The Hunting and Feeding Behavior of Wild Rattlesnakes

Rulon W. Clark

Department of Biology
San Diego State University
San Diego, California 92182-4614, USA.

Correspondence

E-mail: rclark@mail.sdsu.edu
Website: www.bio.sdsu.edu/pub/clark/site/home.html
In this chapter my intent is to review the series of decisions that confront a wild rattlesnake when it is hunting, consuming, and digesting prey. Because these decisions are made in a natural environment they are both dynamic and complex. Specifically, I will discuss and review observations and experiments that my students and colleagues have conducted in the field over the past 10 years. Most of what we know about the hunting and feeding behavior of rattlesnakes derives from laboratory studies, and much of this research has been reviewed in depth. Field studies, on the other hand, are relatively rare, and most reports consist of only single observations and are anecdotal. While the importance of conducting research under controlled settings cannot be overstated - in fact there is no substitute for testing many types of hypotheses under laboratory or semi-captive conditions - studies in nature provide a context that is difficult, or even impossible, to replicate. Overall, both types of approaches are complementary and provide the foundation for constructing a general synthesis. It is my hope that compiling and reviewing data from field studies will be useful for spurring in-depth field and laboratory research of rattlesnake hunting and feeding behavior that is important but not well understood. Many of the behaviors I will discuss herein have been recorded on video, and these recordings do more justice to the behaviors than any verbal descriptions or still figures. Thus, I have posted these videos on the public video sharing site YouTube. The Appendix lists the URLs of all videos cited in the text.
General foraging strategy

Rattlesnakes are carnivorous hunters that seek out and kill live prey using venom. Although there are exceptions, the primary prey of most adult rattlesnakes consists of small mammals and lizards (Klauber, 1972; Beavers, 1976; Wallace and Diller, 1990; Taylor, 2001; Clark, 2002; Holycross and Mackessy, 2002; Holycross et al., 2002a; Avila-Villegas et al., 2007; Sant’Anna and Abe, 2007; Glaudas et al., 2008; LaBonte, 2008; Repp and Schuett, 2009; Dugan and Hayes, 2012). Many species also opportunistically consume birds (Cundall and Greene, 2000), while others specialize on amphibians, invertebrates, and other snakes at some point in their life cycle or throughout life (Klauber, 1972; Taylor, 2001; Schuett et al., 2002; Campbell and Lamar, 2004; Ernst and Ernst, 2012).

Predators are often divided into two types: active versus sit-and-wait (or ambush) (e.g., Huey and Pianka, 1981). Although this dichotomy has some practical utility, most researchers recognize that almost all species do both to varying degree (Perry, 1999). Rattlesnakes are a good example of why the dichotomy is useful, but should be applied with caution. Hunting rattlesnakes occasionally search their environment actively for information that will lead them to their prey, but then spend most of their time waiting patiently in ambush for their prey to come to them. Thus, because rattlesnakes spend the majority of their time sitting and waiting, they can be readily classified as sit-and-wait predators. This classification is useful shorthand when comparing different species, but it should not obscure the importance of the active search stage of their hunting behavior. In adult rattlesnakes the general hunting strategy, which appears to be conserved across many species of vipers, is to: (1) find a place to hide; (2) wait patiently for prey to come within strike distance; (3) envenomate the prey with a rapid strike and immediately release it; (4) employ chemosensory trailing to relocate the envenomated animal; (5) swallow the carcass headfirst; and (6) spend varying amounts of time dedicated to digestion. This basic sequence of events can vary across species and situations. Some aspects of this general predatory strategy have been the subject of extensive research; others are virtually unstudied.

Hunting decisions

I have organized the rattlesnake predatory strategy into a generalized “Decision Tree” illustrating how outcomes of each decision in the sequence alter what the snake might do next (Figure 1). This series of decisions is based on the thousands of hours of video my research group and I have recorded of rattlesnakes hunting in the field as well as on published laboratory experiments (e.g., Duvall et al., 1990; Chiszar et al., 1992; Cundall and Greene, 2000; Kardong and Smith, 2002; Clark, 2004a, b). I will discuss each step in the decision tree in turn, reviewing some of the recent relevant literature and highlighting gaps in our knowledge deserving of further investigation.

Searching for prey cues

Most rattlesnakes have been found to be “mobile ambushers,” sensu Greene (1992). That is, their foraging strategy consists of a mobile search phase and a sedentary ambush phase. During
the mobile search phase, the snake moves through the environment using a number of cues to assess potential ambush locations. Presumably, if chemical and visual information indicates that prey frequently use a site, and the site is also suitable for ambushing, rattlesnakes choose to settle into an ambush posture at that site; if not, they keep searching (Figure 1).

Many field studies across a number of species have documented the basic behavioral pattern of relatively short bouts of chemosensory searching followed by long periods of waiting in stereotyped ambush coils. Following the widespread use of radio-telemetry via surgical implantation pioneered by Reinert and Cundall (1982), Reinert et al. (1984) first described the short-search-long-ambush pattern in the Timber Rattlesnake (Crotalus horridus). Several subsequent field studies using radio-telemetry found similar behaviors in Timber Rattlesnakes (Clark, 2006a; Wittenberg, 2012), Northern Pacific Rattlesnakes (Crotalus oreganus) (Putman et al., 2016), and Sidewinders (Crotalus cerastes) (Clark et al., 2016). I have also observed (R. Clark, unpubl. data) the same general hunting strategy in Western Diamond-backed Rattlesnakes (Crotalus atrox), Red Diamond Rattlesnakes (Crotalus ruber), and Mohave Rattlesnakes (Crotalus scutulatus).

Due to the primacy of the chemosensory system in snake foraging, it has long been assumed that prey-derived chemical cues are one of the principal sources of information guiding the active search and assessment of potential ambush sites. Several behavioral experiments have verified this experimentally. Prairie Rattlesnakes (Crotalus viridis) adopt ambush coils near chemical cues from potential prey, both in the laboratory and in the field (Duvall et al., 1990; Theodoratus and Chiszar, 2000). Pygmy

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**Box 1. Hunting behavior in young rattlesnakes**

