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Evolution and Biomechanics of Specialized Locomotion in Snakes

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of the requirements for the degree of

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in

Evolution, Ecology, and Organismal Biology

by

Jessica L. Tingle

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ABSTRACT OF THE DISSERTATION

Evolution and Biomechanics of Specialized Locomotion in Snakes

by

Jessica L. Tingle

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, September 2021
Dr. Theodore Garland, Jr., Chair

Most animals need to move to find food, escape predators or reproduce. Therefore, locomotion shapes most aspects of an animal's biology. Even though many land-dwelling animals have independently evolved body plans that lack limbs, their locomotion has historically received much less attention than have walking, running, swimming, or flight. Limbless animals move fundamentally differently than do limbed ones, relying entirely on the vertebral column, ribs, and trunk musculature for propulsion. Despite the superficial simplicity of this body plan, one group of limbless terrestrial vertebrates, snakes, have radiated into a wide variety of habitats and can move in more than a dozen different ways.

This dissertation focuses on sidewinding. Several distantly-related viper species have independently specialized in sidewinding, apparently as a way of dealing with shifting sand in their desert habitats. Chapter 1 presents a literature review of sidewinding and an ancestral state reconstruction of specialized sidewinding in vipers. Specialized sidewinding has evolved five times in the Viperidae, and dozens of species across the snake phylogeny can sidewind facultatively, far more than previously appreciated. Chapter 2 presents an analysis of scaling and causal relations of morphology and kinematics in sidewinder rattlesnakes (*Crotalus cerastes*). High-speed videos were used to quantify whole-animal speed and acceleration, the motion of individual marker points along the body, and the body's waveform during sidewinding. Key results include an unexpected positive allometry of wave amplitude in adult sidewinders, as well as evidence from path analysis that body width is positively related to wavelength, that sidewinding snakes increase speed primarily through increases in frequency, and that frequency is correlated with skew angle (the degree to which the wave tilts towards either the head or the tail). Chapter 3 presents a phylogenetic comparative analysis of viper body shape and scalation evolution in relation to sidewinding, arboreality, and climate. Sidewinding specialists do not show differ from non-sidewinders in the traits examined, but arboreal species differ from terrestrial ones in numerous traits, and precipitation is also correlated with several aspects of morphology.

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Introduction

Locomotion provides an ideal behavior for functional and comparative studies because it is both quantifiable and essential to most animals' success. It naturally lends itself to an integrative approach. To move, animals transfer forces between their bodies and the environment, a process heavily influenced not only by lower-level traits such as morphology and physiology, but also by the environment's physical structure and material properties. In turn, an animal's ability to move influences habitat use and interactions with other organisms. These relationships drive the evolution of functional diversity and have far-reaching effects on ecology of the focal species and others in the community.

This dissertation focuses on specialized locomotion and associated morphology in limbless terrestrial vertebrates, specifically snakes. More than 25 clades of tetrapods have evolved a highly elongate, limbless body plan, producing a total of ~4,300 species that represent 19% of terrestrial vertebrate diversity (Wiens et al. 2006; Astley 2020; Bergmann et al. 2020). Not only have these animals achieved a high degree of taxonomic diversity, but some of them display impressive functional diversity: snakes use at least 11 distinct modes of locomotion, which allow them to occupy a wide variety of habitats (Greene 1997; Jayne 2020). Despite the ubiquity and functional distinctiveness of limbless terrestrial vertebrates, studies of limbless locomotion make up less than 0.5% of the locomotion literature (Astley 2020), leaving most of their diversity unexplored. We still have much to learn about how such a superficially simple body plan can generate such extreme locomotor diversity. The answers lie at multiple levels, including the influence of lower-level traits on locomotor behavior and performance, and the evolution of locomotion and related traits on a macro scale.

To better understand locomotor diversity in snakes, I have worked at the interface of biomechanics, functional morphology, and macroevolution (See Fig. 0.1 for a conceptual framework). Biomechanics and functional morphology involve the application of principles from engineering and physics to understand how organisms function and how structure relates to function. Most of my efforts in this area have involved kinematics, a way of describing motion in terms of the changes in spatial relationships among parts (with no regard to the forces involved), as well as quantifying various aspects of morphology so that I can link morphological and kinematic variation. Macroevolution is concerned with understanding patterns of biological diversity across the tree of life. My efforts in this area have largely involved using phylogenetic comparative methods to link morphological evolution with locomotor behavior and/or ecology.

One major theme in this dissertation is the relationship between morphology, behavior, and ecology, as well as the correlated evolution of these traits. Chapter 2 tackles morphology and locomotor behavior at the level of variation within a single species, while Chapter 3 takes a macroevolutionary view of morphology, locomotor behavior, and ecology in vipers.

Another important theme in my dissertation is scaling. An organism's size strongly influences the way it interacts with the environment. This idea has long fascinated humans, as evidenced by the many stories telling of people's adventures when they suddenly change size or when they encounter worlds whose denizens differ greatly in size from themselves

(McMahon and Bonner 1983). Scaling has received extensive scientific attention in the last century (e.g. Thompson 1917; Huxley 1932; Gould 1966; Brown and West 2000), with many studies demonstrating that body size affects morphology, physiology, and even behavior across the tree of life.

Each of my chapters deals with these themes in the context of an unusual mode of snake locomotion called sidewinding, which I have identified as an especially appropriate gait for answering questions about the correlated evolution of specialized behavior and morphology in an ecological context. During sidewinding, a snake alternately holds some sections of its body stationary on the ground while lifting other sections up and forward in loops, eventually anchoring them to new stationary points farther along. Sidewinding resembles lateral undulation, the type of locomotion that most snakes commonly use in terrestrial environments, in that both require the snake to propagate a wave down the length of its body (Jayne 1986). Sidewinding differs from lateral undulation in that it involves static, rather than sliding, contact with the ground, and it includes more pronounced motion in the vertical plane (Jayne 1986). Sidewinding is used by many snake species to varying degrees, and it is closely associated with shifting or smooth surfaces, especially sand. It is not an ancestral locomotor mode, and many snakes cannot perform sidewinding even under duress; yet, several species are highly specialized in sidewinding, and many other species sidewind facultatively with varying degrees of proficiency (Tingle 2020). The continuum of sidewinding provides a promising system for unravelling various aspects of the evolution of functional novelty and associated traits.

For Chapter 1, I conducted a thorough review of the literature on sidewinding. Over the course of that review, I uncovered evidence of sidewinding in far more species than previously appreciated. Although only a handful of viper species use sidewinding as their primary mode of locomotion under natural conditions, dozens of species from across the snake family tree sidewind facultatively to varying degrees and under a variety of conditions, some of them quite well. In addition to providing a literature review, I performed an ancestral state reconstruction of specialized sidewinding in vipers. I discovered that specialization for sidewinding has evolved five times in the family, laying the groundwork for phylogenetic comparative analysis of sidewinding vipers.

For Chapter 2, I examined the scaling of morphology and sidewinding biomechanics in the sidewinder rattlesnake (*Crotalus cerastes*). To do so, I conducted fieldwork near Yuma, Arizona to collect morphological and high-speed video data for 74 sidewinders ranging in size from 8 to 272 grams. I then performed analyses to determine the effects of sex (female vs. male), age class (juvenile vs. adult), and body size (snout-vent length) on morphology and kinematics, as well as the scaling relationships (isometric vs. allometric) of traits that covary with body size. Finally, I used path analysis to understand causal relationships among morphological traits, kinematics variables, and performance.

For Chapter 3, I explored the evolution of viper body shape and scalation in relation to sidewinding locomotion, arboreality, and climatic conditions. To do so, I collected morphological data from several hundred museum specimens representing 86 viper species that have evolved sidewinding locomotion and specialized tree-dwelling habits multiple times, and that live in habitats with a wide range of climatic conditions. I used statistical methods that account for both phylogenetic relationships and intraspecific variation to examine morphological adaptation.

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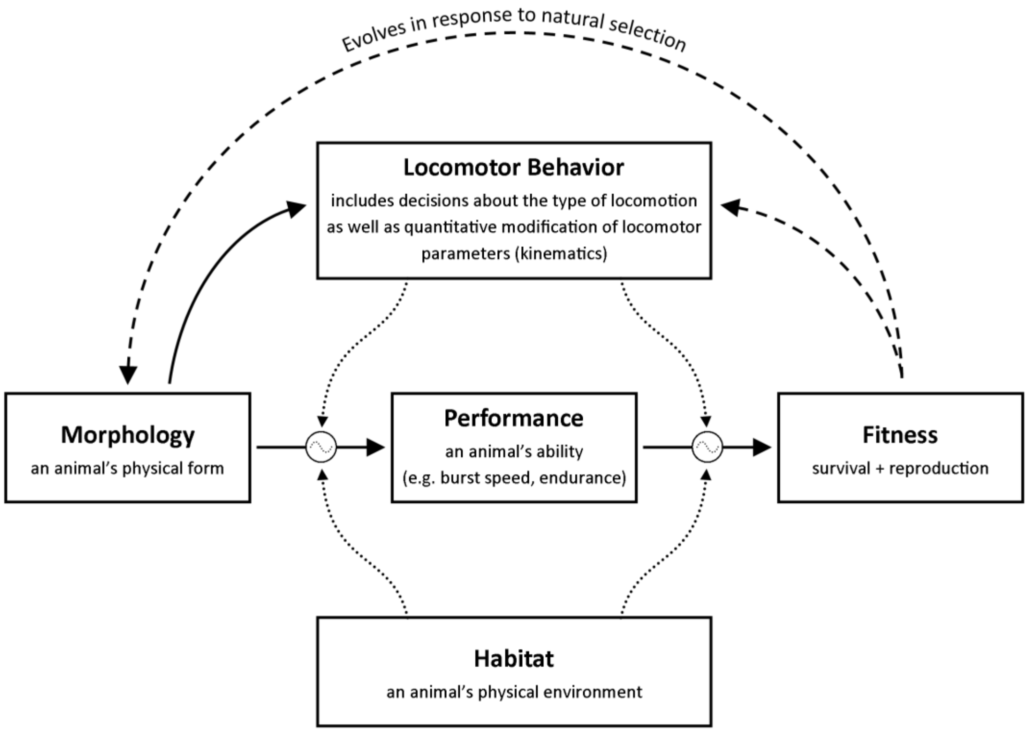
Figure 0.1. Conceptual framework. A. Framework inspired by Arnold's (1983) morphology-performance-fitness paradigm (and later expansions by Garland (1994) and Garland and Losos (1994)). Chapter 1 deals with all of the ideas in this framework. B. The biomechanics scheme characterizes my approach to Chapter 2. C. The macroevolution scheme characterizes my approach to Chapter 3.

A.



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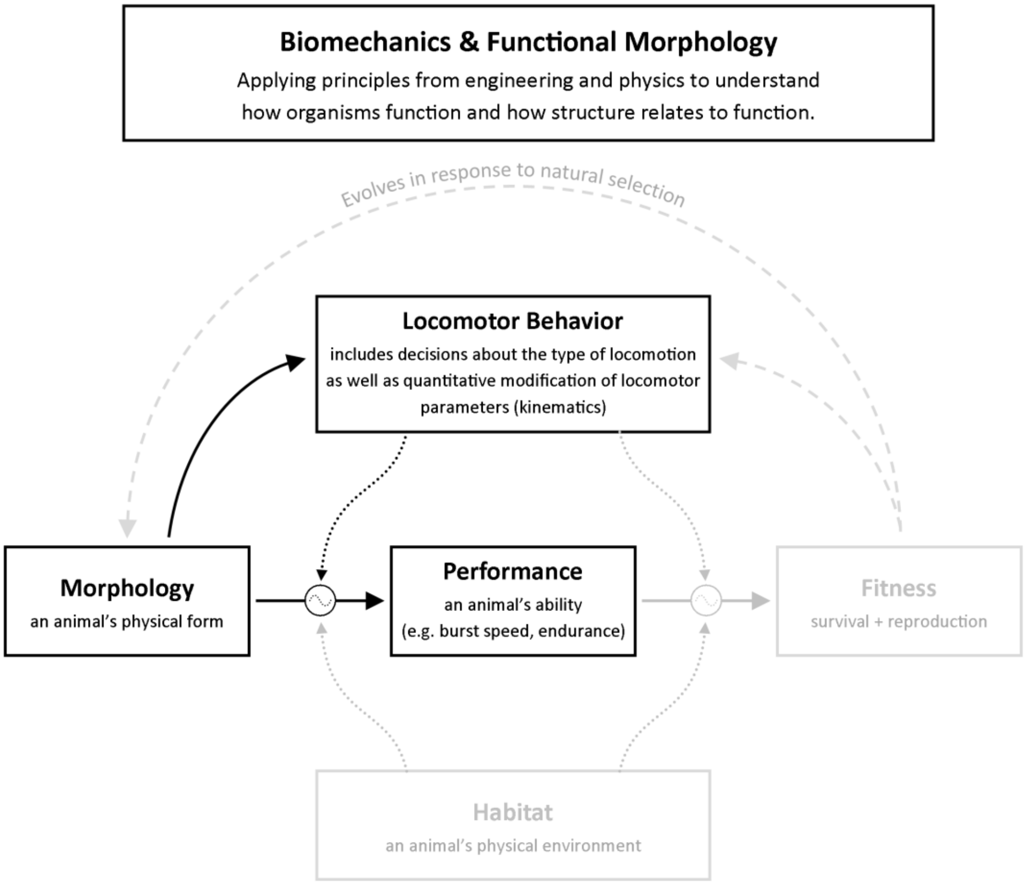
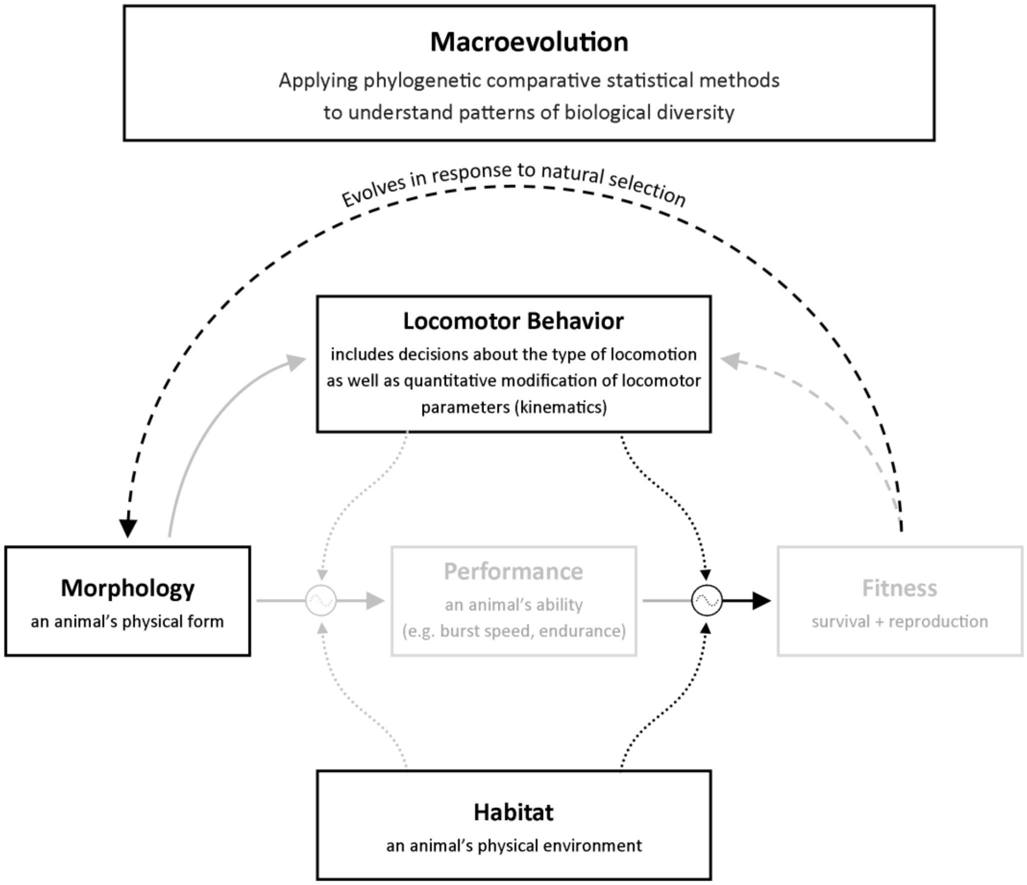

Biomechanics & Functional Morphology
Applying principles from engineering and physics to understand how organisms function and how structure relates to function.
Evolves in response to natural selection
Locomotor Behavior
includes decisions about the type of locomotion as well as quantitative modification of locomotor parameters (kinematics)
Morphology
an animal's physical form
Performance
an animal's ability (e.g. burst speed, endurance)
Fitness
survival + reproduction
Habitat
an animal's physical environment

C.



Macroevolution
Applying phylogenetic comparative statistical methods to understand patterns of biological diversity
Evolves in response to natural selection
Locomotor Behavior
includes decisions about the type of locomotion as well as quantitative modification of locomotor parameters (kinematics)
Morphology
an animal's physical form
Performance
an animal's ability (e.g. burst speed, endurance)
Fitness
survival + reproduction
Habitat
an animal's physical environment

Chapter 1

Facultatively sidewinding snakes and the origins of locomotor specialization

Abstract

Specialist species often possess adaptations that strongly distinguish them from their relatives, obscuring the transitional steps leading to specialization. Sidewinding snakes represent an example of locomotor specialization in an elongate, limbless terrestrial vertebrate. We typically think of sidewinding as a gait that only a handful of very specialized snake species perform, mostly vipers from sandy desert environments. Some of these desert-dwelling vipers are so specialized that they only rarely use more common types of locomotion. However, some non-viper species sidewind facultatively in particular circumstances, and a few may regularly sidewind under natural conditions. Numerous accounts report facultative sidewinding in species that more typically perform other types of locomotion. I have compiled these accounts, uncovering evidence that dozens of species perform sidewinding with varying proficiency under a variety of conditions. These facultative sidewinders can reveal insight into the evolution and biomechanics of sidewinding, and they provide ample opportunities for future study.

