are associated with the carcass? Using captive experiments, I attempted to elucidate these questions further. Normally, the act of striking prey releases enhanced chemosensory searching in rattlesnakes, as they endeavor to relocate the prey that was struck. As mentioned above, some reports of scavenging might actually be relocation of the struck prey item after a prolonged search, lasting up to several days, by which point the carcass will have putrefied (Diller 1990). However, other scavenging episodes involve rattlesnakes feeding on carrion that did not previously strike anything. Such rattlesnakes might locate the carrion by chance, or perhaps they are attracted by the putrescent odor. Because many scavenging events will occur without the snake having struck prey, in my experiments I did not allow the snakes to strike prey before being exposed to the carcasses. This way, rattlesnakes could have a “chance” encounter with carrion, just as they might in the wild.

These experiments highlighted how crucial the act of striking is for rattlesnakes to acquire prey. This action is what activates rattlesnakes’ proficient trailing abilities. Without striking, snakes often did not seem particularly motivated to locate carcasses, and frequently moved about the arena in a random or confused manner. These movements were very similar to those observed in Gillingham and Baker (1981). As mentioned in Chapter 3, rattlesnakes are highly attracted to prey trails that were left by envenomated prey (Chiszar et al. 1982b). Yet it seems that even the presence of venom cues is not enough to facilitate prey-acquisition without striking. Thus, the act of striking prey is more crucial than venom cues to the foraging strategy of a rattlesnake.

A wide range of behavioral responses among the snakes was also observed. Upon commencement of the experiment, some snakes would begin moving right away, whereas some would remain stationary for lengthy periods; some would move quickly to locate the carcass, some would locate it after a very circuitous route, if at all; some would consume carcasses almost immediately after first contact with it, and some would investigate it extensively, leave, and come back, repeating this pattern several times, never ingesting the carcass; some snakes investigated carcass trails, some did not; some would only move along the arena walls, some seemed intent on exploring every square inch of the arena.

This variety of behavioral responses highlights the high degree of behavioral plasticity displayed by rattlesnakes. I was around these snakes almost every day, and these temperamental differences could be observed even as they were lying in their cages, and each snake seemed to have its own “personality.” Such differences in disposition help explain the wide disparity of behavioral responses during the experiments, and these differences are undoubtedly manifested in the wild as well, which is why scavenging behavior in rattlesnakes is very difficult to generalize, as snakes are likely to have contrasting responses to scavenging episodes.

5.2 Chemical crypsis in rattlesnakes

Chemical crypsis has only been confirmed in one terrestrial vertebrate (*B. arietans*) (Miller et al. 2015), which happens to be related to the rattlesnake. Therefore, rattlesnakes seemed a logical choice as a study organism for future testing of chemical crypsis. Miller et al. (2015) speculated that chemical crypsis might be widespread among ambush-foragers, although the number of viperids that are capable of this ability is unknown. However, rattlesnakes might not be as likely candidates for chemical crypsis as *B. arietans*.

A large number of predators prey on *B. arietans* (Miller et al. 2015: table S1), with many of these locating the snakes by olfaction. In response to approaching threats, *B. arietans* employs a defensive strategy of remaining motionless, attempting to avoid detection (Miller et al. 2015). In contrast, rattlesnakes face comparatively fewer predators, and when they feel threatened, they are known to coil into a defensive posture and use their rattles to actively signal their readiness to defend themselves (Klauber 1982; Miller et al. 2015). Both of these key differences in predation pressure and defensive strategies between *Crotalus* spp. and *B. arietans* might render rattlesnakes unlikely to be chemically cryptic to predators.

Nevertheless, I attempted to test for this ability in rattlesnakes, by seeing if *M. ochrogaster* could detect different types of snake scents. Unfortunately, for the reasons described above, this experiment might have been conducted in an improper environmental context. This was not realized until after analysis of the results, which failed to show any significant differences among treatments (active-foragers vs. ambush-foragers).

There were likely many overlapping reasons to account for these results, but broadly, I believe that the following conclusions are most plausible for why *M. ochrogaster* responded as they did in this experiment: 1) The simplest explanation might be that they were simply unable to detect the snake scents. Snakes were placed atop the paper that went into the chambers for 24 hrs prior to each experiment, so I assumed that the odor concentrations would be sufficient. Assuming that *M. ochrogaster* could adequately detect the snake scents, I suggest the following four conclusions that seem the most reasonable: 2) The snake scents were, to some extent, novel to the voles, rendering a relatively unconcerned response, 3) They were unable to properly interpret, assess, and react to the scents, possibly because of confusion that arose from being in the chamber environment, 4) They were aware that no snake was present inside the chamber with them, and consequently did not perceive an immediate risk, and 5) The experimental setup was flawed, providing an improper environmental context for the voles to properly process and respond to the scents.

These conclusions are not mutually exclusive, and the framework that determines how prey perceive predator odors (Parsons et al. 2018) requires that multiple complex variables interact, resulting in numerous outcomes for any given predator-prey experiment. Furthermore, humans have a tendency to anthropomorphize, and frequently misjudge the ways in which prey interpret and respond to scent stimuli (Bleicher et al. 2018). Prey are expected to act a certain way in response to chemical cues, but for the variety of reasons discussed above, do not. Investigation into chemical crypsis still has value, and moving forward can still be attempted, with modifications in the experimental design.

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Vita

Prior to pursuing his educational goals, Mark Teshera was a paratrooper in the United States Army from 2002–2006. He was stationed in Vicenza, Italy and was deployed to Iraq in 2003 and Afghanistan in 2005. After an Honorable Discharge, he was awarded an A.A.S. from Wenatchee Valley College at Omak (Omak, WA) in 2008, a B.S. in Wildlife Ecology from Washington State University (Pullman, WA) in 2010, and a M.S. in Biology from California State University San Marcos (San Marcos, CA) in 2016. He began his Ph.D. in Ecology and Evolutionary Biology at the University of Texas at El Paso in 2016. He received teaching assistant positions every semester, instructing laboratories in Topics in the Study of Life, Organismal Biology, Ecology, Evolutionary Genetics, and Genetics. While at UTEP, he received multiple awards and scholarships, including the Texas Public Educational Grant, Dodson Research Grant, Academic and Research Excellence Departmental Award, and three Frank B. Cotton Trust Scholarships. He also received travel funding to present his research at the Biology of Pitvipers 3 Symposium (Rodeo, NM) in 2019. For professional and community service he served as a graduate student representative on a search committee for a tenure track position in the Department of Biological Sciences at UTEP (2019), and also served as a science judge at multiple science fairs in El Paso. While at UTEP he coauthored two publications and has two more in preparation.

Mark's primary research interests are the evolutionary behavior and feeding ecology of North American pitvipers. Outside of academia he enjoys reading, history (especially the Wild West) and hiking with his akita, Dolly.

This dissertation was typed by Mark Scott Teshera.