Most of the information we have on hunting and feeding behavior of rattlesnakes is derived from studies of adults, mainly because newborn and juveniles are difficult to study via radio-telemetry (see Clark et al., 2016 for an exception). This is likely to change in the near future as transmitter technology advances (see Beaupre, this volume, Monitoring Technologies). Juveniles of many species are known to exhibit ontogenetic shifts in feeding ecology (Taylor, 2001; Mackessy et al., 2003; Glaudas et al., 2008), and these changes are likely accompanied by similar shifts in behavior. Studies of naïve rattlesnakes raised in captivity show that young snakes have innate preferences for chemical cues from syntopic small mammals (Clark, 2004a), but these preferences can be modified by just a single feeding event (Clark, 2004b). Young rattlesnakes of a few species are known to employ at least one unique hunting adaptation: caudal luring as a means of inducing prey to come within strike range (Rabatsky and Waterman, 2005; Reiserer and Schuett, 2008; Farrell et al., 2011; see Reiserer, volume 1, Crotalus cerastes). Additional field studies may uncover other as-yet undiscovered foraging strategies employed by young snakes.
Rattlesnakes (Sistrurus miliarus) were attracted to areas treated with prey chemical cues, in both field (Roth et al., 1999) and laboratory studies (Bevelander et al., 2006). Captive Timber Rattlesnakes recognize and discriminate among chemical cues of potential prey items, favoring those from their natural prey (Clark, 2004a). Captive Southern Pacific Rattlesnakes, Crotalus helleri, adopt ambush coils toward lizard chemical cues as juveniles, and rodent chemical cues as adults (LaBonte, 2008). Captive Prairie Rattlesnakes also display higher rates of tongue flicking toward lizard chemical cues as juveniles, and shift their preference to rodent chemical cues as adults (Saviola et al., 2012); furthermore, this effect seems to be an innate development that is not dependent on body size or experience, as individuals with stunted growth exhibited responses predictive of their chronological age, not their size (Saviola et al., 2013b).

Although these direct observations of snakes in both field and laboratory settings indicate that chemical cues alone are often sufficient for evaluating ambush sites, visual cues are likely to be important in this regard as well, but data here are more limited. Chiszar et al. (1981) exposed a number of captive rattlesnakes of different species (Crotalus enyo, C. viridis, and Sistrurus catenatus) to chemical and or visual cues from live mice. Snakes only exhibited elevated tongue flicking when they could see a live mouse, and their rate of tongue flicking increased over time if both visual and chemical cues were present. Duvall et al. (1990) found that C. viridis in captivity would adopt ambush coils adjacent to chemical stimuli (soiled bedding) from mice, but their responses were much stronger if both chemical and visual stimuli (live mice residing in soiled bedding) were present. After observing C. oreganus hunt Ground Squirrels (Otospermophilus beecheyi), the general conclusion of Hennessy and Owings (1988) was that visual cues from live squirrels are likely an important component of ambush site selection.

Figure 1. Decision tree depicting the hunting process of ambush-foraging rattlesnakes.
Finally, although chemical cues derived directly from prey are certainly a critical source of information for rattlesnakes selecting ambush sites, they can possibly integrate chemical information from other sources. One intriguing possibility is that individuals not only use prey-derived chemical cues, but also pay attention to conspecific-derived chemical cues, and use this as a source of information about their environment (Clark, 2007). A variety of other vertebrate species have been shown to use information derived from conspecifics to assess their environment (reviewed in Valone, 2007; Bonnie and Earley, 2007), and small mammals can transmit food preferences through social cues (Posadas-Andrews and Roper, 1983). Garter Snakes can assess body condition of conspecifics from chemical cues in a courtship context (Shine et al., 2003). Given their exquisite sensitivity to conspecific chemical cues during mating and courtship, snakes may integrate conspecific chemical cues in assessing local prey resources as well.

**Waiting in ambush**

During the sedentary ambush phase, the snake sits in a stereo-typed ambush coil (Figure 2; also see Reinert et al., 2011). Although this waiting stage of the hunting sequence is by far the longest, it has received the least experimental attention, probably because for the majority of that time the snake remains still and nothing happens. Rattlesnakes can wait from hours to days at a given ambush site; Clark (2006a) found that Timber Rattlesnake ambush site residence times ranged from 2 to 67 hours, with a mean ± SD of 17 ± 14 hours. Furthermore, prey encounters can occur at almost any time. Most rattlesnakes are cathemeral hunters, active during both day and night, depending on the favorability of ambient temperatures. This is evidenced both by behavioral studies (Barbour and Clark, 2012a), and by the inclusion of both nocturnal and diurnal rodents in their diets (Wallace and Diller, 1990; Taylor, 2001; Clark, 2002; Glaudas et al., 2008; Dugan and Hayes, 2012).

Although other rattlesnakes I have observed in the field exhibit long site residence times (including *C. cerastes*, *C. scutulatus*, *C. ruber*, *C. atrox*, and *C. oreganus*), *C. horridus* may be somewhat unique in the length of time it can occupy a single site undisturbed. Because they are often sitting under closed canopy woodlands, Timber Rattlesnakes do not always need to retreat from unfavorable daytime temperatures. For all other species I have observed, which occupy hot, arid climates with limited canopy, a typical activity pattern is to emerge from shelter in the afternoon or evening and either adopt an ambush coil at or near the location previously occupied, or abandon the site and enter an extended search phase, exploring the environment for a new ambush site. Thus, even if interrupted by thermoregulatory retreats, individuals of these species will hunt at the same ambush site for several days.

While waiting in ambush coils, rattlesnakes mostly remain almost completely immobile, but this immobility is punctuated by brief bouts of chemosensory exploration, including mouth gaping. Barbour and Clark (2012a) described this behavior as “chemosensory probing” and speculated that this allows the snake to re-evaluate the ambush site and decide whether to stay or leave. In addition to *C. ruber* and *C. oreganus*, I have recorded qualitatively
Figure 2. Stereotypic hunting postures of rattlesnakes. a) A *Crotalus cerberus* coiled in vertically oriented ambush posture at base of log. b) A *Crotalus pyrrhus* coiled in arboreal ambush posture in shrub. c) A *Crotalus “hualapaiensis”* in a vertically oriented ambush posture within rock crevice. d) A *Crotalus cerastes* in an ambush coil partially buried in loose sand. Photos (a, c) Martin J. Feldner, (b) Will Wells, and (d) Rulon Clark.
similar behaviors in *C. scutulatus*, *C. cerastes*, and *C. atrox* (unpubl. data). Diller (1990) also described similar behavior in *C. viridis*. In cathemeral rattlesnakes, chemosensory probing appears to be more common at night than during the day, possibly because the behavior interferes less with crypsis under the cover of darkness. Our knowledge of what cues snakes use to reassess their ambush sites and either stay or abandon is limited, but open to the possibility of experimental investigation. Because rattlesnakes will exhibit these ambush behaviors under captive conditions, laboratory studies could be used to present various prey-derived cues under a controlled setting and examine how they affect rattlesnake behavior.