Introduction

Elongate, limbless body plans appear superficially simple, with few external parts that interact with the environment. In spite of their simple shape, limbless animals can move in an impressive variety of ways, some more common than others (Jayne 2020). All limbless terrestrial vertebrates can employ some version of lateral undulation, which involves the propagation of a side-to-side wave down the length of the body (Gans 1962). Given its ubiquity, researchers often think of lateral undulation as the most generalized mode of limbless vertebrate locomotion. In contrast, we typically think of sidewinding as a gait that only a handful of very specialized species perform, mostly desert-dwelling vipers (Gans and Mendelssohn 1971; see Fig. 1.1 for a description and illustration). Despite this common perception, several authors have pointed out that a wide variety of species might be able to perform at least a crude version of sidewinding under the right conditions (e.g. Bogert 1947; Cowles 1956; Jayne 1988). Yet, no previous study has attempted to assemble a list of all species known to sidewind. Such a list would provide a starting point for understanding the evolution of sidewinding as well as its biomechanical underpinnings. Here, I review the current knowledge of sidewinding, provide an extensive list of species known to sidewind to varying degrees, and use this list to draw some inferences about sidewinding.

A brief history of research on sidewinding

Sidewinding has long baffled human observers, both literary and scientific. A first-century epic poem from the Roman Empire recounted “cerastes which wanders about as its spine makes it turn" (Lucan, trans. Duff 1928, p. 559). Other writers of antiquity, as well as oral traditions in the Middle East and North America, relate the locomotor peculiarities of sidewinding vipers (Klauber 1997, p. 370). Western science took longer to catch on. By the early 20th century, several authors had published very general descriptions of sidewinding in *Cerastes* spp. and *Crotalus cerastes* (e.g. Ditmars 1908, 1910; Cowles 1920; Klauber 1927), but none had described the kinematics in detail. Mosauer and Wallis (1928) provided the first detailed explanation of sidewinding in the western scientific literature, supplementing their very precise verbal description with a schematic drawing and photographs. Mosauer (1930) went on to further describe the motion in *Cerastes vipera*, emphasizing the role of static contact with the ground as well as vertical lifting of the body. Other authors took an interest in sidewinding over the next century, further detailing the kinematics of steady-state sidewinding (e.g. Gray 1946; Gans and Mendelssohn 1971; Jayne 1986; Gans and Kim 1992) as well as the kinematics of particular tasks, such as ascending slopes or turning (Marvi et al. 2014; Astley et al. 2015). In addition to kinematics, researchers have elucidated some aspects of the muscular mechanisms, energetics, and performance of sidewinding locomotion, mainly in the rattlesnake *Crotalus cerastes* (Mosauer 1935; Jayne 1988; Secor et al. 1992), while others have investigated morphological evolution in vipers specialized for sidewinding (Jayne 1982; Tingle et al. 2017).

Research on sidewinding sparked some debate about whether it had derived from concertina locomotion or lateral undulation, both of which are more common than sidewinding. Gans (1974) emphasized the similarity of sidewinding and concertina locomotion in their use of static contact with the substrate. In contrast, Gray (1946, 1968, pp. 180–181) considered sidewinding and lateral undulation to be essentially the same motion, requiring the same fundamental body deformations. Brain (1960) supported Gray's hypothesis with the argument that a sidewinding snake could generate thrust in the same way as a laterally undulating snake does. According to Brain, the main difference is that in sidewinding, a snake pushes on only one side while lifting the other side up and in the direction of travel. Jayne (1986) also supported the idea that sidewinding derived from lateral undulation, pointing out the existence of a "transitional mode combining lateral undulation and sidewinding" in some species. He later used electromyography to demonstrate that both forms of locomotion involve bilateral activity of the spinalis muscle (Jayne 1988). Finally, he emphasized the continuous propagation of waves in these two types of locomotion, in contrast to concertina locomotion. Overall, the body of evidence favors the possibility that sidewinding derives from lateral undulation (Gray 1946, 1968; Brain 1960; Jayne 1986, 1988). A phylogenetic analysis involving a large number of species could provide further insight into the evolution of sidewinding from a more common locomotor mode.

A phylogenetic survey of facultative sidewinding across the snake family tree

Although some vipers use sidewinding as their primary form of locomotion (e.g. the sidewinder rattlesnake, *Crotalus cerastes*, and Peringuey's adder, *Bitis peringueyi*), multiple authors have noted the existence of facultative sidewinding in a variety of other families (e.g. Ditmars 1908; Cowles 1956; Jayne 1986). However, a comprehensive list of facultative sidewinders has not been available. Therefore, I conducted a literature review, solicited observations of facultative sidewinding from colleagues, and searched for evidence of sidewinding in non-traditional sources (e.g. YouTube videos and news articles). I have compiled this evidence into four tables presented in the appendices to this chapter (Appendices 1.1-1.4).

Appendix 1.1 presents species that use sidewinding as a primary mode of locomotion when undisturbed in their natural habitats, and can therefore be considered specialized. Appendix 1.2 presents species that do not specialize in sidewinding, but that regularly sidewind in their natural habitats. Appendix 1.3 presents species that have not been documented sidewinding when undisturbed in nature, but that readily perform sidewinding under specific conditions, such as on smooth or sandy surfaces, or as an escape behavior. Appendix 1.4 presents isolated or uncertain observations of sidewinding or locomotion resembling sidewinding. I classified species given sometimes limited or contradictory information. For example, it was unclear from various accounts whether *Crotalus atrox* belongs in Appendix 1.3 or 1.4. Because one account did not include details except to say it was "far from being a facsimile of the practiced grace of the sidewinder" (Klauber 1997), and the other account mentioned good sidewinding for only one individual (Cowles 1956), I conservatively placed this species in Appendix 1.4. Accounts for some species conflicted, which may reflect differences among populations, a well-documented phenomenon (cf. Garland and Adolph 1991; Kelley et al. 1997; Burbrink et al. 2000). Many species appeared in only one account and/or were mentioned only briefly. In all of these cases, I conservatively placed the species in the highest sidewinding category that I could confidently determine it belonged to. The tables contain details and citations so that readers can evaluate the information. Further studies of more individuals may show that some species in Appendix 1.4 sidewind readily, or that some species in Appendix 1.3 really do use sidewinding regularly in nature. Finally, absence of evidence does not equal evidence of absence: far more species may sidewind capably than are included in this review.

All of the most specialized sidewinders are vipers (at least 10 species; Appendix 1.1). However, sidewinding is by no means limited to a few specialists. Numerous accounts provide evidence we find that facultative sidewinding is far more widespread than previously thought (Appendices 1.2-1.4). Table 1 summarizes the information in the supplemental tables by family. These numbers challenge the idea that only a few species can sidewind competently, highlighting how much is still unknown about sidewinders and sidewinding.

An ancestral state reconstruction suggests that vipers have independently evolved specialized sidewinding locomotion five times (Fig. 1.2). The reconstruction includes only one character with two states, specialized species vs. species that are not specialized for sidewinding. Although it would be instructive to use more fine-grained information on sidewinding behavior for such reconstructions, sufficient data to do this are not yet available. Two papers have presented lists of species that did not sidewind on level or inclined sand, even when other locomotor modes failed (Marvi et al. 2014; Astley et al. 2020; note that the latter paper extends the list presented in the first). Most of the species tested are pit vipers; Astley et al. (2020) also included a handful of species from Boidae, Pythonidae, and Colubridae. Based on tests of only one or a few individuals per species, these studies suggest that many species may not sidewind, but given the likelihood of individual variation and differences among populations, we must interpret such results with caution. For example, Marvi et al. (2014) and Astley et al. (2020) reported that two cottonmouths (*Agkistrodon piscivorus*) never attempted to sidewind; however, juvenile and subadult cottonmouths perform well-coordinated sidewinding under certain conditions, including on a linoleum floor and on an asphalt road (Bruce Jayne, *pers. comm.*).

Inter-specific differences in sidewinding biomechanics

Given that sidewinding spans more snake families than previously thought, perhaps it is also much more diverse in its mechanisms and/or origins. Distantly related species perform a similar motion, but with wide variation in proficiency—some move with elegant ease while others slip or flail. However, detailed biomechanical comparisons are lacking. Based on reports from the literature and observation of sidewinding snakes (including some captured on video), species seem to vary quantitatively with respect to many metrics. The following paragraphs list some quantities that have been observed to vary among individuals or species (see Fig. 1.3 for a visual depiction of most of these).

Peak curvature and vertebral flexion

Snakes differ in how tightly they bend their bodies during sidewinding, which can be quantified as peak curvature or vertebral flexion. These two quantities are related, but not exactly the same. Peak curvature describes the shape of the body, which affects the snake's interaction with the substrate. Vertebral flexion quantifies what happens internally, between body segments. Various aspects of a snake's morphology mediate the two, including: the number of vertebrae for a given body length, the length of the trunk muscles, and the relative width of the body. In one study that quantified vertebral flexion during sidewinding (Jayne 1988), water snakes (*Nerodia fasciata*) had slightly lower maximal vertebral flexion than did sidewinder rattlesnakes (*Crotalus cerastes*), 7° vs. 10°, although the difference was not statistically significant and the comparison involved only two species that were distantly related (see limitations of such studies discussed in Garland and Adolph 1994). Videos of facultative sidewinders show that species bend their bodies to different degrees. In one extreme case, the anaconda shown in a video by Ryerson and Horwitz (2014) makes such tight bends that the lifted body segments press against each other for almost their entire length, giving the appearance of a line rather than a loop of the body projecting forward during a cycle of sidewinding.

Amplitude and wavelength

Because steady-state sidewinding results from waves propagating down the length of the body, one can quantify such elements as amplitude and wavelength (relative to body length). Astley et al (2015) showed that a snakes' wave amplitude changes during some forms of turns, highlighting the functional consequences of wave properties. Wavelength relative to body length helps determine the number of contact points, which affects stability. Future studies could determine how underlying morphological and physiological traits affect wave properties, and how wave properties in turn affect various aspects performance.

Frequency

Frequency is another wave property that can vary during sidewinding. Along with distance moved per cycle, frequency helps determine the speed of sidewinding. Secor (1992) found that sidewinder rattlesnakes, *Crotalus cerastes*, primarily increase their speed by increasing frequency, not the distance moved per cycle, when moving on solid ground. Marvi et al. (2014) confirmed similar results for *C. cerastes* on sand. Additionally, regressions of velocity on frequency for *C. cerastes*, *Nerodia fasciata*, and *Cerberus rynchops* demonstrated a positive slope and high r^2 values, indicating that increased frequency is indeed an important way for multiple species to increase sidewinding speed (Jayne 1986). Like many other aspects of sidewinding, frequency relates to the conditions eliciting the behavior: a snake trying to make a quick escape from a predator needs to use a higher frequency than does a snake on an unhurried, long-distance trek (*pers. obs.*). Although individual snakes do not always use the same frequency, different sidewinding species (both specialized and facultative) could tend towards higher or lower frequencies. Muscular ability could set a maximum limit on frequency, but higher frequency would not necessarily indicate more proficient sidewinding. Higher frequency could correlate with frantic sidewinding that includes lunges or jumps, which leads to rapid exhaustion (discussed in more detail below).

Number of contact points with the ground

The highly specialized sidewinder rattlesnake (*Crotalus cerastes*) normally maintains two, and occasionally three, separate regions of static contact with the ground during sidewinding (Jayne 1988; Burdick et al. 1993; Marvi et al. 2014). In contrast, the unspecialized water snake *Nerodia fasciata* often pivots around a single region of static contact, and the posterior region never establishes static contact with the ground (Jayne 1988). Other facultative sidewinders may similarly vary in the number of regions on the ground at a given time. Having more regions in contact with the ground likely improves stability and control.

Length of contact patches

Independently of the number of regions in static contact with the ground, a snake may vary the length of each region in contact with the ground. Specialized sidewinders increase the length of static contact regions when they move up slopes, which helps prevent slipping or rolling (Marvi et al. 2014). Although data are lacking, species likely differ in this respect. Facultative sidewinders may or may not have precise control over how much of the body touches the ground at any given time.

Track length

Species also differ in how much of the body they use for sidewinding. This quantity is approximately equal to the length of the individual tracks left by normal sidewinding. After observing the rattlesnake *Crotalus cerastes*, Mosauer (1930) pointed out that it forms the anterior curve starting a few centimeters behind the head instead of at the head or neck, as in *Cerastes* spp. Similarly, Brain (1960) found that *Bitis peringueyi* tracks averaged a length 90% that of the snakes' bodies. Based on my own observations, it seems that some

Nerodia species often do not use the most posterior part of the body when they sidewind, and their tails often flail about wildly. Their locomotion contrasts with that of the sidewinder rattlesnake, which controls almost the entire length of the body during sidewinding, even using part of the tail in the posterior region of static contact (*pers. obs.*).

Distance between tracks

A sidewinder's tracks reflect the kinematics of its motion. For example, the distance between tracks, as drawn between successive resting positions of the head, represents the distance travelled over the course of one sidewinding cycle. This distance was significantly smaller in *Nerodia fasciata* than in *Crotalus cerastes* or *Cerberus rynchops* (Jayne 1986), and it also differs among several vipers that specialize in sidewinding (Gans and Kim 1992). The distance between tracks is analogous to stride length in limbed animals.

Track angle

Sidewinding snakes make tracks oblique to the direction of movement, not perpendicular to it (Mosauer 1930). Track angle is defined as the angle between the tracks and the average direction of motion over one cycle, as determined by the vector drawn between successive imprints of the head. It has been shown to vary among species (Table 2). Some of the values in Table 2 are based on only a few cycles of sidewinding, and they may not be fully representative; however, they do suggest that these species vary in their kinematics. Track angles can also vary among and even within individuals (*pers. obs.*). By uncovering the relationship between the track angle and the kinematic properties of the gait, we can open the door to new research opportunities that would not require tracking the animals' motion, which could be especially helpful for field studies.

Height to which the body is lifted

Different snakes may lift the body to different heights during sidewinding (*pers. obs.*). On one hand, lifting the body higher may allow a snake to clear small obstacles that would otherwise impede its progress. On the other hand, lifting the body higher than necessary could increase the energetic cost of transport. Previous studies have not quantified body lifting in sidewinding snakes, leaving this area completely open for future study.

Amount of slipping

An adept sidewinder slips very little when it proceeds at a slow to moderate pace on level ground, even on a shifting or slippery surface. In sand, its track width nearly mirrors the width of the belly, and an observer can clearly see imprints of the ventral scales (pers. obs.; also, see photos in several publications, e.g. Mosauer and Wallis 1928; Van Riper 1955; Gans and Mendelssohn 1971). A snake moving quickly on level ground, or up a steep slope, might slip in its tracks (*pers. obs.*). In specialized species, we would expect all individuals to sidewind adeptly, without slipping. In facultatively sidewinding species, individuals probably show less proficiency and therefore a greater tendency to slip (pers. obs.; see also description of facultative sidewinding by Natrix maura in Gasc 1974, p. 132, details in Appendix 1.3). They may also show greater intraspecific variation in proficiency/slippage. Because slipping leads to energetic loss, it may be useful as one measure of sidewinding ability or efficiency.

Number and continuity of sidewinding cycles

Specialized sidewinders can sidewind continuously for many cycles, rarely pausing (pers. obs.; see also Secor et al. 1992, who tested Crotalus cerastes on treadmills). Accounts of facultative sidewinders indicate that species vary in the number of sidewinding cycles they can or will perform, with some species managing only a cycle or two before switching to some other type of locomotion or taking a pause (pers. obs.; Cowles 1941; Brain 1960; Klauber 1997). Performance of only one or two sidewinding cycles at a time could result from a lack of ability to sustain sidewinding, but it is probably also strongly tied with a snakes' behavioral tendencies (including motivation), and therefore is likely not a good indicator for sidewinding ability.

Presence of frantic, uncontrolled lunges or jumps

When moving very quickly as an escape behavior and/or when the surface is uncomfortably warm, some species have been observed to propel themselves with enough force that they lunge or jump forward. In the viper *Bitis caudalis*, jumping replaces one or more cycles of sidewinding (Gans and Mendelssohn 1971). In species less proficient at sidewinding, lunging or jumping is sometimes associated with obvious attempts to sidewind (pers. obs.; Ditmars 1908, p. 227; Bergman 1951; Helmcke et al. 1962; Scanlon 2001; details in

Appendices 1.3 and 1.4). As with number and continuity of sidewinding cycles, jumping likely relates not just to a snakes' locomotor abilities, but also it its behavioral tendencies.

The foregoing is not an exhaustive list, but it does indicate that sidewinding varies with respect to many kinematic parameters. Kinematic variation has potentially drastic consequences for performance metrics, such as average sustainable speed, maximum speed, peak acceleration of the center of mass, endurance, etc., which in turn are likely to affect success in various natural behaviors, and hence components of Darwinian fitness. The relative importance of various performance metrics likely depends on the ecology and natural history of the animal in question, e.g. whether the snake uses steady-state sidewinding during its regular movements, at moderate pace, or sidewinding as an escape behavior, which generally involves fast movement over shorter distances. Therefore, areas ripe for further study include quantifying and comparing kinematic variation among and within species, as well as determining its effects on performance.

Another step will be to identify differences in the underlying morphology and physiology that produce this kinematic variation. Jayne (1988) made some progress in that direction by using electromyography to show that species differ in their underlying muscular activity during sidewinding. One would expect many other traits to affect sidewinding kinematics. For example, peak curvature could be influenced by relative number of vertebrae, relative length of the trunk muscles, and/or body width relative to length. Ultimately, an understanding of the mechanisms enabling sidewinding will shed light on the evolution of this specialized locomotor mode (cf. Garland and Carter 1994; Zera and Harshman 2001; Autumn et al. 2002).

Possible adaptive origins of sidewinding

Sidewinding may confer various advantages, leading scientists to hypothesize several potential reasons for its origins that are not mutually exclusive. The present survey of facultative sidewinding can facilitate inferences regarding the likelihood of various adaptive explanations.

Sidewinding vipers generally live in sandy deserts, leading many authors to highlight the likelihood of sidewinding as an adaptation to shifting sand (e.g. Ditmars 1908; Cowles 1920; Mosauer and Wallis 1928; Mosauer 1932a, 1932b). Sandy environments can thwart locomotion. Unlike solid ground, sand can behave as either a solid or a fluid (Duran 2000). Many locomotor activities are particularly intensive on sand because not only does the animal have to move its own center of mass relative to the environment, but it also expends energy moving the sand (Lejeune et al. 1998). In extreme cases, an animal's efforts are entirely wasted on moving the sand around, preventing it from making any forward progress. Moreover, the animal deforms the surface of the sand, which creates further challenges for animals that cannot take long enough steps to avoid their own tracks (Schiebel et al. 2019). The difficulty increases on slopes, where the sand must support its own weight in addition to any applied force. Sand begins to flow downhill at a lower force threshold, as compared with level ground, impeding an animal's ability to climb the slope. Marvi et al. (2014) tested 13 species of pit vipers on level and inclined sand, finding that two non-sidewinding species failed to make forward progress on level sand, while 11 non-sidewinding species failed to progress on sand at a 10° incline. Only one species managed to move on inclined sand using a locomotor mode other than sidewinding (a mixture of concertina and rectilinear locomotion). The sidewinder rattlesnake, *Crotalus cerastes*, predictably had no trouble on level or inclined sand. Its ability to move up sandy slopes has ecological relevance because most habitats do not consist entirely of level ground. In many deserts, for example, slopes ranging from small hummocks to large dunes abound.

Despite the efficacy of sidewinding on sand and the strong association between sidewinding and sandy habitats, some authors have disputed the hypothesis that sidewinding represents an adaptation to sand. Cowles (1956) argued most fervently against this hypothesis. Pointing to the fact that several species manage to use "their standard locomotion" on sand without slipping, he posited that sidewinding offers advantages over other types of locomotion only during frantic movements—this claim makes little sense, considering specialized species use sidewinding during routine locomotion. Additionally, nearly all his examples of non-sidewinding species are colubrid snakes whose bodies are quite slender relative to those of most vipers. The possibility remains that although slender species may be able to progress reasonably well on sand using lateral undulation, heavier-bodied species may have no choice but to sidewind if they are to make reasonable forward progress. The present survey of facultative sidewinding provides evidence that substrate plays at least some role in whether a snake sidewinds. Many accounts demonstrate that a species not normally inclined to sidewind will do so when placed on sand, or on a very smooth artificial surface, such as linoleum (e.g. Mosauer 1930; Gray 1946; Gasc 1974, pp.

129–132; Jayne 1986, 1988; Klauber 1997; Scanlon 2001; details in Appendix 1.3). Some species sidewind on mud, which may present some of the same challenges as sand due to its granular nature (although wet granular materials behave differently from dry granular materials, so mud likely also differs from sand in interesting ways) (Wall 1919; Bustard 1969; Jayne 1986; Jayne et al. 1988, 1995; Chim 2009; details in Appendix 1.2). Even among desert species that regularly sidewind in nature, some of them will use sidewinding on sand but switch to other types of locomotion when placed on crushed aggregate (e.g. Echis spp. and Bitis caudalis; Gans and Mendelssohn 1971). These accounts show that substrate characteristics clearly play a role in inducing sidewinding.

Another potential advantage of sidewinding relates to speed, especially on low-traction substrates. Several authors have claimed that sidewinding snakes can move relatively quickly through obstacle-free terrain, allowing them to minimize time spent in dangerous open areas as they move between patches of shade, food resources, or potential mates (e.g. Cowles 1956; Gans and Mendelssohn 1971). Few studies have reported maximum speeds for sidewinding snakes (Table 3). Maximum speeds range from 1.1 to 5.5 km/h in four species, but only two studies (both on *Crotalus cerastes*) aimed to measure maximum speeds under controlled conditions, testing several individuals in more than one trial each (Mosauer 1935; Secor et al. 1992). One of those also tested five sympatric species that use lateral undulation, and they reached maximum speeds of 0.4, 1.2, 1.9, 2.3, and 5.7 km/h (the slowest was a rosy boa, *Lichanura trivirgata*, and the other four were colubrids) (Mosauer 1935). Several studies have quantified maximum burst speed for laterally undulating garter snakes (*Thamnophis* sp.), which ranged from 1.3 km/h in newborns to

>3.6 km/h in some adults (Arnold and Bennett 1988; Garland 1988; Jayne and Bennett 1990). It is not possible to conclusively compare maximum speeds of the two locomotor modes at this time due to the limited number of studies, variation in snake size, and variation in testing conditions (e.g. substrate, temperature, level of motivation). Additionally, the species tested for sidewinding vs. lateral undulation belong to distantly related clades: the sidewinding species were all vipers, whereas those using lateral undulation were all non-vipers.

Other measures besides burst speed might matter for sidewinding snakes, which may rarely reach their top speeds under normal, undisturbed conditions—Mosauer (1935) found an average prowling speed of 0.14 km/h in *Crotalus cerastes*; and Marvi et al. (2014) similarly recorded speeds of <1 km/h in many trials for this species. For species that use sidewinding over long distances, endurance at a given speed may be especially important. However, only one study has quantified it in sidewinders, demonstrating that *Crotalus cerastes* can sustain sidewinding for 33 to >180 minutes at at 0.5 km/h, and 9 to 52 minutes at 0.7 km/h (Secor et al. 1992). The paucity of data invites further, careful studies of the as well as other limbless locomotor modes under various conditions.

Although sidewinding may or may not confer speed, it clearly has a low energetic cost of transport compared to terrestrial lateral undulation, concertina, or terrestrial limbed locomotion (Secor et al. 1992). Lower energetic cost could allow sidewinding snakes to travel greater distances than snakes moving in other ways. Indeed, several studies have documented long movement distances in several sidewinding species. One study reported that *Crotalus cerastes* travelled an annual mean of 173 m per night over the course of three years, with one individual travelling 1269.2 m in a night (Brown and Lillywhite 1992). Another three-year study at the same site found that 805 tracks averaged 146.7 m, with three tracks measuring more than 900 m (Secor 1994). *Cerastes cerastes* are also known to cover large distances when moving, rarely remaining in the same spot on two consecutive days (Schnurrenberger 1957). One researcher reported "a single track of a two-foot specimen of *Cerastes cerastes* apparently representing continuous travel of more than 400 meters after which the snake inspected a tuft of grass and then moved off, sidewinding further" (Gans and Mendelssohn 1971). Another followed tracks of an individual *Cerastes cerastes* more than 3 km before finding the animal (Kramer and Schnurrenberger 1958). Three individuals of *Cerastes vipera* were each tracked 350–450 m prior to capture (Mermod 1970), and one publication reported that this species makes daily movements on the order of a kilometer or more (Saint Girons and Saint Girons 1959). *Cerastes gasperettii* regularly travels a kilometer or more during a single night (Gasperetti 1988). These distances far exceed those reported for non-sidewinding species, most of which average well under 100 m of movement per day (Landreth 1973; Macartney et al. 1988; Carfagno and Weatherhead 2008; Waldron et al. 2016; although see Brattstrom et al. 2016 for an observation of two Western diamondback rattlesnakes (*Crotalus atrox*) moving 3.28 km over the course of four days). Sidewinding specialists with known daily movement distances fall within the range of values observed for lizards of similar body size, whereas the daily movement distance of many non-sidewinding snakes falls below that range (Garland and Albuquerque 2017).

At least one author has asserted that sidewinding represents an adaptation to hot surfaces: because the lifting motion inherent to sidewinding reduces the proportion of the body in direct contact with the ground, whereas other locomotor modes involve constant contact between the entire body and the ground, sidewinding would hypothetically minimize heat transfer from a hot surface to the snake (Cowles 1956). He had previously noted that three colubrid species, when placed on sand at 60°C, "were stimulated to their utmost speed" and approximated sidewinding (Cowles 1941). Gans (1962) pointed out the need for experimental testing of Cowles' fervently argued but empirically unsupported hypothesis; however, in the ensuing decades, no one has published results for such a test. Considering that many (perhaps all) of the sidewinding desert vipers adopt nocturnal habits during the hottest parts of the year, scorching sand seems unlikely to present a thermoregulatory challenge while the snakes go about their usual ramblings. Moreover, the world's deserts provide a home to not only sidewinders, but also to snake species that use lateral undulation, exposing them to constant full-body contact with the sand. Many of these are slender colubrid species, which generally have a higher surface area to volume ratio than do the sidewinding vipers, and should therefore face a stronger danger of overheating quickly; yet, some of them are diurnal even during hot times. Finally, laterally undulating snakes have been shown to lift portions of their bodies during trials on smooth and rough surfaces at lab temperature, demonstrating that lifting during lateral undulation is not a response to hot surfaces (Hu et al. 2009).

Although I find it highly unlikely that sidewinding evolved to minimize heat transfer on hot surfaces, it could provide some benefits in hot climates. If a snake is forced out of a hiding place during the day when temperatures are high, then the ability to move quickly through open areas may increase the probability that it will find a new refuge before it succumbs to excessive heat or burns its skin. Temperature may also play some role in provoking snakes to sidewind. For example, Gans and Mendelssohn (1971) noted that some vipers used lateral undulation, concertina, or rectilinear on shaded sand, but switch to sidewinding under warmer conditions. Causes other than avoidance of contact with the hot surface could explain this switch. For example, it is well known that ectotherm locomotor performance depends strongly on body temperature, with temperature affecting muscle function such as power output and the maximum force (Bennett 1985, 1990). As sidewinding requires a snake to lift part of its body off the ground, it probably requires relatively high peak muscle force near the apex of the wave. Therefore, a snake whose body temperature is too low may not have the muscle capacity to sidewind. Even the sidewinder rattlesnake, *Crotalus cerastes*, which favors sidewinding over other types of locomotion in nearly all circumstances, may not use sidewinding at low temperatures. They normally do not become active until temperatures reach 17.5–19.5°C, but they have been documented to move at 16°C, at which temperature they use often use rectilinear locomotion (Cowles and Bogert 1944). Therefore, temperature may play a role in eliciting sidewinding because snakes may be unwilling or unable to sidewind below some threshold temperature, which may differ among species. Future studies could explore this hypothesis and its causal mechanism.

Finally, by creating pauses in head movement, sidewinding could plausibly increase acuity of sensory perception. To my knowledge, this hypothesis has not previously appeared in the literature on sidewinding, but it would be consistent with our knowledge of other animals' locomotor behavior. Many animals compensate for motion blur during locomotion by making controlled eye or head movements (e.g. pigeons; Frost 1978; Davies and Green 1988; Troje and Frost 2000), and indirect evidence suggests that other species might use pauses during intermittent locomotion to gather and process sensory information (see Kramer and McLaughlin 2001 for a review). Sidewinding contains intervals where the snakes' head holds still, potentially improving sensory perception compared to lateral undulation, which involves continuous movement of the head. These built-in pauses could improve the snakes' ability to collect visual information, infrared information (for species with heat-sensing pits), and/or chemical information. Not only could sidewinding improve sensory perception by creating pauses in head movement, but it also allows snakes to point their heads in a direction other than the direction of travel. Lastly, sidewinding snakes can move in an apparently backwards fashion, retreating while maintaining eye contact with an aggressor (*pers. obs.*; Brendan Schembri, *pers. comm.*, details in Appendix 1.3). A laterally undulating snake cannot move in reverse.

Based on the existing evidence, sidewinding seems most likely to have arisen in response to difficult substrates and/or the necessity of long-distance travel through wide open spaces. Species that use sidewinding for one of these primary reasons may experience additional benefits. Disentangling the adaptive benefits and causal mechanisms of sidewinding remains a potentially fertile area for further study, one that would benefit from close examination of species that sidewind facultatively in addition to specialized species.

Conclusion

So far, research on sidewinding has mostly focused on a few specialized species, leaving many opportunities to explore its full diversity. Even a cursory look at facultative sidewinding in non-specialized species reveals biomechanical differences. Not only do non-specialized species differ in their biomechanics, but they also differ in their tendency to sidewind and in the conditions that will elicit sidewinding. We can leverage this diversity to deepen our understanding of the evolution of sidewinding, its biomechanics, and underlying neural and physiological mechanisms. More generally, species that sidewind facultatively provide ample opportunities to study coadaptation of sidewinding with other aspects of behavior, physiology, morphology, and life history.

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Table 1.1. A summary of sidewinding observations, by family. For details and citations, see Appendices 1.1-1.4.

	Specialized sidewinders (Appendix 1.1)	Not specialized, but regularly sidewind in nature (Appendix 1.2)	Sidewind under specific conditions (Appendix 1.3)	Isolated or uncertain reports of sidewinding (Appendix 1.4)
Boidae	–	*Candoia aspera*	–	*Boa constrictor* *Eunectes murinus*
Colubridae	–	–	*Natrix maura* *Natrix natrix* *Nerodia fasciata* *Nerodia rhombifer* *Nerodia sipedon* *Nerodia taxispilota* *Opisthotropis typica* *Regina septemvittata* *Storeria dekayi* *Thamnophis* sp. (*elegans or sirtalis infernalis*) *Thamnophis ordinoides* *Thamnophis sirtalis* *Pseudoxenodon macrops*	*Phyllorhynchus decurtatus* *Sonora occipitalis* *Hypsiglena ochrorhynchus* *Thamnophis hammondii*
Elapidae	–	–	*Cryptophis nigrostriatus* *Denisonia devisi* *Ephalophis greyae* *Parasuta dwyeri* *Suta punctata*	*Acanthophis antarticus* *Laticauda colubrina* *Naja tripudians* *Suta suta*
Homalopsidae	–	*Bitia hydroides* *Cerberus australis* *Cerberus rynchops*	*Homalopsis buccata*	*Fordonia leucobalia*
Lamprophiidae	–	–	*Boaedon fuliginosus*	–

Pythonidae	–	–	*Aspidites ramsayi*	*Python bivittatus* *Python curtus*
Tropidophiidae	–	–	*Tropidophis haetianus* *Tropidophis melanurus*	–
Viperidae	*Crotalus cerastes* *Bitis caudalis* *Bitis peringueyi* *Cerastes cerastes* *Cerastes gasperettii* *Cerastes vipera* *Echis carinatus* *Eristicophis macmahoni* *Pseudocerastes fieldi* *Pseudocerastes persicus*	*Crotalus catalinensis* *Bitis cornuta* *Bitis schneideri* *Echis coloratus*	*Agkistrodon piscivorus* *Bothrops ammodytoides* *Bothrops jararaca* *Echis pyramidum*	*Crotalus atrox* *Crotalus helleri* *Crotalus pyrrhus* *Crotalus ruber* *Crotalus scutulatus* *Crotalus viridis* *Bitis arietans* *Bitis gabonica* *Trimeresurus gramineus* *Vipera latastei*
Total	**10**	**8**	**27**	**23**

Table 1.2. A comparison of track angles among species.

Species	Track angle	Source
Bitis peringueyi	mean: 36° (range: 21-47°)	(Brain 1960)
Cerastes cerastes	mean: 26.3° (range: 26-28°)	(Gans and Kim 1992)
Cerberus rynchops	mean: 38.2° (range: 28-47°)	Jayne 1986
Crotalus cerastes	mean: 26° (range: 17-40°)	Brain 1960
	mean: 26.5° (range: 16-42°)	Jayne 1986
Echis carinatus sochurecci	mean: 16.3° (range: 14-19°)	Gans and Kim 1992
Eristicophis macmahoni	mean: 25° (range: 24-26°)	Gans and Kim 1992
Nerodia fasciata	mean: 48.3° (range: 34-55°)	Jayne 1986
Pseudocerastes fieldi	mean: 34.3° (range: 32-37°)	Gans and Kim 1992

Table 1.3. Reported maximum speeds of specialized sidewinding snakes.

Species	Speed	Notes	Source
Bitis caudalis	5.5 km/h	no details on conditions for eliciting speed; two individuals (apparently), unknown number of trials	Hoffmann 1988
Crotalus cerastes	3.3 km/h	burst speed trials on sand, with unknown ambient temperature; several individuals, several trials each	Mosauer 1935
	3.7 km/h	burst speed trials on a track with rubber matting, endurance trials on a treadmill covered in rubber-impregnated cloth; all trials at 30°C ambient temperature; several individuals, two trials each	Secor et al. 1992
Echis coloratus	1.1 km/h	no details on conditions for eliciting speed; unclear how many individuals were tested/observed	Mendelssohn 1965
Pseudocerastes fieldi	1.3 km/h	trials on a serpentarium floor at 30°C ambient temperature; two individuals, apparently one trial each	(Mendelssohn 1965)

Figure 1.1. Sidewinding kinematics. During sidewinding, a snake alternately holds some sections of its body stationary on the ground while lifting other sections up and forward in loops, eventually anchoring them to new stationary points farther along (Mosauer 1930; Gray 1946; Jayne 1986). Drawing traced from high-speed video of *Crotalus cerastes* (~0.6 s intervals).