A final intriguing set of observations from field studies indicates that, while waiting in ambush, rattlesnakes will even modify physical elements of their habitat, presumably to maximize their ability to successfully strike any prey that come within range. Greene (2006) described an adult male *Crotalus molossus* extend out of his ambush coil and use his body to bend down a dried fern that was in the path of a potential strike. Breanna and I recorded similar behavior in an adult male *C. oreganus* in an ambush coil within a dense bunch of dried grass (Putman and Clark, 2015a). After a Ground Squirrel (*O. beecheyi*) passed by the front of the snake, he moved out of his ambush coil and used his head and upper body several times to move the dead grass up and out of the way of a potential strike path (Video 1). These observations cry out for experimental investigation. Such experiments may tell us whether rattlesnakes are truly able to anticipate future predatory encounters and modify their habitat in ways that are more likely to make those encounters successful.

**Strike preparation**

While rattlesnakes are waiting in ambush coils, they are usually immobile, other than the chemosensory assessment described above. However, just prior to prey encounters, they often exhibit subtle but distinct movements that indicate they are anticipating an encounter. These movements include small changes in the orientation of the head and upper body as well as a slow tightening of the ambush coil (Video 2). Although these behaviors have not been quantified, I have observed them in all rattlesnake species studied to date with fixed videography, and they occur regardless of whether the snake attempts a strike toward the prey or not. However, these preparatory movements are not necessary for successful strikes, as I have recorded several successful strikes where snakes remained completely immobile until striking. Further observations and experiments would be necessary to adequately characterize under what conditions rattlesnakes may reorient or recoil prior to striking, and how these behaviors may affect the outcome of the strike.

Once prey begin approaching rattlesnakes closely (within about a meter in my recordings), preparation/orientation movements cease and the snake remains motionless until it strikes or the prey leaves. Rattlesnakes appear to have a somewhat limited effective strike range. In an analysis of strikes of free-ranging rattlesnakes (including *C. ruber*, *C. scutulatus*, *C. oreganus*, and *C. horridus*), the furthest distance at which a snake attempted to strike a prey was ~50 cm (an adult *C. horridus* attempting to strike a Tree Squirrel, *Sciurus carolinensis*). However, the furthest distance at which a snake successfully struck prey was 25 cm (an adult *C. horridus*...
striking a Tree Squirrel, *Sciurus carolinensis*), and most (>80%) successful strikes were within 15 cm. Snakes also showed a significant propensity to strike prey that had just started moving past them. That is, when prey animals were moving laterally in front of a coiled snake (as opposed to directly toward the snake), snakes were much more likely to strike prey after the animal had moved passed its head (Clark et al., 2012).

In our quantitative analysis of field strikes the most significant factor affecting strike success was prey movement initiated after the rattlesnake began to strike (Clark et al., 2012). This is because many prey animals detected oncoming strikes and exhibited evasive maneuvers that displaced them from the path of the strike (Video 3). In a laboratory study using wild Deer Mice (*Peromyscus maniculatus*), Hayes (1992a) also found that rattlesnakes (*C. viridis*) frequently missed strikes due to evasive maneuvers of mice. These observations indicate that rattlesnakes may strike at prey in ways that minimize the ability of prey to dodge out of the way. Although missed strikes are probably not expensive in terms of energy expenditure, there are significant opportunity costs involved in a missed strike. Any prey that comes within strike range is probably unaware or at least uncertain about the presence of a rattlesnake nearby. Thus, from the perspective of the snake, delaying a strike might result in the prey moving even closer and increasing the probability that the eventual strike is successful. However, if the snake strikes early and misses, it will unambiguously reveal its presence and the likelihood of that prey item coming back within strike range is very low—the rattlesnake has then missed any future opportunities it may have had if it had waited.

Clearly, the decision of if and when to initiate a strike is critical to the success of the rattlesnake hunting strategy, and there are probably many factors that play into this decision. Rattlesnakes may be sensitive to the speed, position, orientation, and other behavioral indicators of the prey animal that indicate strike success or likelihood of dodging. Indeed, California Ground Squirrels (*O. beecheyi*) appear to take this relationship one step further and actively signal their vigilance toward the possibility of snake attack by tail flagging (Barbour and Clark, 2012b; Putman and Clark, 2015b); rattlesnakes respond by decreasing the distance at which they initiated strikes toward tail flagging squirrels compared to non-tail flaggers. In addition to these behavioral factors, the decision to strike is likely also affected by temperature, ambient light, body condition, and relative prey size. Future research efforts could examine the interplay between these factors and how they influence rattlesnake strikes.

**Strike**

The strike behavior of rattlesnakes and other vipers has received significant attention from functional morphologists (reviewed in Kardong and Smith, 2002). Kardong and Smith (2002) divide the strike behavior into the following four stages: (1) ‘Extend’: the snake rapidly straightens its coiled neck and upper body, propelling the head toward the prey while the mouth opens and the fangs are rotated forward; (2) ‘Contact’: the head of the snake contacts the prey, the jaws close to embed the fangs into prey tissue, and venom is expelled through the hollow fangs; (3) ‘Release’: the jaws open and disengage from the prey, breaking contact; (4) ‘Retract’: the head withdraws from the vicinity of the
prey. This entire sequence is extremely rapid, typically taking place in less than 0.5 seconds. Detailed kinematic studies of this behavior using high-speed video recordings have shown that this basic sequence is not just typical of rattlesnakes, but holds for vipers in general (Janoo and Gasc, 1992; Vincent et al., 2005; Cundall 2008; Herrel et al., 2011).

The purpose of the strike is to inject venom that will immobilize and kill the prey. How effectively this occurs depends on the site of injection, the amount of venom injected, and the physiological effect of the venom:

**Injection site.** To date, most field recordings of snake strikes are not detailed enough for us to quantify where on their body prey are struck. Laboratory studies indicate that rattlesnakes often strike the head/thorax region of lab mice, and mice die more quickly when struck in this region compared to strikes to the body or rump (Kardong, 1986). However, lab mice apparently do not try to dodge strikes often. William Hayes (Hayes, 1992a) examined strikes toward wild-caught field mice and found that the site of injection was variable, which he attributed to evasive maneuvers of the mice. When mice were injected with experimental doses of venom, they were immobilized much more quickly if injected in the head/neck region or near vital organs (Hayes, 1992a). The site of injection can also be altered during the course of the bite. High speed video recordings show that rattlesnakes often are not able to embed fangs upon initial contact with prey, but they can rapidly reposition their fangs during prey contact to achieve more effective envenomation (Cundall, 2008).

**Amount of venom injected.** The amount of venom rattlesnakes inject during bites is variable and appears to depend on several factors, including the size and species of rattlesnake, the size and species of prey, and physical interactions between the target tissue and the snake fangs. Hayes (Hayes, 1992a, 2008) found that the dose of venom injected during predatory bites can vary anywhere from 5 to 25 mg. Several studies have found that under laboratory conditions, rattlesnakes inject larger quantities of venom into larger prey, indicating that rattlesnakes may adjust the quantity of venom they use to some optimal level (Hayes, 2008; but see Young, 2008).