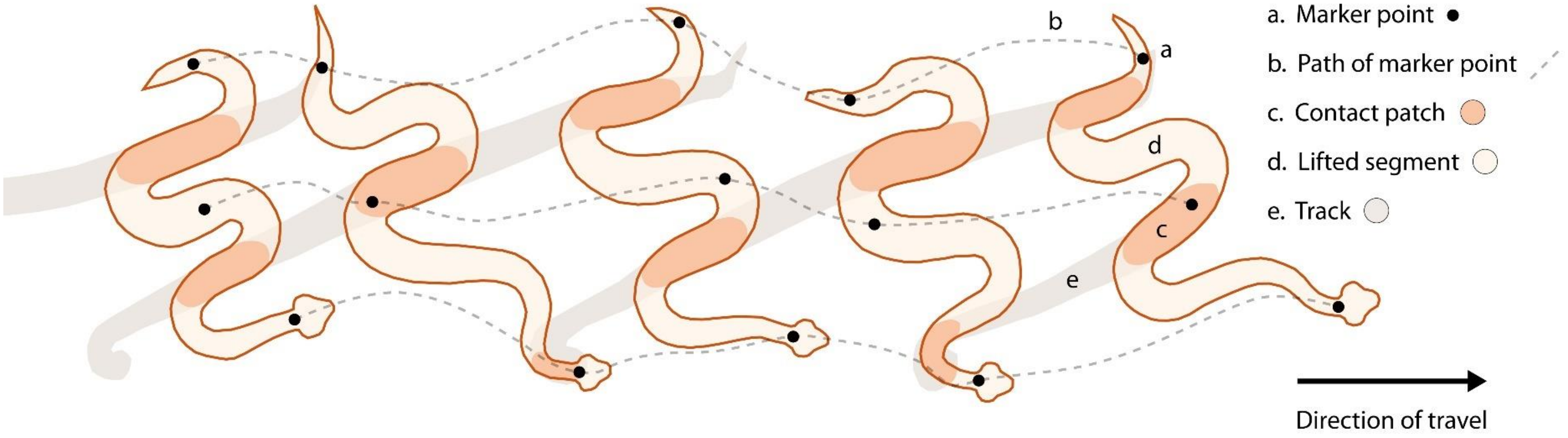
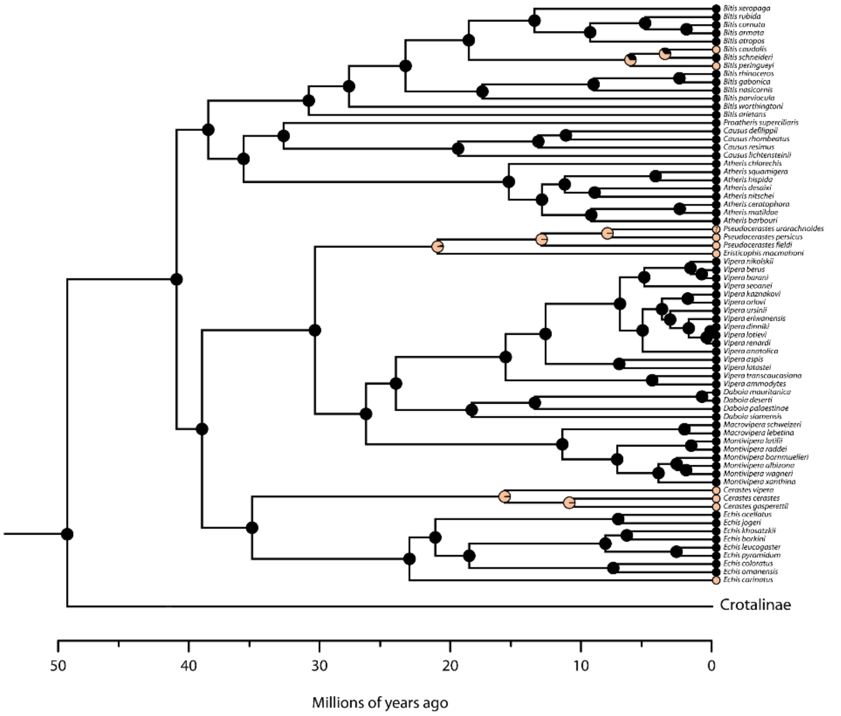


Figure 1.2 Ancestral state reconstruction. Ancestral state reconstruction of sidewinding specialization using maximum likelihood estimates for discrete characters (Pagel 1994), as implemented by the ace function of the R package APE (Paradis et al. 2004). Pie charts at nodes show the likelihood of a specialization for sidewinding locomotion vs. a generalist state. We used the phylogeny from Alencar et al. (2016) and the narrowest categorization of sidewinding specialization, coding species listed in Appendix 1.1 as sidewinding specialists. If we assume that all nodes with >50% likelihood of having the sidewinding state were in fact sidewinders, then specialized sidewinding has evolved 5 times, potentially with a reversal (*Bitis schneideri*, which may show population differences in sidewinding tendency, Appendix 1.2). Note that one species in a sidewinding clade, *Pseudocerastes urarachnoides*, was only recently described (Bostanchi et al. 2006) after having been previously been mistaken for one of its congeners, and it is therefore uncertain whether it is similarly specialized for sidewinding. Panel A (this page) shows the viper subfamily Viperinae. Panel B (next page) shows the viper subfamily Crotalinae.



A. Viperinae

B. Crotalinae

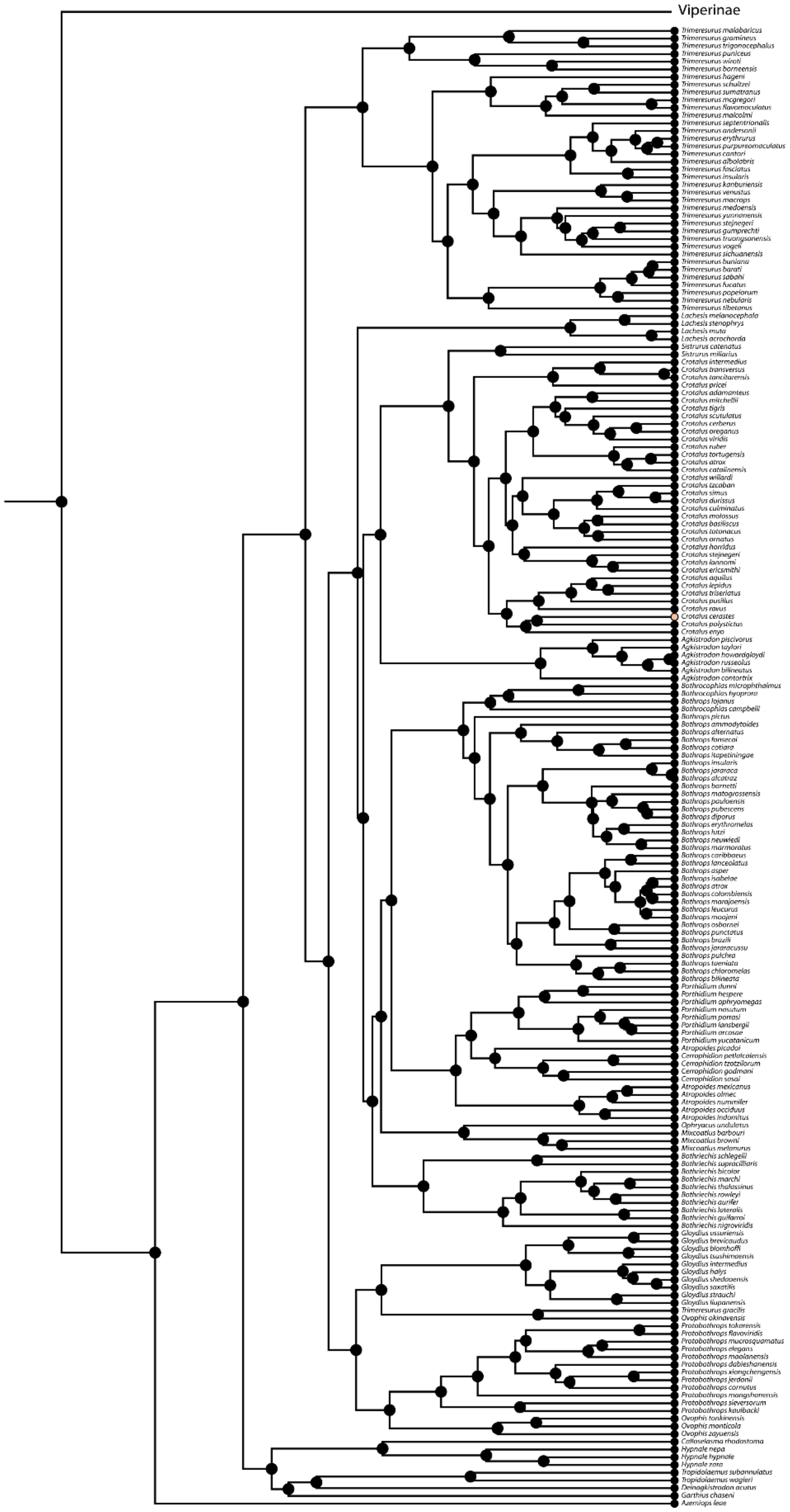
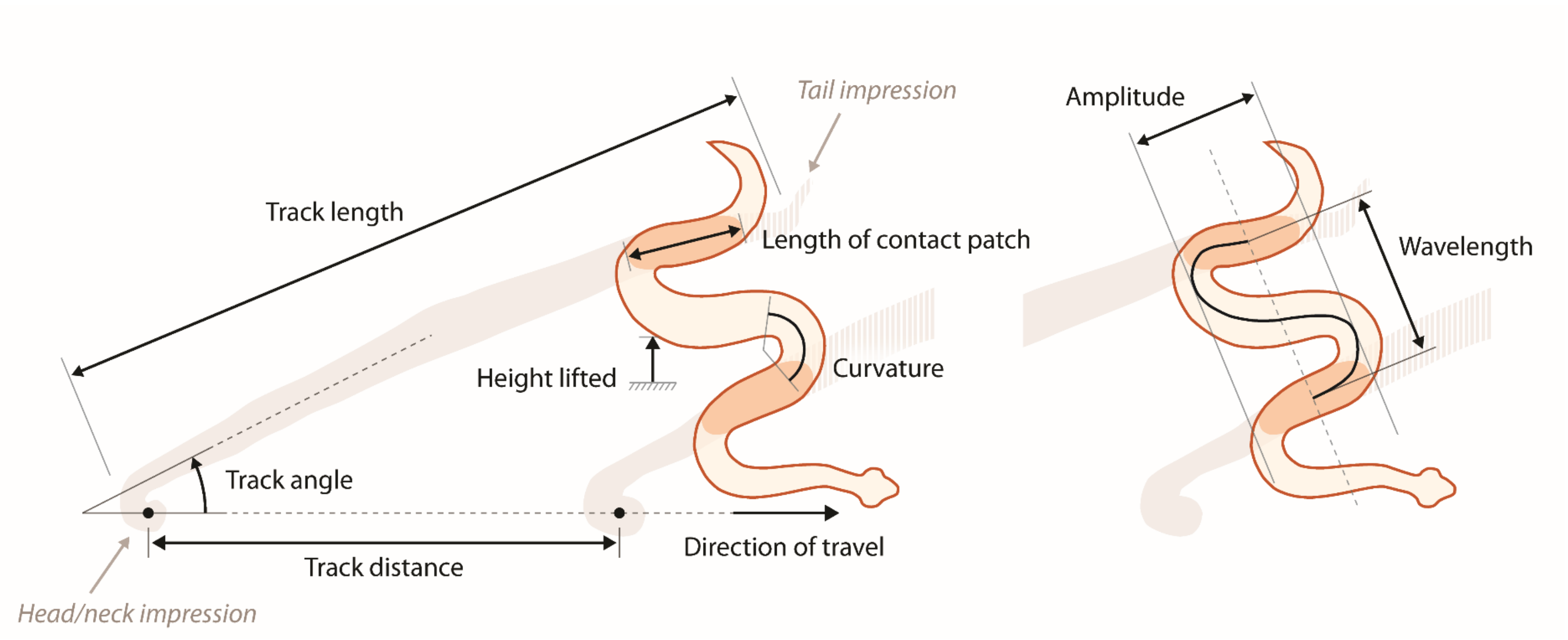


Figure 1.3. Sidewinding variables. This diagram shows some metrics that vary among sidewinding species.



Appendices

Appendix 1.1. These species use sidewinding as a primary mode of locomotion when undisturbed in nature, and can therefore be considered specialized.

family	species	notes	source
Viperidae (Crotalinae)	*Crotalus cerastes*	This species has long been famous for its specialization for sidewinding, earning its common name as early as 1875.	Klauber 1997, p. 371
		It uses sidewinding on almost any terrestrial surface, except when entering and exiting burrows or in very cluttered area around the base of bushes.	Klauber 1997, p. 376; *pers. obs*.
		The young sidewind at birth.	Klauber 1997, p. 376
		Many detailed kinematics studies have focused on this species.	Jayne 1986; Marvi et al. 2014; Astley et al. 2015
Viperidae (Viperinae)	*Bitis caudalis*	"*Bitis caudalis* tends to move across flat surfaces by utilizing lateral undulations, sometimes combined with rectilinear locomotion. When animals are disturbed, and when the surface area to be crossed has been warmed by the sun, specimens tend to utilize sidewinding with the distance between tracks increasing with body temperature." Some specimens will also jump while sidewinding: "The jumping motion, here described, always occurs as a substitution for one or more sidewinding sequences; most of the time the snake is either excited or unusually warm, and it had often engaged in a relatively rapid, but ineffective, sidewinding sequence."	Gans and Mendelssohn 1971
		Uses sidewinding in soft sand, "but not to the same degree of perfection as in Peringuey's adder (*Bitis peringueyi*)."	Broadley 1983

[continued]	[continued]	"The three specimens collected by the author were found on loose gravel and sandy surfaces. Two specimens behaved as follows: when approached, this adder dispelled its seemingly lethargic characteristics by propelling itself across the surface, away from the author, in a side-winding manner (undulations of its body in lateral curves) at a speed calculated at 1.5m/sec. or approximately 5.5km/hour. On sandy surfaces the frictional marks of these undulatory movements were readily observable."	Hoffmann 1988
Viperidae (Viperinae)	*Bitis peringueyi*	When moving rapidly, it uses only sidewinding locomotion. Its tracks are slightly curly compared to those of the horned viper or the sidewinder rattlesnake.	Mertens 1955
		Favors sidewinding over other types of locomotion regardless of "the hardness of the surface over which it moves."	Brain 1960
		Uses sidewinding on sand. They were also tested on crushed aggregate, but the authors did not report their locomotion.	Gans and Mendelssohn 1971
		Newborn individuals used sidewinding on sand immediately upon breaking free of the membranes surrounding them at birth.	Robinson and Hughes 1978
		It is "essentially a sand-living creature", and has perfected the sidewinding motion, with which it can move startling quickly. It manages to sidewind up dune slopes as steep as 45°.	Broadley 1983
Viperidae (Viperinae)	*Cerastes cerastes*	*Cerastes cornuta* (= *Cerastes cerastes*) shows remarkable convergence to *Crotalus cerastes* in its sidewinding locomotion	Mosauer 1932
		Schnurrenberger described field observations on *Cerastes cerastes* and published photographs of sidewinding tracks. This species often travels long distances in the wild. It seems to prefer areas with fine sand (as opposed to coarse sand), but it sometimes occurs in areas where the ground is hard.	Schnurrenberger 1957

[continued]	[continued]	One individual was followed for over 3 km in the wild. Its route consisted of both fine and coarse sand, and where they met, the snake skirted the edge, apparently avoiding the coarse sand in favor of the fine sand.	(Kramer and Schnurrenberger 1958)
		This species used sidewinding during locomotion trials on sand. They were also tested on crushed aggregate, but the authors did not report whether they retained sidewinding or switched to other locomotor modes.	(Gans and Mendelssohn 1971; Gans and Kim 1992)
Viperidae (Viperinae)	*Cerastes gasperettii*	"It is a true sidewinder, never having been seen to employ any other type of locomotion."	(Gasperetti 1988)
Viperidae (Viperinae)	*Cerastes vipera*	A "flourishing colony" lived at the New York Zoological Park (now the Bronx Zoo) in the early 20th century, distinguishing themselves by their tendency to sidewind rapidly about their cage. Given that the zoo also possessed multiple *Cerastes cerates*, and the curator in charge of reptiles did not mention any observations of sidewinding for the latter species, *Cerastes vipera* may show a stronger tendency to sidewind than does *C. cerastes*.	(Ditmars 1910, p. 329), p. 329
		Early studies to clarify sidewinding kinematics focused on this species.	(Mosauer and Wallis 1928; Mosauer 1930)
		Tracks for three separate individuals showed that they had each travelled 350-450 m in a single night, using sidewinding.	(Mermod 1970)
Viperidae (Viperinae)	*Echis carinatus*	"Being an inhabitant of sandy biotopes, *Echis carinata* probably developed sidewinding locomotion as an adaptational mechanism, enabling it to move over sandy terrain, as did other sidewinders." Like *E. colorata*, *E. carinatus* uses sidewinding on sand or smooth surfaces, or when hurrying. However, *E. carinatus* tends to lift its body higher during sidewinding than does *E. coloratus*, "as the typical sidewinders do."	Mendelssohn 1965

[continued]	[continued]	The subspecies *E. carinatus carinatus* "shows almost no sidewinding" while *E. c. leakeyi*, *E. c. sochureki* and *E. c.* sp. from Ethiopia and Northern Kenya do. Additionally, although many *Echis* species use sidewinding on sand, they switch to other modes on crushed aggregate.	(Gans and Mendelssohn 1971)
Viperidae (Viperinae)	*Eristicophis macmahoni*	It is "well adapted to life on shifting sands," including the evolution of "the very specialized habit of sinking into the sand," a behavior observed in few other sand-dwelling species.	(Mendelssohn 1965)
		They used sidewinding when tested on sand; although they were also tested on crushed aggregate, the authors did not report the results.	(Gans and Mendelssohn 1971; Gans and Kim 1992)
Viperidae (Viperinae)	*Pseudocerastes fieldi*	"It is a sidewinder and uses side winding more than *Echis colorata* does, in the typical way, lifting its coils clear off the ground. It uses side winding when moving on a level surface of sand, or, sometimes, on hard, level ground, especially if the surface is smooth, e.g. on a road or on a floor. On such ground the snake sidewinds, especially when frightened, or when ill at ease, for instance, if it is put on such a surface during the day, exposed to the full glare of the sun." "*Pseudocerastes* pays much attention to other sidewinding snakes, whether of its own or of other species. Upon sighting a sidewinding snake it adopts the same type of movement to pursue and overtake the latter, and then uses its tongue to probe and inspect it... Crawling specimens do not arouse the same interest as do sidewinding ones."	(Mendelssohn 1965)
		Uses sidewinding on sand. They were also tested on crushed aggregate, but the authors did not report their locomotion.	(Gans and Mendelssohn 1971; Gans and Kim 1992)

Viperidae (Viperinae)	*Pseudocerastes persicus*	"Capable of sidewinding." Note: this source considered *P. persicus* and *P. fieldi* as two subspecies of *P. persicus* - it seems probable that they are similar in their sidewinding behavior.	(Spawls and Branch 1995)

Appendix 1.2. These species don’t specialize in sidewinding, but they regularly sidewind in nature.

family	species	notes	source
Boidae	*Candoia aspera*	Regularly uses sidewinding to cross soft, wet mud. Based on a verbal description and a figure drawn from a film of the locomotion, *Candoia* may throw itself forward during this motion, rather than employing a smooth, controlled motion like that of sidewinding vipers like *Crotalus cerastes* or *Bitis peringueyi*.	Bustard 1969
Homalopsidae	*Bitia hydroides*	"Similar to *Cerberus*, we observed *Bitia* using lateral undulatory swimming through water and loose mud and using proficient sidewinding on the surface of harder mud."	Jayne et al. 1995
Homalopsidae	*Cerberus australis*	"When progressing along the ground, a coil of the body is thrown forwards in advance of the head, and then the head is advanced. This action reminds one of the action of the American sidewinder."	Kinghorn 1956
Homalopsidae	*Cerberus rynchops*	A primarily aquatic snake, many individuals were observed on a mud flat exposed after the tide ran out. In this situation, "Its mode of progression is curious. The body is thrown forward in a curve in advance of the head, and the head subsequently advanced, the body being again thrown forward before the snake quite extends itself. It gives the impression of moving sideways."	Wall 1919

[continued]	[continued]	"During field work, I frequently observed sidewinding by undisturbed *Cerberus*on tidal mud flats in Malaysia." This species will readily perform sidewinding as well as lateral undulation on sand, apparently without the need to frighten a snake to elicit sidewinding (unlike for *Nerodia fasciata* in the same study). It may also use sidewinding and lateral undulation when moving on sand: "This snake made a series of parallel tracks (impressions in the sand) grossly resembling the shape and orientation of those produced during sidewinding. During one cycle of activity, the snake displayed R, L, R movement which normally indicates sidewinding. Yet, this snake never established static contact with the substrate and hence was combining aspects of sidewinding with lateral undulation. Rather than the snake stopping as it touched the end, the snake slid within each track (parallel to the length of the track)." "As *Cerberus* increased its speed while moving on sand, pure lateral undulation, lateral undulation combined with sidewinding and then pure sidewinding were used." Kinematics of *Cerberus* sidewinding on sand differ somewhat from kinematics of *Crotalus cerastes*.	Jayne 1986
		In their natural habitat in Malaysia, "snakes usually performed sidewinding locomotion on mud that was firm enough to support their weight. If snakes sank in mud past the first few dorsal scale rows, then lateral undulation was used for surface locomotion as well as swimming through the mud slightly below its surface."	Jayne et al. 1988

[continued]	[continued]	An individual was observed sidewinding on tidal mudflats at a wetland reserve in Singapore.	Chim 2009
Viperidae (Crotalinae)	*Crotalus catalinensis*	“Often sidewinds when moving rapidly across the ground and climbs into vegetation to escape.”	Grismer 2002, p. 326
Viperidae (Viperinae)	*Bitis cornuta*	A captive specimen from the Cape Province, apparently a juvenile only a few weeks old, was observed sidewinding.	Mertens 1955
		"Like *B. xeropaga*, this species is commonly found on rocky mountain sides, but like *Bitis peringueyi and caudali*, it is very fond of burying itself in the sand…" "Together with *caudalis* it displays a sidewinding movement over loose sandy surfaces, but not to the same degree of perfection as Peringuey's or Namid adder (*Bitis peringueyi*).	Broadley 1983
		"It rarely sidewinds or shuffles into loose sand."	Branch 1988
Viperidae (Viperinae)	*Bitis schneideri*	"A specimen collected about 20 km W of Aurus Mountain, Diamond Area 1, was photographed sidewinding up a dune" "It frequently sidewinds and also buries itself in sand."	Haacke 1975
		When moving, "it uses the characteristic rapid sidewinding locomotion that adapts it to its sandy environment."	Hurrell 1981
		"It frequently sidewinds and also buries itself in the sand."	Broadley 1983
		"It sidewinds readily."	Branch 1988
		“South African *schneideri* never showed any signs of sidewinding (over three years of following tracks). However, several of the animals that we found in Namibia did show 'sidewinder' type tracks. This was mostly across largish gaps in the vegetation.”	Bryan Maritz, *pers. comm.*

Viperidae (Viperinae)	*Echis coloratus*	"*Echis colorata* is a sidewinder, like most other desert viperids. Species which show this kind of locomotion are generally inhabitants of more or less sandy areas, *Echis colorata* apparently being the only exception." Mendelssohn hypothesized that the ancestor of *Echis colorata* probably lived on sandy soils and used sidewinding, and that *Echis colorata* retained sidewinding even though it prefers rocky slopes and "is never actually encountered on sandy soils." "Side winding is not an efficient means of locomotion in the typical biotope of *Echis colorata* and is not regularly used by this species. The employment of sidewinding depends to a certain degree on the substrate on which the snake is moving, and on its state of stimulation." "On hard, level ground, e.g., on a smooth road or on a floor, pure side winding is used when the snake is hurrying, otherwise serpentine and rectilinear movements are combined with side winding. On level, rough ground, *Echis colorata* progresses by serpentine and rectilinear movement, side-winding only being resorted to if the snake is extremely frightened." "*Echis colorata* tends less to lift its coils, but rather to push them ahead on the ground."	Mendelssohn 1965
		They used sidewinding when tested on sand, lateral undulation on crushed aggregate.	Gans and Mendelssohn 1971

Appendix 1.3. These species have not been documented sidewinding when undisturbed in nature, but they readily sidewind under specific conditions.

family	species	notes	source
Colubridae (Natricinae)	*Natrix maura*	When it performed sidewinding on a smooth surface in the lab, it maintained three regions of static contact with the ground at any given time. It differed from sidewinding vipers like *Cerastes cerastes* in that it moved more quickly, and it maintained shorter segments of the body in static contact with the ground, while the raised segments of the body were relatively long. It appeared to waste considerable energy due to slippage. Sidewinding appears to have been induced as an escape behavior.	Gasc 1974, pp. 129-132
Colubridae (Natricinae)	*Natrix natrix*	"When a grass snake moves over a relatively smooth and uniform surface its mode of progression tends to be irregular, and serpentine movement is replaced either by side-winding, or by concertina movement, or a combination of the two. The precise mechanical conditions of the substratum necessary for the elicitation of sidewinding in its most characteristic form cannot be defined at present, but an instance is shown in PI. 6(C), in which the animal is moving over a painted metal plate." This species would not or could not sidewind on sandpaper.	Gray 1946
		Performed sidewinding on a smooth surface in the lab (fig. 106 shows *Natrix natrix*; most of the rest of the discussion in this paper seems to focus on *Natrix maura*).	Gasc 1974, pp. 129-132

Colubridae (Natricinae)	*Nerodia fasciata*	Small individuals readily performed a combination of lateral undulation and sidewinding when placed on sand, but they normally had to be frightened to perform pure sidewinding. Velocity profiles showed that when sidewinding, it was more variable than either *Crotalus cerastes* or *Cerburus rynchops* in terms of when, during a cycle, it reached its maximum speed. It remained in static contact with the ground for less time than did *Crotalus cerastes*.	Jayne 1986
		Jayne used electromyography to characterize the muscular activity of *N. fasciata* sidewinding on a linoleum floor.	Jayne 1988
		Some neonates sidewind when placed on sand, with varying proficiency.	*pers. obs.*
Colubridae (Natricinae)	*Nerodia rhombifer*	Some large *Nerodia rhombifer* (~450 g) used sidewinding "on an unpaved road that consisted of compacted clay and rounded gravel. Although most of the sidewinding was high-speed and nearly jumping, at one point they slowed down and had a beautifully coordinated pattern of sidewinding."	Bruce Jayne, *pers. comm.*
		Some neonates sidewind when placed on sand, with varying proficiency. Some larger individuals also sidewind on sand.	*pers. obs.*
Colubridae (Natricinae)	*Nerodia sipedon*	Some neonates sidewind when placed on sand, with varying proficiency.	*pers. obs.*
Colubridae (Natricinae)	*Nerodia taxispilota*	Some neonates sidewind when placed on sand, with varying proficiency.	*pers. obs.*
		Several have been observed sidewinding quickly and proficiently across a paved road as an escape behavior.	Noah Carl, *pers. comm.*

Colubridae (Natricinae)	*Opisthotropis typica*	An adult performed proficient sidewinding when placed on a flat cement floor in captivity. Two sections of the body were in contact with the floor at a given time, and the front of the body was lifted well above the floor while moving. Was "easily induced to perform this sidewinding motion continuously" except when exhausted.	Mori 1993
Colubridae (Natricinae)	*Regina septemvittata*	Some neonates sidewind when placed on sand.	Bruce Jayne, *pers. comm.*
Colubridae (Natricinae)	*Storeria dekayi*	"Capable of adopting a movement essentially like the sidewinding of *Cerastes vipera* when they are obliged to move on a smooth floor."	Mosauer 1930
Colubridae (Natricinae)	*Thamnophis* sp.	Ditmars reported sidewinding in "*Eutaenia elegan*s variety *infernalis*," which may refer to either *Thamnophis elegans* or *Thamnophis sirtalis infernalis*." "It progresses in a rapid series of close, S-shaped movements and generally in an oblique direction to that in which the head is pointing-an evolution performed, though at greatly reduced speed, by the 'side-winder' rattlesnake. While making off in this fashion, if the snake is closely pursued, it will actually leap forward, for a distance of nearly a foot, by suddenly straightening the body." "Of a large number of specimens, comprising three separate shipments, all displayed the same agile movements."	Ditmars 1908, p. 227
		They "sidewind with considerable success" when placed on a smooth surface.	Klauber 1997, p. 375

Colubridae (Natricinae)	*Thamnophis ordinoides*	Higham captured video for several (~10) adult individuals from a population on Vancouver Island, which sidewind readily and very proficiently when placed on soft beach sand.	Tim Higham, *pers. comm.*
Colubridae (Natricinae)	*Thamnophis sirtalis*	"Capable of adopting a movement essentially like the sidewinding of *Cerastes vipera* when they are obliged to move on a smooth floor."	Mosauer 1930
		They occasionally use sidewinding when attempting to escape rapidly while on a linoleum floor.	Bruce Jayne, *pers. comm.*
		Performs incipient sidewinding. If the snake is rushed, this movement turns into jumping with a stretched body.	Helmcke et al. 1962
Colubridae (Pseudoxeno-dontinae)	*Pseudoxenedon macrops*	A young individual performed proficient sidewinding when placed on a flat cement floor in captivity. Two sections of the body were in contact with the floor at a given time, and the moving portions of the body were lifted only slightly, such that they slid along the ground. Was "easily induced to perform this sidewinding motion continuously" except when exhausted.	Mori 1993
Elapidae	*Cryptophis nigrostriatus*	Sidewinds in a manner similar to *Parasuta dwyeri* and *Suta punctata* except that “the anterior part of the more elongate body forms more regular waves”	Scanlon 2001
Elapidae	*Denisonia devisi*	When tested on a smooth wooden table, it “has a relatively slow and ‘deliberate’ sidewinding pace, at least as an adult. This was observed within hours after obtaining a specimen… so it is surprising that it has not been recorded previously.”	Scanlon 2001
Elapidae	*Ephalophis greyae*	A video recording shows one individual sidewinding slowly and deliberately across sand, with well-coordinated movements.	Brendan Schembri, *pers. comm.*

Elapidae	*Parasuta dwyeri*	When tested on a smooth wooden table, they “have a rapid style of sidewinding in which the posterior body and tail appear to ‘flick’ against the substrate, reminiscent of the saltational escape locomotion of [the pygopodid lizard] *Delma* spp.”	Scanlon 2001
Elapidae	*Suta punctata*	When tested on a smooth wooden table, they “have a rapid style of sidewinding in which the posterior body and tail appear to ‘flick’ against the substrate, reminiscent of the saltational escape locomotion of [the pygopodid lizard] *Delma* spp.”	Scanlon 2001
Homalopsidae	*Homalopsis buccata*	The following description applies to an unspecified number of individuals, apparently observed on a tiled laboratory floor: "On dry land, the animal rises the first third of the body, takes the head a little backwards and projects it then forward with some strength so that the body seems to be dragged after it. This is repeated and the animal proceeds thus more or less litterally [sic] with leaps and bounds. However the movement can be swift and makes then at first the impression of gliding with waves in a vertical plane, more than that of jumping."	Bergman 1951
Lamprophiidae	*Boaedon fuliginosus*	Normally uses lateral undulation, but "when released on a smooth surface, devoid of adequate superficial projections, resorts to sidewinding which allows fairly rapid locomotion. The movement is, however, seldom regular and is punctuated by frequent stops. This fact makes it difficult to obtain a satisfactory track on sooted cardboard since after producing two or three parallel lines, the snake is inclined to rest and then on starting again, to erase the existing tracks with its tail. Fortunately, some undamaged records have been obtained and these do not differ substantially from the ones made by Peringuey's adder."	Brain 1960

Pythonidae	*Aspidites ramsayi*	A video shows one individual sidewinding very slowly on apparently firm, open ground, keeping its body behind its head relative to the person recording the video.	Brendan Schembri, *pers. comm.*
Tropidophiidae	*Tropidophis haetianus*	Two juveniles and one adult male, all captured in the wild, used sidewinding as an escape behavior. "All three animals used the same pattern of locomotion on a variety of substrates, including a tile floor, carpet, a tightly stretched sheet, poured concrete, grass, and sand. The adult female was gravid and resisted all attempts to induce movement by refusing to uncoil from a defensive ball. The sidewinding pattern (Fig. 1) resembled that of *Crotalus cerastes* and left a similar track in sand. It differed, however, in that the direction of movement was more parallel to the long body axis than in sidewinding rattlesnakes. Individuals 'looped' their bodies to either the left or right as they moved in a forward direction."	Smith et al. 1991
Tropidophiidae	*Tropidophis melanurus*	It "is a far more capable sidewinder than any colubrid that I have seen.”	Bogert 1947
Viperidae (Crotalinae)	*Agkistrodon piscivorus*	When placed on a linoleum floor, a juvenile performed well-coordinated sidewinding with several successive cycles of movement, allowing Jayne to collect EMGs (unpublished data). On another occasion, he observed similarly nice sidewinding of sub-adults on an old asphalt road in southern Florida.	Bruce Jayne, *pers. comm.*
Viperidae (Crotalinae)	*Bothrops ammodytoides*	They sidewind across both sand and gravel as an escape behavior.	Robert Espinoza, *pers. comm.*; YouTube: gavensmar

Viperidae (Crotalinae)	*Bothrops jararaca*	Small individuals have been observed using “a locomotor mode similar to sidewinding (apparently combined with lateral undulation)” when “found away from cover and fleeing over open areas with smooth surfaces, such as sandy trails.”	Sazima 1992
Viperidae (Crotalinae)	*Echis pyramidum*	"When agitated may also sidewind, moving at astonishing speed!"	Spawls and Branch 1995

Appendix 1.4. This table includes isolated or uncertain observations of sidewinding or locomotion resembling sidewinding.

family	species	notes	source
Boidae	*Boa constrictor*	Gans and Mendelssohn claimed to have footage of a medium-sized "*Constrictor*" (presumably *Boa constrictor*) performing "a primitive form of sidewinding."	Gans and Mendelssohn 1971
Boidae	*Eunectes murinus*	One individual resorted to sidewinding in an attempt to escape humans on firm, grassy ground (captured on video).	Ryerson and Horwitz 2014; YouTube
Colubridae: Colubrinae	*Phllorhynchus decurtatus*	When placed on very hot sand (60°C), they "were stimulated to their utmost speed" and approximated sidewinding, but based on a photograph of their tracks, they performed only a limited number of cycles in between bouts of lateral undulation, and they did not lift their bodies completely off the ground as a proficient sidewinder would.	Cowles 1941
Colubridae: Colubrinae	*Sonora occipitalis*	When placed on very hot sand (60°C), they "were stimulated to their utmost speed" and approximated sidewinding, but based on a photograph of their tracks, they performed only a limited number of cycles in between bouts of lateral undulation, and they did not lift their bodies completely off the ground as a proficient sidewinder would.	Cowles 1941
Colubridae: Dipsadinae	*Hypsiglena ochrorhynchus*	When placed on very hot sand (60°C), they "were stimulated to their utmost speed" and approximated sidewinding, but based on a photograph of their tracks, they performed only a limited number of cycles in between bouts of lateral undulation, and they did not lift their bodies completely off the ground as a proficient sidewinder would.	Cowles 1941
Colubridae: Natricinae	*Thamnophis hammondii*	Secondhand report of sidewinding over hard, open ground.	Cowles 1956