**Physiological effect of venom.** The physiological effect of venom depends on both the biochemical composition of the venom and the degree to which the prey resist the effects of that venom. This issue is complicated by the fact that both of those factors can vary substantially within species.

Venoms function primarily as offensive weaponry for rattlesnakes, used to kill and immobilize prey. Rattlesnake venoms are complex cocktails of enzymes and peptides that can have hemorrhagic, neurotoxic, and hemostatic effects (Tu, 1996). These compounds break down tissue, causing massive hemorrhaging and organ system failure, that leads to rapid immobilization and death. Several studies have found venom composition can vary both ontogenetically (Mackessy, 1988) and intraspecifically (reviewed in Chippaux et al., 1991). Rattlesnake venoms are probably even more variable than we realize, because the venoms of most species have only received cursory examination.
In addition to the substantial intraspecific variation in venom, several small mammals that are the primary prey for different rattlesnake species have been shown to exhibit some degree of innate physiological resistance to rattlesnake venom (reviewed in Biardi, 2008). The most thoroughly studied example is the California Ground Squirrel (\textit{O. beecheyi}). Ground Squirrels that have coevolved with rattlesnake predators exhibit strong physiological resistance, but that resistance is lost in populations that are not sympatric with rattlesnakes (Poran et al., 1987). Laboratory studies have estimated some rattlesnake prey, such as Ground Squirrels or Woodrats, to be resistant enough to easily recover from doses of venom larger than what is injected during a typical rattlesnake strike (Perez et al., 1979; Poran et al., 1987). However, because these studies used venom samples pooled from many rattlesnake populations, they may obscure adaptation rattlesnake venom has undergone for efficacy against local prey. Genetic and genomic data indicate snake venom is under strong positive selection (Sanz et al., 2006; Vonk et al., 2013), and intraspecific variation may be a result of adaptation to local prey resources (Daltry et al., 1996).

**Hold or release prey**

There are a variety of complex factors discussed above that determine how effective any given envenomation event is from the perspective of the rattlesnake. Because envenomation attempts vary in their effectiveness, rattlesnakes are confronted with a series of decisions after striking that will determine how likely it is that they will actually be able to locate and ingest the envenomated prey. The seemingly most effective mechanism of securing prey following envenomation is also the most straightforward: hold the prey until it is immobilized. However, this is not what usually happens, both because prey often struggle free and or are immediately released by rattlesnakes after envenomation.

The decision to release prey may not always be made by the snake. In several instances, we have recorded rattlesnakes striking relatively large prey that exhibit explosive escape behaviors (e.g., leaping into the air and pulling the snake out of its ambush coil) (Video 4). In such cases, it is doubtful a snake would be capable of holding the prey if it attempted to do so.

In cases where prey are released and or struggle free, it is often impossible to quantify the degree to which a snake that grasped prey in its jaws during a strike actually embedded fangs and envenomated prey. We have recorded several snakes striking prey that immediately leapt or struggled free. After these apparently successful strikes, the snake usually began the process of strike-induced chemosensory searching (SICS) to relocate the presumably envenomated prey (Videos 4, 5, and 8); however, occasionally the snake simply recoiled in its ambush site, or moved a short distance and adopted a new ambush coil (Video 6). In these cases, we assume that the rattlesnake did not effectively envenomate prey during the strike, although we have not verified this experimentally. Laboratory studies of SICS also indicate that the decision to try and trail prey is made independently of the decision to strike at it (Chiszar et al., 1991). Thus, snakes know, to some degree, if they have successfully envenomated prey during the strike and apparently only attempt SICS following successful envenomations.
Box 2. Infrared sensing

Rattlesnakes are pitvipers and thus possess a specialized heat-sensing facial pit. Animals that possess sensory capabilities that humans lack are inherently fascinating, as they literally see a different world than we do. In the case of pitvipers, a recent comprehensive review of the neuroanatomy of this sensory system concluded that the pits operate essentially as an extra pair of eyes that give the snakes sensitive vision that extends into the infrared wavelengths (Goris, 2011).

There are no known photosensitive pigments in nature for near infrared light, so rattlesnakes do not directly detect the photons in infrared light like regular eyes do; instead, pitvipers detect those photons by the incident warming that occurs when they are absorbed by the membrane in the pit organ. Because the heat given off by small endotherms is miniscule at best (imagine warming your hands on a cold night by holding them up to a live mouse), the pit organ must be extremely sensitive to temperature contrast to produce thermal images of prey. Physiological studies have indicated that the pit membrane is sensitive to changes at least as small as 0.001°C (de Cock Buning et al., 1981), with behavioral studies indicating even greater sensitivity (Ebert and Westhoff, 2006). The pit membrane is full of temperature-sensitive nerve endings, which are apparently studded with temperature-gated cation channels. Molecular studies have identified at least one temperature sensitive cation channel involved in this process (Gracheva et al., 2010), although the properties of this cation channel alone cannot explain the extraordinary sensitivity of the pit membrane. Additional behavioral and physiological study will likely continue to shed light on how this sensitivity is achieved. In one intriguing recent example, pitivipers were found to increase the sensitivity of the pit membrane by using evaporative respiratory cooling of the rostrum (Cadena et al., 2013). Rostral cooling was accomplished by changes in breathing patterns when snakes became alert.

The sensory information from the pit is integrated in the optic tectum with information from the visual system, producing an image that includes infrared light. Various behavioral studies have been conducted with rattlesnakes that have had either their eyes or pits occluded, and these studies show that snakes with their eyes covered can still see mice well enough to strike and envenomate (Kardong, 1992; Chen et al., 2012). However, anatomical and modeling studies by Bakken and others indicate that the ability to form detailed images with the infrared-sensing pit alone is limited (Bakken and Krochmal, 2007; Bakken et al., 2012). It is likely that the effective range of this sense is small (~50–100 cm), and the resolution is low. Thus, a small mammal probably gives off a general heat “glow” at close range that rattlesnakes can use to increase their ability to see and target that animal for envenomation.