Elapidae	*Acanthophis antarticus*	"H. Ehmann (pers. comm., 1999) records sidewinding in two additional species not covered by my own observations. In about 1970 he observed (and filmed) sidewinding by a hot and agitated adult *Acanthophis antarcticus* (Southern Death Adder): 'It was a recently captured SA coastal adult released to "perform" on a bare and rather warm dense, fine red sand dune about 400 km inland.'"	Scanlon 2001
Elapidae	*Laticauda colubrina*	Twenty-four Banded Sea Kraits were found together in a sandy area, in close association with tracks resembling sidewinder tracks. The tracks appeared to have been made by at least eight different individuals.	Heatwole and Abbott 1998
Elapidae	*Naja tripudians*	Wall reported a secondhand observation of "peculiar progression" that "moved along like a huge caterpillar, hunching his back, and then using his head as a fulcrum to draw himself along" - it is unclear whether this locomotion represents sidewinding, and it is also unclear whether the snake moved strangely in a desperate escape attempt, or whether it may have been injured.	Wall 1907
Elapidae	*Suta suta*	"Ehmann (pers. comm.) also states that *Suta suta* (Curl Snake) sidewinds, 'at least big/fat/gravid ones'."	Scanlon 2001
Homalopsidae	*Fordonia leucobalia*	"Two specimens were found under a pile of timber at an aboriginal camp site on a sandbank in a mangrove swamp at Cape Don. Their presence was indicated by tracks made in the sand early in the morning; the tracks indicate that this species progresses by a distinctive 'sidewinding' locomotion."	Cogger and Lindner 1974

Pythonidae	*Python bivittatus*	A python (presumably a Burmese Python) was captured on video using a sidewinding-like motion to cross a smooth floor after it fell through the ceiling of a Chinese bank. The snake does not perform many cycles of the motion. This video was shared on YouTube, and many news outlets reported the story.	e.g. BBC, Global News, The Independent, NDTV, Science Alert, YouTube: CCTV
Pythonidae	*Python curtus*	In tests of crawling endurance involving nine wild-caught individuals, they soon switched from lateral undulation to sidewinding.	Rozar 2010

Viperidae: Crotalinae	*Crotalus* spp. *(atrox, helleri, pyrrhus, ruber, scutulatus, viridis)*	Klauber placed several rattlesnake species on "polished wood or linoleum floors to determine the degree to which they would adopt sidewinding on surfaces unsatisfactory for ordinary snake locomotion. In general, although it was noted that all of these rattlers could and did sidewind, the motion was far from being a facsimile of the practiced grace of the sidewinder. First, the coils were not as widely thrown, and they were more nearly perpendicular to the axis of the body rather than at a sharp angle, as with the sidewinder. The several elements of motion were not even and continuously flowing; rather, they tended to be spasmodic and separate. The result was a much reduced efficiency, as measured by speed and expended effort. Some of the rattlers were virtually reduced to purposeless thrashing, or at least to a continuous effort to find irregularities in the floor surface that might serve as pegs against which to push the body." "In my experiments, I found that much depended on the snake's objective and the degree of its alarm. Those that were not unduly frightened tried all forms of locomotion, at times simultaneously with different elements of the body; they mixed all combinations-undulatory, sidewinding, rectilinear, and concertina-in their endeavors to get a purchase on the smooth floor."	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus atrox*	One individual gave “a seemingly perfect duplication of sidewinding,” apparently on a hot surface.	Cowles 1956

[continued]	[continued]	See Klauber’s description under *Crotalus* spp. "Dr. R.B. Cowles has advised me by letter that one western diamond back (*C. atrox*), a snake that lives in sidewinder territory, but does not ordinarily sidewind, when placed on linoleum went into perfect sidewinding and flowed across the floor without the slightest effort or confusion." (this account may correspond to the same individual mentioned in Cowles 1956)	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus helleri*	See Klauber's description under *Crotalus* spp. "One southern Pacific rattler (*C. v. helleri*) was fairly successful" at sidewinding when placed on a smooth floor.	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus pyrrhus*	Young of this species have been observed to resort to sidewinding (or something resembling it) in situations of extreme fear or discomfort.	Cowles 1941
		See Klauber's description under *Crotalus* spp.	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus ruber*	See Klauber's description under *Crotalus* spp.	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus scutulatus*	See Klauber's description under *Crotalus* spp.	Klauber 1997, p. 375
Viperidae: Crotalinae	*Crotalus viridis*	See Klauber's description under *Crotalus* spp.	Klauber 1997, p. 375
Viperidae: Viperinae	*Bitis arietans*	"When forced to move rapidly on a flat surface even *Bitis arietans* resorts to sidewinding, but it is a crude performance compared to that of *Crotalus cerastes*."	Bogert 1947
		"When attempting to escape it can move quickly, in a rather stiff-bodied lateral undulation that is reminiscent of sidewinding."	Spawls and Branch 1995

Viperidae: Viperinae	*Bitis gabonica*	Ditmars described it as a “looper” or “sidewinder” without stating the source of his information. He also called it a creature of "sterile, sandy places" when they are now known to primarily inhabit rainforests, leading one to question the veracity of his account.	Ditmars 1910, p. 325
Viperidae: Viperinae	*Trimeresurus gramineus*	“One brought to me alive moved in a remarkable manner. It threw forward its body, and then advanced the head and forebody till straight, and repeated the action. It thus appeared to progress sideways, and did so in a laboured fashion.”	Wall 1926
Viperidae (Viperinae)	*Vipera latastei*	A book on the wildlife of Andalusia shows a photograph of *V. latastei* tracks in the sand at Coto Doñana. These tracks clearly do not correspond to sidewinding locomotion.	Vaucher 1967
		“The southern subspecies, *V. l. gaditana* is a good sidewinder in the sand dunes of Coto Donana in southern Spain.”	Mallow et al. 2003
		The information in Mallow et al. (2003) comes from the observations of one of the book's authors, who has seen tracks associated with *V. l. gaditana* in sand dunes on several occasions.	Göran Nilson, *pers. comm.*

Chapter 2

Scaling and relations of morphology and kinematics in the sidewinder rattlesnake *Crotalus cerastes*

Abstract

The movement of terrestrial animals with a snakelike body differs fundamentally from that of limbed animals, yet few scaling studies of their locomotor kinematics and morphology are available. We examined scaling and relations of morphology and kinematics in sidewinder rattlesnakes (*Crotalus cerastes*), which move using an unusual gait suited to the challenges of shifting sand. During sidewinding, a snake lifts sections of its body up and forward while other sections maintain static contact with the ground. We used high-speed video to capture variables describing whole-animal speed and acceleration; the height to which body sections are lifted; and the frequency, wavelength, amplitude, and skew angle of the wave made by the body. With snout-vent length (SVL) as a covariate, several morphological traits were sexually dimorphic, but sidewinding kinematics were not. Body width, head length, and neck width deviated significantly from isometry. Most kinematic variables did not deviate from isometry, but wave amplitude was disproportionately higher in larger adults. Path analysis of residuals (from log-log regressions on SVL, sex, and/or age) supported a hypothesized causal relationship between body width and wavelength, indicating that stouter snakes do not curve their bodies as tightly during sidewinding. It also supported a strong causal relationship between frequency of sidewinding cycles and whole-animal speed, along with weaker effects of

wavelength (positive) and amplitude (negative) on speed. We suggest that sidewinding snakes may face a limit on stride length (to which amplitude and wavelength both contribute), beyond which they sacrifice stability. Thus, increasing frequency is an inherently better way to increase speed for this type of locomotion. Finally, frequency and skew angle were strongly related, a result that points to future studies of sidewinding kinematics and physiology.

Introduction

Previous studies of terrestrial locomotion have demonstrated how aspects of kinematics scale with body size inter- and intraspecifically for walking, running, and jumping (e.g. Heglund et al. 1974; Pennycuick 1975; Emerson 1978; Irschick and Jayne 2000; Toro et al. 2003; Day and Jayne 2007; Smith et al. 2010). However, many terrestrial animals navigate the world without limbs, and they face different locomotor challenges than do limbed animals. A limbless body plan has evolved >25 times in terrestrial vertebrates and represents 19% of terrestrial vertebrate diversity (~4,300 species) (Wiens et al. 2006; Astley 2020; Bergmann et al. 2020). Of the limbless terrestrial vertebrates, which include caecilians as well as numerous squamate reptiles, none surpasses snakes in their locomotor diversity. Slithering, crawling, climbing, and even gliding, snakes manage a remarkable variety of motions (Jayne 2020).

Some snake species from sandy desert environments have convergently evolved a type of locomotion called sidewinding. Sidewinding snakes move in a direction oblique to axis of their bodies, propagating waves that have a horizontal as well as a vertical component. At any given time, some sections of the body remain in static contact with the ground while other sections are lifted up and forward to a new contact patch (Fig. 2.1A). Several aspects of sidewinding locomotion have received attention (see Tingle 2020 for a review), including general kinematics (e.g. Gray 1946; Jayne 1986; Gans and Kim 1992), as well as mechanisms for ascending slopes (Marvi et al. 2014), turning (Astley et al. 2015), and negotiating obstacles (Astley et al. 2020). One study dealt with scaling of sidewinding performance (Secor et al. 1992), but none has focused on the scaling of sidewinding kinematics, despite the ubiquity of scaling effects on other types of locomotion (Pedley 1977; Garland and Albuquerque 2017; Cloyed et al. 2021).

Limbless terrestrial animals differ from limbed ones in fundamental ways that likely influence the scaling of kinematics during locomotion. For example, limbed terrestrial animals face high postural costs at larger body sizes because mass increases with length cubed while limb cross-sectional area increases with only length squared. To deal with the disproportionate demands of locomotion at larger body sizes, they may evolve morphological solutions, such as thicker limbs, they may alter their behavior in the gross sense, such as avoiding especially taxing tasks like jumping or climbing, and/or they may alter kinematics parameters, such as posture (sprawling vs. upright) or duty factor (e.g. Biewener 1989; Hutchinson et al. 2006; Day and Jayne 2007; Cieri et al. 2021). In contrast, limbless animals can (and usually do) keep their bodies largely in contact with the ground, so one would expect them to incur lower postural costs, even at relatively large body sizes. Thus, they may not face such drastically different demands at small vs. large body sizes.

Dynamic similarity has been used to understand the scaling of limbed locomotion (Alexander and Jayes 1983; Alexander 1991). For a motion to scale with dynamic similarity, all lengths describing the motion must be directly proportional to some characteristic length of the animals in question. This idea relates very closely to that of geometric similarity for morphology. In the case of sidewinding kinematics, linear dimensions include variables describing the shape of the wave made by the body, such as wavelength, amplitude, and the height of vertical lifting (Fig. 2.1B). If limbless animals do not face disproportionate locomotor demands at larger sizes (or at least not to the degree that limbed animals do), then we might predict geometric similarity, with an expected scaling exponent of 1 vs. snout-vent length for these linear dimensions. In addition to simple linear dimensions, the waveform of a sidewinder's body can vary in the degree to which it tilts towards either the head or the tail, which we call skew angle (Fig. 2.1C and 2.1D). Skew angle has not previously been considered, but it might be expected not to vary systematically with body size under geometric similarity.

For the frequency of a sidewinding cycle, it is more difficult to predict scaling. On one hand, frequency generally decreases with body size for locomotion involving oscillation, such as flapping flight, swimming via tail beats, and running (e.g. Bainbridge 1958; Heglund and Taylor 1988; Rayner 1988; Drucker and Jensen 1996; Smith et al. 2010; Norberg and Norberg 2012). This relationship exists due to physical laws and the intrinsic properties of muscles. On the other hand, sidewinding involves a travelling wave, and so is qualitatively quite different from these locomotor modes. With only one previous study on the muscular mechanisms of sidewinding (Jayne 1988), we do not have sufficient information to form a hypothesis for the scaling of frequency. Finally, following the arguments presented in a seminal paper by Hill (1950), we might reasonably predict that whole-animal speed and acceleration would not change with body size. However, it would also not be surprising for larger sidewinders to achieve higher speeds, since intraspecific analyses of a variety of animals indicate that routine and maximal speeds often increase with size (Cloyed et al. 2021).

After accounting for body size, morphological variation may lead to kinematic and performance variation. Previous studies have shown that sidewinding viper species have some morphological specializations (Jayne 1982; Tingle et al. 2017; Rieser et al. 2021; but see Tingle and Garland 2021); however, none has explored the link between morphology and sidewinding locomotion at the intraspecific level. Sidewinding snakes form curves along the body (Fig. 2.1B), and a snake's maximum potential curvature might depend on such morphological traits as body width and number of vertebrae (both of which vary intraspecifically). Additionally, the tail does not seem to contribute to force production during sidewinding (Jayne 1988), so relatively long tails may inhibit performance, for example by reducing the frequency of sidewinding cycles. The contributions of various kinematic parameters to performance, as well as the relationships among kinematic parameters, also merit further exploration to improve our mechanistic understanding of sidewinding. For example, we do not currently know the degree to which various wave shape parameters contribute to "stride length," i.e., distance travelled during a cycle of sidewinding (Fig. 2.1B).

Here, we use morphological and high-speed video data to examine factors influencing the kinematics of sidewinding locomotion in the sidewinder rattlesnake, *Crotalus cerastes*. We first explore the effects of size, sex, and age class (juvenile vs. adult) on morphology and kinematics. Then we use path analysis to explore causal relations of residual variation in morphology, kinematics, and performance.

Methods

Data collection

We collected sidewinder rattlesnakes (*Crotalus cerastes*) on the Barry M. Goldwater Range near Yuma, Arizona, USA in June and July 2016. Our sample included 74 female and male snakes ranging from small juveniles (young of the year) up to large adults.

We anesthetized snakes by placing them in a tube with a cotton ball soaked in approximately 1 mL of isoflurane per 500 g of snake mass (never <0.125 mL isoflurane). While the snakes were anesthetized, we determined sex by cloacal probing and collected the following measurements: mass (to 1-5 g of accuracy with Pesola scales or a digital scale); snout-to-vent length (SVL) and tail length (both to the nearest mm with measuring tape); width at 25%, 50%, and 75% of the SVL (to the nearest mm with calipers); neck width, head width at the corners of the mouth, and head length from the anterior edge of the first ventral scale (to the nearest mm with calipers); number of ventral scales (following the convention of Dowling 1951); number of subcaudal scales; and number of dorsal scale rows. Table 2.1 lists all of the morphometric and meristic traits that were measured. Finally, we painted 10 markers along the dorsum from the head to the tip of the tail (before the rattle) with White-Out brand correction fluid and black permanent marker as a visualization aid for the videos.

Approximately one day passed between the time of recovery from isoflurane and time of kinematics data collection. We recorded sidewinding sequences indoors in a sandbox measuring 1.15 x 1.15 m with two Edgertronic high-speed cameras (Model SC1; San Jose, California), synchronized at 500 frames per second, with a resolution of 1,264 by 1,008 pixels. Cameras were placed ~1.5-2 m away from the sandbox, with one camera on a low tripod for a lateral view, while the other camera was placed on a higher tripod for a more dorsally-oriented view. Linear dimensions in videos were calibrated in the MATLAB program DLTdv5 (Hedrick 2008) with a large object of known dimensions (several metal rods fixed to each other and to a metal base plate), which we placed in the middle of the sandbox. We recorded substrate and snake body temperatures for each trial. Substrate temperatures ranged from 20.4 to 27.2 °C, while snake body temperatures ranged from 20.1 to 27.3 °C, well within the active range observed in free-living sidewinders (Cowles and Bogert 1944; Moore 1978; Signore et al. *In press*). Trials took place between the hours of 11:45 and 23:28. Sand came from the Barry M. Goldwater Range about 14.5 km from where snakes were captured. Sand in the box measured 2 cm deep. We recorded sidewinding sequences that had at least 2-3 full cycles within the frame of recording. For each snake, we took three recordings. Snakes were given the minimum motivation necessary to elicit sidewinding; in some cases, it was enough to place them on the sandbox, whereas other cases required waving snake tongs, or tapping the tongs on either the substrate or the snake's tail. In between trials, we raked and smoothed the sand to create an uncompressed, level surface.

Video data pre-processing

We recorded trials for 64 individuals, aiming to obtain a final sample of 25-30 individuals for kinematics trials and knowing that not all trials would be usable. Of those, we chose to digitize videos based on a number of factors. First, we eliminated individuals that refused to perform multiple sidewinding cycles, whose painted markers had rubbed off, or whose trials suffered from poor video or calibration quality (e.g., because a camera had been bumped). Of the remaining individuals, we chose ones that provided good representation from the total size range (evaluated based on both SVL and mass): the 3-5 largest females and males, the 3-5 smallest females and males, and several individuals of both sexes distributed throughout the middle of the size range. Our final digitized sample comprised 14 females and 12 males.

Because the raw videos were very large files, and 500 frames per second was more than necessary to adequately quantify the motion, we converted the raw files from .mov to .mp4 format and then used Adobe Premiere to trim the videos and remove every other frame. Then we exported the trimmed videos as 30 fps mp4 files. We calibrated and digitized videos using the MATLAB programs DLTcal5 and DLTdv5 (Hedrick 2008), which yielded files containing x, y, and z coordinates of each tracked point at each frame.

We smoothed the data using a custom MATLAB program. The program used a Savitzky-Golay filter (Savitzky and Golay 1964), implemented by the built-in MATLAB function sgolayfilt. Displacement was smoothed using a 3-pass fourth order Savitzky-Golay filter with a uniform weight distribution. Velocity and acceleration were computed from smoothed displacement using the finite difference method (first and second order central differences, respectively), and then smoothed using a single-pass fourth order Savitzky-Golay filter with a uniform weight distribution. In all cases (displacement, velocity, and acceleration), we used a span of 143 points in time in the smoothing functions. To eliminate edge effects, we dropped 150 time points at the beginning of each sequence and 100 points at the end. This process produced smoothed displacement, velocity, and acceleration for each of the 10 markers.

Extracting kinematic variables

We used a custom MATLAB program to extract kinematic variables from the smoothed data. Some of these variables describe the whole snake's motion, some describe the motion of the 10 discrete markers painted on the body, and some describe the waveform of the snake's body. Table 2.2 lists all of the kinematic variables that were quantified, along with scaling expectations under geometric similarity.

To understand whole-snake speed and acceleration, we used the centroid of the 10 painted markers as the best approximation we could make for center of mass. First, we computed the displacement of the centroid at each frame using the smoothed displacements of the painted markers. Next, we calculated the velocity of the centroid in each frame using the central difference formula. Finally, we computed speed from velocity and took the average and peak speed over the whole trial. We calculated mean and peak centroid acceleration in a similar manner, using the second order central difference of centroid displacement.

For each of the 10 painted markers, we calculated peak speed (cm/s) as well as maximum amplitude in the vertical direction (cm), i.e. the maximum height to which the marker was lifted over the course of the trial. We then used values from individual markers to calculate the mean value of those markers' peak speeds and heights lifted for a given trial. We did not use all 10 painted markers to calculate these mean values because we wanted to capture locomotor behavior, and the head and tail can be involved in non-locomotor behaviors. Therefore, we needed to determine how many markers to discard from the head and tail regions. For each variable, we first replaced the raw data with z scores, which provide a sense of how far from the mean a data point is. Z scores were calculated as:

$$\frac{(an\ individual\ marker's\ value - the\ mean\ value\ of\ all\ 10\ markers\ for\ that\ trial)}{standard\ deviation\ of\ all\ 10\ markers\ for\ that\ trial}$$

For each of the ten markers, we calculated the mean z score across all trials for all individuals. We then determined which of the markers were most consistently close to the mean values (consistently had the lowest z scores). For peak speed, markers 3-7 were consistently closest to the trial mean, so we calculated an average value of peak speed for each trial based on those markers. For height lifted, we used markers 2-8.

Finally, to examine the body's waveform, we measured three common wave properties (frequency, wavelength, and amplitude), plus skew angle, which describes the degree to which the wave slants towards either the head or the tail (Fig. 2.1). We calculated these based on painted markers 4-9 because the head/neck region (markers 1-3) and the tail (marker 10) moved less predictably than the rest of the body did, as explained above. For frequency, we used smoothed displacement data to measure the period of the wave for each sidewinding cycle, and then calculated the frequency as the reciprocal of the median period for the trial. With only 10 painted markers, we could not create a spline that accurately represented the shape of the body. However, the high temporal resolution of our data allowed us to estimate wavelength, amplitude, and skew angle without reconstructing the snake's midline. To do so, we had to assume that snakes were moving at steady-state, and that body shape of a sidewinding snake is a traveling wave where one mode dominates. Each of the painted markers had to pass through the extrema of interest (the crests and troughs of the wave) at some point during a sidewinding cycle. When the angle formed by any three points was at a minimum, the middle point was assumed to be at an extreme (crest or trough). Given these times and locations of the extrema in a subset of frames, we estimated the locations of the extrema at all points in time using simple linear interpolation.

Wavelength is the distance between successive maxima (crests) or successive minima (troughs). If we draw a triangle whose corners are two minima and the maximum in between them (or two maxima and the minimum in between them), then the altitude of the triangle is the wave's peak to peak amplitude, and the angle between the altitude and the median is the skew angle (Fig. 2.1C). We calculated the median directly from our estimated extrema locations: one endpoint of the median is the midpoint of the line connecting the minima (or the maxima), and the other endpoint of the median is the maximum in between those two minima (or the minimum between the maxima). The skew angle is the angle between the median and any line perpendicular to the line connecting the minima (Fig. 2.1C). A positive skew angle indicates that the waves are tilted towards the head, while a negative skew angle indicates that the waves are tilted towards the tail (Fig.

2.1D). Note that sidewinding shows “handedness,” in that the snake’s trunk can be positioned either to the left or the right of its head, and the program used to extract kinematics variables could not distinguish between left- and right- “handed” trials when determining the sign of skew angle. Therefore, we had to manually change the sign of skew angle for all left-handed trials prior to statistical analysis. The altitude/amplitude is the median times the cosine of skew angle (Fig. 2.1C). The reported values of wavelength, amplitude, and skew angle for each trial are the average over all points and frames where values could be calculated.

As the MATLAB program processed each trial, it displayed an animation of digitized points (using the smoothed displacements) and the interpolated wave extrema locations. This allowed us to qualitatively verify the extracted variables to check for anomalies, which can result from violations of the steady-state movement assumption (e.g., if a snake turned partway through a trial rather than proceeding along a relatively straight path). In cases where we detected anomalies, we either truncated the trial to omit the affected frames and re-analyzed it, or we discarded the trial entirely prior to statistical analysis. Our final sample included 63 total trials for 26 individuals; some of these trials were missing one or more variables because wave properties could not be calculated if a trial was too short.

Statistical analysis

All statistical analyses were implemented in R 3.6.0 (R Core Team 2019) except where otherwise stated. We $\log_{10}$-transformed morphological traits prior to analyses.

Initially, we checked for outliers using standardized residuals obtained by regressing each trait on SVL + sex, for juveniles and adults separately. If a standardized residual exceeded ~3 in magnitude and/or was >1 SD from the next value, then the individual snake was removed as a statistical outlier for all further analyses involving that trait.

We used ANOVA to test for sex differences in SVL, examining juveniles and adults separately. We then used ANCOVA (package *car*; Fox and Weisberg 2019) with Type III sums of squares to test for effects of SVL, sex, and age class (juvenile vs. adult) on all morphological traits, except for dorsal row count, which showed minimal variation, and ventral scale count, which violated the assumption of homogeneity of variance (Levene's test F(3,69) = 4.071, p = 0.010). For each trait, we started with a full model that included SVL + sex + age + SVL*sex + SVL*age + sex*age + SVL*sex*age, and we then eliminated predictor variables in a stepwise fashion, starting with interaction terms, to determine the best-fitting model for each trait based on AICc. In two cases where two models had AICc values within 2 (width at 25% SVL and head length), we chose the model that included more predictor variables to facilitate a more granular view of scaling relationships that might differ among groups. We then separated the sample into the subgroups suggested by the best model for each trait and calculated reduced major axis (RMA) slopes (R 3.6.0, package *lmodel2*; Legendre 2018). Confidence intervals for RMA slopes were calculated in *lmodel*2 using the formula from Jolicoeur and Mosimann (1968), and we identified deviations from isometry by determining whether those confidence intervals contained the expected value under isometry (3 for mass; 1 for linear measurements).

For ventral scale count, we used ANCOVA to test for sexual dimorphism in juveniles and adults separately, with SVL as a covariate (package *car*; Fox and Weisberg 2019). Because ventral scale count did not show a statistically significant relationship with SVL in either age group, we did not examine scaling.

For statistical analysis of kinematic data, we chose one representative trial for each individual. To determine which trials would serve as representatives, we first ruled out those with incomplete data (unless all trials for an individual had incomplete data, in which case we considered trials that had the least missing data). We then watched the remaining videos and ruled out any with obvious issues (e.g., part of the body out of frame or obscured from view during part of the video). Finally, we counted the number of sidewinding cycles in each of the remaining videos, and we chose the video that maximized the number of cycles and the path length (the video with the most cycles almost always had the longest path length).

We then compared ANCOVA models as for the morphological variables, but for the kinematic variables we included an additional set of models with snake body temperature as a predictor (we did not consider interactions between body temperature and other predictors). Based on these models, only three kinematic variables were significantly related to SVL: wavelength, amplitude, and height lifted. For these variables, we tested for isometric vs. allometric scaling using the best combination of predictor variables, as we did for morphological traits.

To calculate relationships of morphological and/or kinematic variables, we log transformed them (except for skew angle, which is signed), regressed each variable on log

SVL (including sex and/or age class as predictors in the regression if they appeared in the best ANCOVA model for a given variable: Tables 2.3 and 2.5), and then used the residuals to compute Pearson correlation coefficients and to conduct a path analysis. Previously-identified outliers were removed prior to computing residuals.

We conducted path analyses in Ωnyx (Onyx) (von Oertzen et al. 2015) to estimate parameters in a causal model of relationships involving morphology, kinematics, and performance (Fig. 2.2). We used mean centroid speed as our measure of performance; we did not include additional measures of speed or acceleration because all measures of speed and acceleration were tightly correlated. Speed equals frequency times stride length (i.e. distanced travelled per cycle). Stride length is determined in part by both wavelength and wave amplitude as a result of the oblique angle between the sidewinder's direction of travel and the axis of the wave made by its body; Fig. 2.1C. The degree to which wavelength and amplitude contribute to stride length is determined in part by the wave's skew angle. Therefore, we hypothesized causal relationships of frequency, wavelength, amplitude, and skew angle with mean centroid speed. We included height lifted as an additional kinematic variable because the snake has to allocate part of its finite length to displacement in the vertical direction as well as in the horizontal plane, so height lifted, amplitude, and wavelength may therefore be correlated.

Additionally, we hypothesized that morphological traits affecting a snake's maximum potential body curvature may show causal relationships with amplitude and/or wavelength. One such trait is vertebral count (which is equal to ventral scale count). Another would be the stoutness of a snake's overall body shape, which could be described by mass and/or a width measurement. Finally, because the tail does not seem to contribute to force production during sidewinding (Jayne 1988), we hypothesized that longer tails might inhibit sidewinding, reducing frequency.

Our sample size limited us to models with only seven total variables. Given that we identified ten potential variables of interest, we compared models with different combinations of those variables. All models included causal paths from frequency, wavelength, and peak-to-peak amplitude to mean centroid speed, because we had strong reason to think that those variables would show the clearest relationships. In addition to those four variables, the models included all possible combinations of tail length, ventral scale count, mass, and width at 50% SVL with their hypothesized effects on kinematics (except mass plus width at 50% SVL, which are redundant as measures of stoutness). We rejected nine of the 16 models because they had significant lack of fit. Of the remaining models, six had RMSEA of zero. Of the variables included in those six models, skew angle and body width consistently had strong relationships with other variables, whereas height lifted and mass did not (models with vertebral count always showed significant lack of fit). We therefore present the model that includes skew angle, body width, and height lifted, which also had the lowest AIC of the six models with RMSEA of zero (Fig. 2.2).

Results

Tables 2.1 and 2.2 present descriptive statistics for morphological traits and kinematic variables, respectively.

Juveniles did not show sexual dimorphism for snout-vent length (F(1,44) = 2.251, p = 0.141), but adult females were longer than adult males (F(1,25) = 7.231, p = 0.0126). Sex was a significant predictor in the best ANCOVA models for tail length, head length, and subcaudal scale count, indicating sexual dimorphism in those traits (Table 2.3). The ANCOVA models also indicated SVL as a significant predictor for all morphological traits except scale counts. Additionally, age class was a significant predictor in the best models for mass, tail length, and head width. The interaction between SVL and age class was a significant predictor for tail length, indicating different scaling relationships in juveniles vs. adults. The ANCOVAs for ventral scale count in juveniles and adults showed significantly higher values in females vs. males in both age groups (F(1,43) = 11.234, p = 0.002 in juveniles; F(1,24) = 18.499, p = 0.0002 in adults), and no relationship between SVL and ventral scale count in either age group (F(1,43) = 0.465, p = 0.499 in juveniles; F(1,24) = 0.023, p = 0.881 in adults).

For scaling relationships, we focus on RMA results (Table 2.4; Fig. 2.3). The scaling of most traits did not deviate significantly from isometry, including mass, tail length, width at 25% SVL, and head width. Neck width scaled with negative allometry. Head length scaled with negative allometry in females, but with isometry in males. Width at 50% SVL and 75% SVL scaled with positive allometry. Ventral and subcaudal scale count had no significant relationship with SVL in either sex, so they were not included in the scaling analysis.

The best ANCOVA models showed the majority of kinematic variables were not significantly predicted by body temperature, SVL, sex, age class, or interactions between them (Table 2.5). Snake body temperature was not a significant predictor for any kinematic variable (Table 2.5). None of the kinematic variables showed sexual dimorphism. Snout-vent length was a significant predictor of amplitude, wavelength, and height lifted. Additionally, age class and SVL had an interactive effect on amplitude, indicating different scaling relationships in juveniles vs. adults. Wavelength and height lifted scaled isometrically (Table 2.6; Fig. 2.4). Amplitude scaled with isometry in juveniles, but with positive allometry in adults (Table 2.6; Fig. 2.4).

Several kinematic variables were correlated with each other and with morphological variables. All performance variables (centroid mean and peak speed, centroid mean and peak acceleration, peak speed of individual marker points) were highly correlated ($r \geq 0.880$ for all pairs). Sidewinding frequency was highly correlated with each of these performance variables ($r \geq 0.786$). Body width at 25% SVL was moderately correlated with performance variables ($0.440 \leq r \leq 0.564$) and frequency ($r = 0.508$). Body width at 50% SVL was correlated with wavelength ($r = 0.601$).

Our path model (Fig. 2.2) had no significant lack of fit ($x^2 = 1.148$, d.f. = 2, $p = 0.563$; RMSEA classic = 0.0). Sidewinding frequency had the largest effect on centroid mean speed (estimate: 0.912 ± 0.077; likelihood ratio test $x^2 = 48.334$, $p < 0.00001$). Wavelength and amplitude had much lesser effects in opposite directions (estimates: 0.140 ± 0.068 and -0.140 ± 0.066, likelihood ratio test results $x^2 = 3.946$, $p = 0.047$ and $x^2 = 4.127$, $p = 0.042$, respectively). Skew angle did not have an effect on centroid mean speed (estimate: -0.039 ± 0.080; likelihood ratio test $x^2 = 0.240$, $p = 0.624$), but it was strongly correlated with frequency (estimate: 0.548 ± 0.223; likelihood ratio test $x^2 = 9.301$, $p =$

0.002). Body width at 50% SVL had a positive effect on wavelength (estimate: 0.588 ± 0.159; likelihood ratio test $x^2 = 10.808$, $p = 0.001$).

Discussion

Sexual dimorphism in morphological traits

Although we did not find sexual size dimorphism in juvenile sidewinders, adult females were significantly larger than adult males. Female-biased size dimorphism has previously been documented in adult sidewinder rattlesnakes (Klauber 1937, 1944) and in many other snake species (e.g. Semlitsch and Gibbons 1982; Shine 1993, 1994; Hendry et al. 2014), and is generally hypothesized to result from sex-specific natural selection, especially fecundity selection.

Female sidewinders also had more ventral scales, which correspond 1:1 with trunk vertebrae (Alexander and Gans 1966). Several studies have found sexual dimorphism in ventral scale (vertebral) count, often corresponding to sexual size dimorphism, sometimes female-biased (e.g. Klauber 1943; Lindell et al. 1993; Lindell 1996; Shine 2000) and sometimes male-biased (e.g. Arnold 1988; Arnold and Bennett 1988; Dohm and Garland 1993). A study of the European viper *Vipera berus* demonstrated evidence for selection against individuals with lower ventral scale counts – such individuals are apparently less likely to survive to adulthood (Lindell et al. 1993). Similar selection may be at play in our sample. Juveniles had greater variance in ventral scale count for females (Levene's test: $F(1,41) = 10.396$, $p = 0.002$) but not males (Levene's test: $F(1,28) = 2.040$, $p = 0.164$), perhaps indicating that only females face detectable selection on ventral scale count in this population.

Male sidewinders had longer tails and higher subcaudal scale counts than did females, with this pattern manifesting in both juveniles and adults. Numerous studies have documented longer tails in males of many snake species, pointing out several possible explanations that are not mutually exclusive: the necessity of accommodating hemipenes at the base of the tail, selection on females to have a more posterior cloaca to maximize relative length of the body cavity, and selection related to male behavior involving the tail during courtship (e.g. Klauber 1943; Kaufman and Gibbons 1975; King 1989).

Males also had longer heads, relative to their body size. Because they swallow their prey whole, a snake's range of potential prey items is limited by its gape (Pough and Groves 1983; Forsman and Lindell 1993). If head length corresponds to underlying musculoskeletal traits that contribute to gape, then an increased relative head length could be a way for males to compensate for their smaller body size and expand their otherwise restricted prey options. Indeed, previous studies have found that longer heads enable snakes to more readily consume larger prey (Shine 1991; Forsman and Lindell 1993).

Scaling of morphological traits

We found that sidewinders of different sizes were not scale models; some traits scaled allometrically. For example, body width measured at 50% SVL and at 75% SVL scaled with positive allometry, meaning that shorter sidewinders are relatively slender and longer sidewinders are relatively stout. If this increased stoutness in larger snakes results from positive allometry of muscle cross-sectional area, then it would likely have implications for locomotion. Because our study did not include data on muscle morphology, this could be a fertile area for future study.