Of course, being able to detect infrared light is useful in contexts outside of prey capture. For example, Aaron Krochmal and others (Krochmal and Bakken, 2003; Krochmal et al., 2004) have shown that pitvipers can locate heat sources or thermal refuges using the pit organ. Future investigations may reveal other novel ways in which pitvipers use infrared light as a source of information about their environment.
Even if the struck prey does not struggle or bite during the strike, rattlesnakes still often chose to immediately release prey. In fact, rattlesnakes usually even strike and release completely inert prey (pre-killed rodents or artificial models of rodents) that cannot struggle or retaliate (Melcer and Chiszar, 1989; Hayes and Duvall, 1991; Hayes and Hayes, 1993). This is especially true for mammalian prey, although laboratory studies are somewhat variable in the degree to which they have found that rattlesnakes hold on to prey after the strike. Kardong (1986) found that the majority of the time (83% of strikes) *C. oreganus* striking live laboratory mice released them immediately, although this proportion was higher (90%) for smaller snakes. In this same study, mice only bit back during the strike 6% of the time. When mice were held they died more quickly, indicating that more venom may be injected when snakes do not release prey. Radcliffe et al. (1980) also found relative prey size to be an important factor, with rattlesnakes releasing relatively larger prey more often. Deufel and Cundall (2006) also suggested that the propensity to release prey was modified by prey size, as snakes in their study also tended to release larger prey that could mount more effective struggles or retaliatory attacks. Anecdotal evidence and one experimental study indicate that rattlesnakes are more likely to hold birds than small rodents, presumably because of the difficulties involved in post-strike trailing of prey that could fly (Hayes, 1992b). Under field conditions, 1 of 25 successful strikes we recorded in Clark et al. (2012) resulted in a rattlesnake holding on to its prey (Video 7).

Thus, under both laboratory and field conditions, even if struck prey do not struggle free rattlesnakes still usually choose to immediately release small mammals after envenomation. Although this helps to avoid retaliatory bites, it leads to the problem of relocating an envenomated animal that has fled some distance.

**Strike-induced chemosensory searching (SICS)**

When prey are released, rattlesnakes often remain still for a variable period of time (the quiescent stage in Kardong and Smith, 2002) and then initiate strike-induced chemosensory searching (SICS), the process by which the snake locates the chemosensory trail left by the envenomated prey. SICS is a robust behavioral phenomenon that has been studied extensively in the laboratory under a variety of experimental paradigms (reviewed in Chiszar et al., 1992; Kardong and Smith, 2002; Chiszar and Smith, 2008). A large number of experimental studies on SICS focus on determining how rattlesnakes can identify the specific chemosensory trail that will lead them to the prey animal that was envenomated, and thereby avoid following a chemical trail that was left by that animal before it was struck, or following a trail left by some other individual. Overall, this research has revealed that rattlesnakes integrate at least three different types of information in a hierarchical fashion: (1) Envenomation: rattlesnakes can discriminate the trail of an envenomated animal from one that has not been injected with venom; (2) Prey odor: rattlesnakes can identify and follow the distinct chemical cues associated with the individual they struck; (3) Mechanical damage: rattlesnakes can identify and follow distinct chemical cues associated with a mammal that has been mechanically damaged via puncture, as occurs during envenomation. When confronted with contrasting information among these sources in experimental treatments, rattlesnakes prioritize envenomation over mouse odor and mouse odor over mechanical damage.
Recent studies continue to fine-tune our understanding of SICS. Experiments with specific venom components have shown that a particular class of venom molecules, disintegrins, appears to mediate the responsiveness of rattlesnakes to envenomated prey during SICS (Saviola et al., 2013a). It may be that these molecules, crotatroxin 1 and 2, evolved specifically as a biochemical “tag” to facilitate post-strike relocation of envenomated prey.

Although SICS has been studied almost exclusively in a laboratory setting, field data confirm that the same basic sequence of behaviors occurs under natural settings (Klauber, 1972; Diller, 1990; Goode et al., 1990; Clark, 2006b). However, relocating prey via SICS under field conditions does appear to be more time-consuming and variable in outcome. Some field strikes can lead to immobilization of prey within a few centimeters, requiring very little time for relocation. Others can result in prey moving many tens of meters, resulting in a SICS process that lasts over 24 hours. Because published field data are limited in this area, I believe it would be useful to present a brief summary of field observations of my own and of colleagues who have had occasion to observe SICS and prey ingestion in the field. The quantitative aspects of these narratives are summarized in Table 1.

**Crotalus horridus**

In a field study of Timber Rattlesnakes, I observed two full post-strike trailing events: one snake took 12 min to trail a nocturnal rodent that had fled 0.75 m, and another took 41 min to trail a Red-backed Vole (*Clethrionomys gapperi*) 7 m (Clark, 2006b).

**Crotalus scutulatus**

Michael Cardwell (unpubl. data) documented SICS leading to post-strike prey relocation on several occasions in his field study of Mohave Rattlesnakes, *C. scutulatus* (see Cardwell, volume 1, *Crotalus scutulatus*). One snake took 43 min to relocate an envenomated Merriam’s Kangaroo Rat (*Dipodomys merriami*) that had fled approximately 15 m before becoming immobile. Another took 21 min to relocate a *D. merriami* that had fled 9.5 m. However, on two other occasions, Cardwell observed *C. scutulatus* searching for and swallowing rigored *D. merriami* carcasses several hours after sunrise, indicating a more prolonged prey relocation time. In my own field studies, I recorded a *C. scutulatus* striking a *D. merriami* several hours before sunrise (Video 8); this individual was then seen consuming a rigored *D. merriami* carcass 18 m away at 1845 h the next evening. *Crotalus scutulatus* is well known for having a particularly potent venom neurotoxin in at least some populations (Glenn et al., 1983). Cardwell and others have speculated that *C. scutulatus* evolved this neurotoxin as an adaptation for quickly immobilizing their primary prey, Kangaroo Rats (*Dipodomys* spp.), which are likely to leave a discontinuous chemical trail due to their saltatory locomotion (see Cardwell, volume 1, *Crotalus scutulatus*). These field observations confirm that, at least occasionally, *C. scutulatus* has difficulty readily relocating struck kangaroo rats.

**Crotalus lutosus**

Diller (1990) observed a Great Basin Rattlesnake (*C. lutosus*) engaging in SICS-like behavior for over 24 hours until finding and consuming a rigored Cottontail Rabbit (*Sylvilagus nuttallii*). This
### Table 1

Summary of field observations that quantified the time rattlesnakes take to relocate and ingest prey after envenomation.

<table>
<thead>
<tr>
<th>Rattlesnake species</th>
<th>Prey species</th>
<th>Prey relocation time (minutes)</th>
<th>Prey distance (meters)</th>
<th>Ingestion time (minutes)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crotalus horridus</em></td>
<td>Small nocturnal rodent</td>
<td>12</td>
<td>0.75</td>
<td>39</td>
<td>Cundall and Greene (2000); Kardong and Smith (2002); Clark (2006b); Chiszar and Smith (2008)</td>
</tr>
<tr>
<td><em>Crotalus horridus</em></td>
<td>Clethrionomys gapperi (Red-backed Vole)</td>
<td>41</td>
<td>7</td>
<td>18</td>
<td>Clark (2006b)</td>
</tr>
<tr>
<td><em>Crotalus horridus</em></td>
<td><em>Peromyscus</em> spp. (field mouse)</td>
<td>8</td>
<td>0.25</td>
<td>21</td>
<td>R. W. Clark, unpubl. data</td>
</tr>
<tr>
<td><em>Crotalus lutosus</em></td>
<td><em>Sylvilagus</em> nuttallii (Cottontail Rabbit)</td>
<td>1560 (minimum)</td>
<td>–25</td>
<td>–90</td>
<td>Diller (1990)</td>
</tr>
<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>165</td>
<td>15</td>
<td>90</td>
<td>Putman et al. (2016)</td>
</tr>
<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>266</td>
<td>27</td>
<td>–25</td>
<td>Putman et al. (2016)</td>
</tr>
<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>179</td>
<td>21</td>
<td>not located</td>
<td>Putman et al. (2016)</td>
</tr>
<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>105</td>
<td>7</td>
<td>20</td>
<td>Putman et al. (2016)</td>
</tr>
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<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>123</td>
<td>20</td>
<td>unknown</td>
<td>Putman et al. (2016)</td>
</tr>
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<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>140</td>
<td>1.3</td>
<td>20</td>
<td>Putman et al. (2016)</td>
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<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>25</td>
<td>5</td>
<td>unknown</td>
<td>Putman et al. (2016)</td>
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<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>&gt;1200</td>
<td>unknown</td>
<td>not located</td>
<td>Putman et al. (2016)</td>
</tr>
<tr>
<td><em>Crotalus oreganus</em></td>
<td><em>Otospermophilus beecheyi</em> (California Ground Squirrel)</td>
<td>&gt;360</td>
<td>unknown</td>
<td>unknown</td>
<td>Putman et al. (2016)</td>
</tr>
<tr>
<td><em>Crotalus ruber</em></td>
<td><em>Peromyscus</em> spp. (field mouse)</td>
<td>Held</td>
<td>Held</td>
<td>10</td>
<td>R. W. Clark, unpubl. data</td>
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<tr>
<td><em>Crotalus scutulatus</em></td>
<td><em>Dipodomys merriami</em> (Merriam’s Kangaroo Rat)</td>
<td>21</td>
<td>9.5</td>
<td>~15</td>
<td>M. Cardwell, unpubl. data</td>
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<tr>
<td><em>Crotalus scutulatus</em></td>
<td><em>Dipodomys merriami</em> (Merriam’s Kangaroo Rat)</td>
<td>43</td>
<td>15</td>
<td>17</td>
<td>M. Cardwell, unpubl. data</td>
</tr>
<tr>
<td><em>Crotalus scutulatus</em></td>
<td><em>Dipodomys merriami</em> (Merriam’s Kangaroo Rat)</td>
<td>960</td>
<td>18</td>
<td>18</td>
<td>R. W. Clark, unpubl. data</td>
</tr>
</tbody>
</table>
field observation is bolstered by laboratory experiments that confirm that *C. lutosus* will engage in SICS for up to 24 hours post-strike (Smith et al., 2000).

*Crotalus oreganus*

My research group has spent several summers observing predator-prey interactions between California Ground Squirrels (*Otospermophilus beecheyi*) and Northern Pacific Rattlesnakes (*C. oreganus*). We observed several instances of successful and unsuccessful relocation following SICS.

**Successful relocation**

1. An adult male snake struck the flank of a juvenile squirrel, which fled 15 m before becoming immobilized. The snake waited 12 min to initiate SICS, and circled back twice to the site of the bite before successfully locating the dead squirrel 165 min post-strike. The snake then took 90 min to successfully swallow the squirrel carcass.

2. An adult male snake struck a juvenile squirrel, which travelled 27 m to a burrow. The snake waited 29 min to initiate SICS, after which it explored multiple burrows in the area before locating the burrow with the squirrel 266 min post-strike. The snake was seen to strike something (presumably the same squirrel) a second time at the entrance to the burrow, then move inside the burrow and emerge 25 min later with a noticeable food bolus.

3. An adult female snake struck a juvenile squirrel which travelled 7 m to tall vegetation. The snake waited 65 min to initiate SICS, after which it located the squirrel 105 min post strike and took 20 min to swallow the carcass.

4. An adult male snake struck an adult squirrel which travelled 20 m to a burrow. The snake waited 36 min to initiate SICS, after which it located the burrow of the squirrel 123 min post strike.

5. An adult female snake struck a juvenile squirrel, which travelled 1.3 m before becoming immobile. The snake waited 135 min to initiate SICS, after which it located the squirrel 140 min post strike and took 20 min to swallow the carcass.

6. An adult female snake struck a squirrel of indeterminate size, which travelled 5 m to a burrow. The snake waited 1 min to initiate SICS, after which it found the squirrel’s burrow 25 min post strike.

**Unsuccessful relocation**

1. An adult rattlesnake struck an adult squirrel in the head region. The squirrel fled ~21 m to a burrow. The snake initiated SICS but could not locate the burrow used by the squirrel; after 179 min of searching (while also being repeatedly approached by tail flagging squirrels), the snake entered a burrow 27 m from the site of the strike, and 15 m from the squirrel’s burrow. The following day the snake was observed to resume ambush hunting, and the struck squirrel was observed moving normally, having apparently successfully resisted the effects of the venom.

2. An adult female snake struck a juvenile squirrel, which travelled an indeterminate distance following the strike. The snake waited 2 min to initiate SICS, after which it searched for ~7 hours before retreating to a burrow. This snake was observed exhibiting SICS-like searching until 1120 h the next day, after which it appeared to give up SICS and resume ambush hunting.
3. An adult male snake struck a juvenile squirrel which travelled an indeterminate distance. The snake waited 101 min to initiate SICS, after which it was observed to search for at least 6 hours. We were not able to determine if the snake was successful in recovering the struck prey after this time.

The general pattern to emerge from these observations is that, despite their sophisticated sensory mechanisms for chemical trailing, rattlesnakes have a surprisingly difficult time trailing ground squirrels post-strike, and are not able to successfully relocate struck prey a significant portion of the time. Fitch and Twining (1946) also reported finding two squirrel carcasses and two Kangaroo Rat carcasses dead “for some time” that had been envenomated but not recovered by snakes. This is no doubt due in large part to the physiological venom resistance of squirrels allowing them to travel further than typical envenomated prey. However, several other key rattlesnake prey species are also at least somewhat resistant to snake venom (Biardi, 2008), and (as discussed previously) rattlesnake envenomation success can be widely variable, so post-strike trailing difficulty may be more common than we realize. Another factor identified from these field observations is that under circumstances where venom immobilizes prey, but the prey is still alive upon relocation, rattlesnakes may envenomate prey again before attempting to swallow it.

**Ingestion**

Upon successfully relocating prey (or finally releasing immobilized prey that was held during the strike), rattlesnakes begin the process of swallowing the carcass whole. This process almost always begins by the snake investigating the carcass extensively via tongue-flicking in an apparent attempt to identify the head. Anecdotal reports and a few published studies indicated that rattlesnakes will occasionally strike, envenomate, trail, and attempt to swallow items that are too large for them to ingest (Pough and Groves, 1983; Kardong, 1986). However, overestimating the size of ingestible prey appears to be relatively rare. A morphometric analysis examining ingestible prey size of whole rodents suggests that this may be because the cross sectional area of a live rodents is significantly reduced once it is forced into a tube, as essentially occurs during ingestion by a snake (Close and Cundall, 2012); thus, snakes estimating prey size visually may underestimate ingestible size.

The functional mechanics of prey swallowing by snakes are reviewed extensively by Cundall and Greene (2000). Rattlesnakes have highly kinetic skulls that allow them to ingest large prey. Briefly, rattlesnakes swallow prey by using alternating left-right movements of the jaw, essentially using their head muscles to “crawl” over their prey in small steps (Cundall and Greene, 2000). Rattlesnakes can swallow relatively massive carcasses in this manner—prey that are even bigger around than the head of the snake itself.

Rattlesnakes almost always swallow prey headfirst—especially so for relatively large mammalian prey (Loop and Bailey, 1972; Taylor, 2001; Clark, 2002; Glaudas et al., 2008), although it is still unclear what cues are being used for identifying the head of mammalian prey items (Ashton, 2002). One intriguing field observation indicates that, in some cases, head location may be nec-
ecessary for successful ingestion. Breanna Putman observed an adult female *C. oreganus* investigating the carcass of a juvenile squirrel that had been decapitated, presumably by a hawk (Putman, unpubl. data) (Video 9). The snake investigated the carcass for about 7 minutes, occasionally opening its jaws to “mouth” different parts of the carcass, but always stopping and letting go before beginning ingestion. Eventually, the snake left the area without ingesting the carcass. Although it is unclear to what extent the lack of a head was a factor in the snake rejecting the carcass, it seems plausible (and open to experimental investigation) that the snake was unable or unwilling to proceed with ingestion because it could not find a head. It may be that snakes use the wedge-like shape of the prey rostrum to push the elastic elements of the skull open as they walk their jaws over the head and body. In other words, without the head present, the shoulder girdle could be too large to begin the swallowing process, even if the snake would be able to squeeze its head over the shoulders of the prey had it been able to start at the smaller rostrum.

Because the jaws are used for ingestion, snakes are essentially defenseless while swallowing prey and would presumably benefit from being able to complete the process relatively quickly. Nevertheless, field observations indicate that rattlesnakes may require long periods of time to ingest large prey. For example, the *C. lutosus* observed by Diller (1990) took over 90 min to swallow the rigored *S. nuttallii*. Field observations across a range of species indicate that even swallowing small prey under field conditions can take longer than what is often observed in captivity (Table 1, Clark, 2006b). Perhaps for this reason, rattlesnakes will often grab prey in their jaws and drag it to a sheltered location (such as a mammal burrow) before attempting ingestion (Clark, Putman, and Barbour, unpubl. data) (Videos 5 and 10).

**Digestion**

Like other snakes that feed infrequently on relatively large prey, rattlesnakes upregulate their digestive system after ingestion, and the concomitant specific dynamic action can last for many days (reviewed in Secor, 2008). Under field conditions, rattlesnakes often stop hunting for several days after swallowing a large meal and retreat to favorable basking sites to digest and thermoregulate. There are several possible benefits to this behavior. Not only do large prey take more time and energy to digest, but the distention of the body associated with ingestion can interfere with effective antipredator behavior, such as rapid fleeing and the ability to recoil for a defense strike. Anecdotal reports indicate that extremely large meals may at least occasionally lead to mortality (Pauly and Benard, 2002; Mulcahy et al., 2003; Shepard et al., 2004). Thus, rattlesnakes probably benefit by investing time in thermoregulation to aid rapid digestion, until they have digested enough of the meal to restore functional mobility. Additionally, prey that is not digested quickly may decompose, leading to regurgitation (Naulleau, 1983).

Our understanding of post-prandial thermoregulation in free-living snakes is limited. Several studies have shown that captive snakes usually increase their body temperature through behavioral thermoregulation after feeding (reviewed in Blouin-Demers and Weatherhead, 2001), but only a few studies have
been conducted in the field. Beck (1996) found that the body temperatures of six rattlesnakes (C. molossus, C. atrox, and Crotalus tigris) that were experimentally fed small mammals (meals ranged from 16–45% of snake mass) were significantly higher between 1200 and 1600 h, indicating a postprandial upregulation in temperature that lasted for several days. The fed snakes also showed decreased mobility and retreated to sheltered sites after eating. We have observed similar behaviors in C. oreganus, C. horridus, and C. ruber that have ingested large meals (Clark, Putman, and Barbour, unpubl. data). However, after ingesting relatively small prey (i.e., items that do not lead to a noticeable mid-body bulge), rattlesnakes often resume foraging more or less immediately. The relatively large adult C. horridus and C. ruber in the Appendix that ingested small nocturnal rodents all continued to exhibit ambush-foraging behavior immediately after ingestion. Because small prey do not interfere with mobility and are not likely to decompose before digestion, rattlesnakes may be able to digest these meals without interfering with hunting behavior.

Additional aspects of rattlesnake predatory behavior

Seasonal migrations
Several rattlesnakes exhibit seasonal migrations between overwintering habitat and feeding habitat, especially in less temperate parts of their geographic range. Prairie Rattlesnakes at high altitude sites in Wyoming make lengthy (~5 km) straight line movements from dens to habitats containing prey (Duvall et al., 1985). Timber Rattlesnakes in the Northeast United States move from dens located in south-facing rocky outcrops to surrounding woodlands to forage (Brown et al., 1982; Reinert, 1984). These seasonal migrations are an important aspect of the predatory behavior of rattlesnakes, since they appear to primarily involve long-distance movements to locate patches of abundant prey.

Alternative predatory strategies
Although the mobile ambushing strategy detailed above is certainly the dominant hunting behavior of most rattlesnakes, alternative foraging strategies are also employed. Like many predators, rattlesnakes appear to be opportunistic, and will sometime scavenge carcasses that they have not killed (reviewed in DeVault and Krochmal, 2002). Given their relatively sedentary lifestyle, I think it is unlikely that scavenging is a significant source of food—most rattlesnakes move only short distances once every few days (Duvall et al., 1985; Beaupre, 1995; Hardy and Greene, 1999; Holycross et al., 2002b; Prival et al., 2002; Reed and Douglas, 2002; Clark, 2006a; Tozetti et al., 2009; Wastell and Mackessy, 2011; Wittenberg, 2012), and so are simply unlikely to encounter many dead animals that they did not kill themselves.

Rattlesnakes will also occasionally engage in more active “stalking” behavior, moving slowly toward an area containing prey, and then surprising the prey with a quick strike. For example, Cardwell observed a free-ranging C. scutulatus uncoil
and move slowly toward an adult Pocket Mouse (*Perognathus* spp.), strike, hold, and rapidly ingest it (M. Cardwell, unpubl. data). This behavior is very similar to the “approach” behavior frequently observed in captive rattlesnakes presented with live mice (de Cock Buning, 1983; Kardong and Smith, 2002). Putman (unpubl. data) also observed a large adult *C. oreganus* follow a nestling squirrel, which was making distress calls, out of a squirrel burrow. The snake approached and struck the pup, and promptly swallowed it. Other observations also indicate rattlesnakes will occasionally raid small mammal nests and consume nestlings (Fitch and Twining, 1946; Funk, 1965; Klauber, 1972; Brown, 1990).

**Concluding remarks**

> We should venture on the study of every kind of animal without distaste, for each and all will reveal to us something natural and something beautiful.

-Aristotle

Rattlesnakes are not ideal for classical methods of studying animal behavior. They are cryptic, secretive, and largely sedentary. If you were to venture into the hills with binoculars and a notepad, you would be lucky to find a single subject to watch, and even luckier still if you kept from frightening it underground. Even with the use of radio-telemetry to readily relocate subjects for observation, you could carefully watch a snake for hours and see nothing but an impressive display of stillness. Then, while you were looking down to tie your shoe, a chipmunk would scamper by, get struck, envenomated, released, and flee, leaving you with nothing but an outstretched snake and a mystery when you looked up.

As high-energy endotherms, we are ill equipped to study rattlesnake hunting behavior without the use of some technology. We need video recording equipment to quantify both the prolonged time periods of waiting as well as the almost instantaneous burst of activity comprising a predation attempt. The use of video cameras to record rattlesnakes in the field turns the sedentary nature of their hunting behavior into an asset. Because video recording technology is now relatively inexpensive, it is feasible for a single researcher to deploy several unmanned cameras simultaneously at a field site, thereby assembling large data sets on potential and actual encounters with prey.

Field data on predation in most systems is rare—any taxa that can be readily studied in this regard is likely to contribute broadly to our knowledge of predator-prey interactions and co-evolution. Even though they exhibit a major predatory influence in many communities, rattlesnakes are not well represented in the literature on predator-prey dynamics and top-down control (Nowak et al., 2008). This may stem in part from a dearth of field studies of predation. Rattlesnakes already serve as model systems in physiological ecology, habitat selection, sensory ecology, and life history variation (Beaupre and Duvall, 1998). I believe they can also be models for our understanding of the expression and evolution of complex behaviors in nature, a field that is currently dominated by studies of birds and mammals.
Acknowledgments

I am indebted to numerous undergraduate and graduate students for aid in field studies, but especially Matthew Barbour and Breanna Putman. I thank Michael Cardwell, Matthew Barbour, and Breanna Putman for providing me with their unpublished data on rattlesnake behavior. This manuscript was greatly improved by comments from Gordon Schuett, Shannon Hoss, Matthew Barbour, Breanna Putman, and Valerie Clark. I thank Kraig Adler for his mentorship during my dissertation research, which spawned all of my subsequent studies on rattlesnake behavior. I thank Harry W. Greene for his early willingness to foster the efforts of an inexperienced rattlesnake fanatic, as well as his continued inspiration to maintain a research focus on the study of animals in nature. San Diego State University, the National Geographic Society Waitts Grant (W17-08), the National Science Foundation (DBI-0951010 and DDIG-0308919), and the Kieckhefer Adirondack Fellowship funded my work on rattlesnake hunting behavior.

References


Clark, R. W. 2006b. Post-strike behavior of Timber Rattlesnakes (Crotalus horridus) during natural predation events. Ethology 112: 1,089–1,094.


## Appendix

Descriptions and Uniform Resource Locator (URL) of video files cited in text.

<table>
<thead>
<tr>
<th>Video</th>
<th>Description</th>
<th>URL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Video 1</td>
<td><em>Crotalus oreganus</em> uses head and upper body to move dead grass out of the way of a potential strike path.</td>
<td>youtu.be/hx_9OT3frpA</td>
</tr>
<tr>
<td>Video 2</td>
<td><em>Crotalus oreganus</em> makes subtle movements reorienting head prior to striking California Ground Squirrel.</td>
<td>youtu.be/Y8teBmV6wTY</td>
</tr>
<tr>
<td>Video 3</td>
<td><em>Crotalus cerastes</em> attempts to strike Desert Kangaroo Rat, which exhibits evasive dodge to avoid strike.</td>
<td>youtu.be/GUyhnAjwxVkJ</td>
</tr>
<tr>
<td>Video 4</td>
<td>Juvenile <em>Crotalus cerastes</em> strikes adult whiptail lizard (<em>Aspidoscelis tigris</em>) and is physically pulled out of ambush coil by struggling lizard before prey is released.</td>
<td>youtu.be/hREihZCiCd8</td>
</tr>
<tr>
<td>Video 5</td>
<td><em>Crotalus oreganus</em> strikes squirrel, exhibits SICS, relocates carcass, and drags carcass into shaded area to consume.</td>
<td>youtu.be/lxvdYNMhCUG0</td>
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<tr>
<td>Video 6</td>
<td><em>Crotalus cerastes</em> misses strike at Desert Kangaroo Rat and recoils back in same ambush location.</td>
<td>youtu.be/i51tvjnm-VYE</td>
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<tr>
<td>Video 7</td>
<td><em>Crotalus ruber</em> striking field mouse (<em>Peromyscus</em> spp.) and holding on to mouse during envenomation.</td>
<td>youtu.be/fUMeNER2Ocw</td>
</tr>
<tr>
<td>Video 8</td>
<td><em>Crotalus scutulatus</em> strikes and releases Merriam’s Kangaroo Rat (<em>Dipodomys merriami</em>), initiates SICS, circles back to starting location twice, and is found the next evening consuming <em>D. merriami</em> carcass.</td>
<td>youtu.be/dSIQE4BzUKg</td>
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<tr>
<td>Video 9</td>
<td><em>Crotalus oreganus</em> investigating and attempting ingestion of decapitated California Ground Squirrel carcass.</td>
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<td>Video 10</td>
<td><em>Crotalus oreganus</em> begins ingesting squirrel carcass, then drags carcass into retreat site (squirrel burrow) to complete consumption.</td>
<td>youtu.be/HlvWEXzsZ34</td>
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