Head length scaled with negative allometry in females; thus, the head was disproportionately large in smaller individuals. Many studies have found evidence for negative allometry of head dimensions, both interspecifically (e.g. Tingle and Garland 2021) and intraspecifically (e.g. Phillips and Shine 2006). As noted above, snakes with longer heads can consume larger prey (Shine 1991; Forsman and Lindell 1993), so negative allometry could allow smaller individuals to eat relatively larger meals.

Scaling of sidewinding kinematics

In the absence (or considerable reduction) of postural costs, which strongly influence the scaling of morphology and locomotion in limbed animals, we hypothesized that the scaling of kinematics of sidewinding snakes would follow expectations derived from geometric similarity (Table 2.2). Consistent with this expectation, most kinematic variables did not deviate significantly from geometric similarity, with one exception: amplitude scaled with positive allometry in adult sidewinders (but not in juveniles), meaning that larger individuals had disproportionately large wave amplitude (Table 2.6). In general, deviations from isometry often occur either because allometry serves as compensation to maintain functional equivalency, or because some size-dependent constraint prevents isometric scaling.

Our results do not suggest maintenance of functional equivalency as an explanation for the positive allometry of wave amplitude, but they also do not rule out the possibility. Regarding the potential for size-dependent constraint, this situation often arises in locomotion due to size effects on relative muscle force production. Under geometric similarity, muscle cross-sectional area and hence force-generating ability should scale as body length squared, whereas body mass scales as length cubed, so larger animals have reduced mass-specific force-generating ability. For muscular constraint to explain positive allometry of wave amplitude, lower-amplitude waves would have to require greater force production; we think that is unlikely to be the case, so muscular constraint in larger sidewinders seems like an unlikely explanation for the pattern in our data. On the other hand, we did find positive allometry of body width, indicating stouter bodies in larger individuals. We do not know what changes in internal anatomy might underlie this trend; if it results from a disproportionate increase in muscle tissue, then it would invalidate our expectation of geometric scaling of kinematics. Here, it is worth noting that some species of lizards have positive allometry of thigh muscle mass, which may relate to their positive allometry of endurance capacity (Garland 1984; Garland and Else 1987). Future studies could examine whether scaling and/or variation in muscle morphology contributes to sidewinding kinematics and performance.

Another possible explanation for the positive allometry of wave amplitude relates to the peculiarities of limbless terrestrial locomotion. The entire body can be used to generate ground reaction forces (as opposed to discrete limbs), affording limbless animals greater flexibility in how they use different sections of their bodies. Perhaps adult sidewinders use sections of their bodies differently as they get larger. For example, smaller snakes may use a greater percentage of the neck region to help them assess their destination, removing that length from the total amount available for sidewinding. Additionally, snakes are not infinitely long, so they may also face trade-offs among wave amplitude, height lifted, number of waves present on the body (not measured in the present study), or other waveform parameters. Consider a finite length of string as a 2-dimensional analogy: if you lay the string on the table in the shape of a wave, and then increase the amplitude of the wave, you must also change either the wavelength or the number of wave cycles. Height lifted scales with a slope lower than 1 (Fig. 2.4), which might suggest a trade-off, but the slope is not statistically <1. Moreover, the magnitude of height lifted is so much smaller than that of amplitude that its contribution to body length usage would be trivial (see Table 2.2 for descriptive statistics; on average, amplitude was ~8 times greater than height lifted). Therefore, we do not think a trade-off with height lifted explains why amplitude does not scale isometrically in adult sidewinders. Additionally, we did not find significant relationships between amplitude and any other variables in either the pairwise correlation or in the path analysis (accounting for body size). Future work should consider additional parameters that we could not include, such as curvature, length or number of contact patches.

Causal relations of morphology, kinematics, and performance

The path analysis of residual (individual) variation supported four of our six hypothesized causal relationships among morphology, kinematics, and performance (Fig.

2.2). First, it supported the positive relationship between body width and wavelength. Increasing wavelength without changing amplitude creates a wave with lower curvature. Thus, this relationship could plausibly exist because stouter snakes might not be able to curve their bodies as tightly as thinner snakes do.

Sidewinders in our study increased speed mainly by increasing the frequency of sidewinding rather than stride length (distance moved per cycle) (Fig. 2.2). Frequency explained 83% of the variation in mean centroid speed, whereas wavelength and amplitude explained only about 2% each (based on squared path coefficients). This result aligns with Secor et al.'s (1992) finding of increasing frequency with increasing speed between 0.3 and 0.8 km/hr. It makes sense that sidewinders would increase speed through changes in frequency rather than through wave parameters related to stride length, given that a sidewinding snake cannot increase its stride length beyond a certain point without reducing the number of body segments in contact with the ground. Sidewinding snakes normally maintain at least two contact points with the ground (Jayne 1988; Burdick et al. 1993; Marvi et al. 2014); any fewer, and they lose stability while lifting their bodies, pivoting around their sole contact point (Jayne 1988). Increasing frequency instead of stride length does not necessitate such a sacrifice in stability. This restriction on increased stride length in sidewinders contrasts with creatures from crawling maggots to galloping mice (or horses) to swimming fish, which can increase their speed by changing either stride length or frequency (or both simultaneously) (Bainbridge 1958; Heglund et al. 1974; Berrigan and Pepin 1995).

Skew angle varied considerably, from -6.3° (a slight tail-wards tilt) to 31.7° (a strong head-wards tilt). Skew angle likely contributes to stride length in conjunction with wavelength, amplitude, and other wave parameters not captured in this study. Given that speed equals stride length times frequency, we therefore expected that skew angle would be one of the variables affecting speed. Contrary to expectations, we found no relationship between skew angle and speed in the path analysis (Fig. 2.2). We did find that wavelength and amplitude predicted speed (positively and negatively, respectively), though they explained very little of the total variation in speed. Future studies could clarify the physical basis of stride length in sidewinders. In particular, a model that more fully describes the body's waveform could elucidate how various aspects of wave shape, including ones we could not measure here, contribute to stride length.

The relationship between skew angle and sidewinding frequency (Fig. 2.2) could have a physical and/or physiological basis, but our data do not allow us to explore that possibility. From a physical standpoint, mathematical relationships between skew angle and other variables are certainly complex and involve wave parameters that we did not characterize. From a physiological standpoint, increasing our knowledge of muscular mechanisms of sidewinding could clarify how sidewinders control skew angle, and the consequences for ground reaction forces. Moreover, negative and positive skew angle are likely qualitatively different; we suspect they may involve activity of different muscles, in addition to different degrees of contraction of the same muscles. Therefore, it may not be appropriate to treat the entire range of sidewinder skew angle on a linear scale, but our sample size does not allow us to pursue more complicated schemes for scoring skew angle.

Thus, future studies have much to explore with respect to the role of skew angle in sidewinding.

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Table 2.1. Descriptive statistics for morphological traits**.**

trait	expected scaling exponent vs. SVL	group	n	mean	range	standard deviation	coefficient of variation (%)†
SVL (mm)	-	adult females	22	600.9	440–710	76.3	12.7
		adult males	5	506.0	466–553	37.9	7.5
		juvenile females	21	323.0	253–426	44.2	13.7
		juvenile males	25	303.6	226–415	48.3	15.9
mass (g)	3	adult females	22	184.5	86–310	64.2	19.1
		adult males	5	133.2	94–165	27.3	20.8
		juvenile females	21	27.4	11–64	12.6	20.5
		juvenile males	25	25.4	12–61	13.7	16.6
tail length (mm)	1	adult females	22	38.0	30–47	5.2	6.8
		adult males	5	46.6	40–52	5.0	3.1
		juvenile females	21	19.8	5–28	5.0	28.3
		juvenile males	25	23.7	9.5–35	5.8	18.2

width at 25% SVL (mm)	1	adult females	22	19.5	14–29.6	3.4	11.2
		adult males	5	17.8	13.5–22.9	3.5	18.7
		juvenile females	20	9.9	8.2–14.5	1.7	6.4
		juvenile males	25	9.5	6.8–12.8	1.6	10.6
width at 50% SVL (mm)	1	adult females	22	27.9	17.9–36	4.6	8.8
		adult males	5	24.3	19.5–28.9	3.3	13.7
		juvenile females	20	13.8	10–19.5	2.5	12.0
		juvenile males	25	13.2	9.5–19.6	2.7	10.2
width at 75% SVL (mm)	1	adult females	22	27.3	18–36.2	4.6	12.1
		adult males	5	25.3	20.3–29.9	3.5	13.5
		juvenile females	20	13.4	9.8–19.9	2.6	9.4
		juvenile males	25	13.0	9.1–19.7	3.1	12.3
neck width (mm)	1	adult females	21	11.3	9.1–14.2	1.4	7.7
		adult males	5	9.4	8.2–10.7	1.0	9.6
		juvenile females	21	6.8	5.4–8.8	0.9	7.6
		juvenile males	25	6.5	4.9–8.6	0.9	9.7

head width (mm)	1	adult females	22	26.7	20.4–31.1	3.1	5.4
		adult males	5	22.9	18.6–25.9	2.9	10.2
		juvenile females	21	14.4	9.5–18.5	2.1	11.5
		juvenile males	25	13.8	11.2–18.2	1.9	4.2
head length (mm)	1	adult females	21	28.5	22.7–35.1	3.4	7.0
		adult males	5	26.8	23.1–29.3	2.8	3.9
		juvenile females	21	17.4	12.8–24.2	2.5	7.4
		juvenile males	25	16.9	13.3–23.7	2.6	5.6
ventral scale count	-	adult females	22	146.0	143–150	1.6	1.1
		adult males	5	142.2	141–145	1.6	1.1
		juvenile females	21	144.3	138–149	3.1	2.2
		juvenile males	25	141.4	135–148	2.9	2.0
subcaudal scale count	-	adult females	22	14.1	11–17	1.5	11.0
		adult males	5	19.0	18–20	1.0	5.3
		juvenile females	21	14.7	13–17	1.1	6.9
		juvenile males	25	18.9	16–22	1.7	8.6

dorsal row count	-	adult females	22	22.6	21–25	1.0	4.2
		adult males	5	23.0	23	0.0	0.0
		juvenile females	20	22.4	21–23	0.9	4.1
		juvenile males	25	22.2	21–23	1.0	4.5

Means, ranges, standard deviations, and coefficients of variation for morphological traits, presented separately by sex and age class.

†For all traits except SVL, coefficient of variation = 2.3026 x the standard deviation of residuals from allometric equations x 100%. This method for calculating coefficient of variation allows comparison of the relative variability of different characters after removing variation related to size (Garland 1984).

Table 2.2. Descriptive statistics for kinematic variables.

variable	expected scaling exponent vs. SVL	group	n	mean	range	standard deviation	coefficient of variation (%)†
centroid mean speed (cm/s)	0	adults	9	22.2	8.2–60.7	16.8	66.5
		juveniles	17	17.6	6.8–34.1	8.6	49.4
centroid peak speed (cm/s)	0	adults	9	32.3	12.6–78.3	21.3	63.7
		juveniles	17	26.9	9.6–56.8	13.8	53.7
centroid mean acceleration (cm/s^2)	0	adults	9	41.9	11.1–132.7	39.5	86.7
		juveniles	17	32.0	8.5–89.8	21.5	67.9
centroid peak acceleration (cm/s^2)	0	adults	9	98.3	29.6–272.8	77.7	74.1
		juveniles	17	87.8	17.2–319.2	74.7	76.6
frequency (Hz)	?	adults	9	0.9	0.3–2.2	0.7	82.5
		juveniles	17	0.9	0.4–1.8	0.4	43.9
approximate wavelength (cm)	1	adults	9	12.0	5.8–16.4	3.0	22.5
		juveniles	16	6.6	3.5–9.4	1.6	21.5
approximate amplitude (cm)	1	adults	9	11.4	8.4–15.8	2.6	4.4
		juveniles	16	6.0	3.9–7.9	1.0	11.3
skew angle (degrees)	0	adults	9	13.0	-1.0–31.7	10.2	‡
		juveniles	16	6.4	-6.3–24.1	9.5	‡
avg height lifted (cm) markers 2-8	1	adults	9	1.2	0.8–1.7	0.3	24.3
		juveniles	17	0.9	0.5–1.1	0.1	17.9
avg peak marker speed (cm/s) markers 3-7	0	adults	9	50.1	20.0–98.2	27.6	58.9
		juveniles	17	42.1	15.3–77.6	19.4	48.7

Means, ranges, standard deviations, and coefficients of variation for kinematic variables, presented separately by age class. Expected scaling exponent assumes geometric similarity.

†See Table 2.1 footnote.

‡ We do not present coefficient of variation for skew angle because it is signed and therefore the mean potentially can be zero or near zero, thus leading to pathological inflation of the CV.

Table 2.3. Best-fitting ANCOVA models for morphological traits.

trait		sum of squares	Df	B	F	p
log(mass)	intercept	1.25	1	-5.09	172.20	1.2E-20
	sex	-	-	-	-	-
	adult	0.06	1	0.14	8.29	0.0053
	log(SVL)	2.02	1	2.59	277.41	1.16E-20
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.52	71	-	-	-
	adjusted r^2	0.96	-	-	-	-
	AICc	-148.77	-	-	-	-
log(tail length) *five outliers removed (adltJ, juv45, juv41, juv39, juv112)	intercept	0.04	1	-1.09	28.88	1.2E-06
	sex	0.10	1	0.10	67.12	1.6E-11
	adult	0.00	1	0.01	0.16	0.6891
	log(SVL)	0.20	1	0.96	141.23	9.7E-18
	sex*adult	0.01	1	0.06	6.68	0.0121
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.09	63	-	-	-
	adjusted r^2	0.93	-	-	-	-
	AICc	-243.93	-	-	-	-

log(width at 25% SVL) *three outliers removed (adltB, ad147, and juv39)	intercept	0.08	1	-1.32	68.87	7.0E-12
	sex	-	-	-	-	-
	adult	0.00	1	0.03	3.08	0.0837
	log(SVL)	0.24	1	0.92	208.34	3.0E-22
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.08	67	-	-	-
	adjusted r^2	0.95	-	-	-	-
	AICc	-269.30	-	-	-	-
log(width at 50% SVL) *one outlier removed (juv31)	intercept	0.62	1	-1.62	332.11	2.8E-28
	sex	-	-	-	-	-
	adult	-	-	-	-	-
	log(SVL)	1.94	1	1.10	1034.53	1.1E-43
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.13	70	-	-	-
	adjusted r^2	0.94	-	-	-	-
	AICc	-243.27	-	-	-	-

log(width at 75% SVL)	intercept	0.68	1	-1.69	246.61	8.5E-25
	sex	-	-	-	-	-
	adult	-	-	-	-	-
	log(SVL)	2.03	1	1.13	735.03	3.5E-39
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.20	71	-	-	-
	adjusted r^2	0.91	-	-	-	-
	AICc	-218.70	-	-	-	-
log(neck width)	intercept	0.31	1	-1.14	222.71	1.4E-23
	sex	-	-	-	-	-
	adult	-	-	-	-	-
	log(SVL)	0.97	1	0.79	709.10	1.1E-38
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.10	71	-	-	-
	adjusted r^2	0.91	-	-	-	-
	AICc	-269.63	-	-	-	-

log(head width) *one outlier removed (juv44)	intercept	0.04	1	-0.93	77.34	6.3E-13
	sex	-	-	-	-	-
	adult	0.00	1	0.04	7.27	0.0088
	log(SVL)	0.21	1	0.83	385.97	3.4E-30
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.04	70	-	-	-
	adjusted r^2	0.97	-	-	-	-
	AICc	-336.80	-	-	-	-
log(head length)	intercept	0.12	1	-0.82	139.20	3.3E-18
	sex	0.00	1	0.02	3.89	0.0526
	adult	-	-	-	-	-
	log(SVL)	0.83	1	0.82	973.45	2.1E-42
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.06	69	-	-	-
	adjusted r^2	0.94	-	-	-	-
	AICc	-299.05	-	-	-	-

log(subcaudals)	intercept	0.31	1	1.32	203.86	2.0E-22
	sex	0.18	1	0.11	116.52	1.5E-16
	adult	-	-	-	-	-
	log(SVL)	0.00	1	-0.06	3.07	0.0839
	sex*adult	-	-	-	-	-
	sex*log(SVL)	-	-	-	-	-
	adult*log(SVL)	-	-	-	-	-
	sex*adult*log(SVL)	-	-	-	-	-
	residuals	0.11	70	-	-	-
	adjusted r^2	0.70	-	-	-	-
	AICc	-261.51	-	-	-	-

The best-fitting ANCOVA model for each morphological trait (based on AICc) resulting from a comparison of models with various combinations of predictor variables and their interactions (see Methods for details). Note that we did not compare ANCOVA models for ventral scale count due to heteroscedasticity, so ventral scale count does not appear in this table. Instead, we analyzed juveniles and adults separately, using ANCOVA models that included sex + SVL (see Methods and Results).

Table 2.4. Scaling of morphological traits (RMA) in relation to body length (SVL).

trait	sample	# outliers removed	n	r	p	RMA intercept	RMA slope	RMA CI lower	RMA CI upper	expected slope
mass	juveniles	0	47	0.917	1.3E-19	-6.183	3.035	2.694	3.420	3
	adults	0	27	0.836	5.5E-08	-4.985	2.607	2.084	3.262	
tail length	juvenile females	2	19	0.728	4.1E-04	-1.723	1.210	0.858	1.707	1
	adult females	1	21	0.914	7.0E-09	-1.148	0.983	0.810	1.192	
	juvenile males	2	23	0.852	2.4E-07	-1.630	1.215	0.961	1.537	
	adult males	0	5	0.960	0.010	-2.256	1.451	0.884	2.382	
width at 25% SVL	juveniles	1	45	0.894	1.4E-16	-1.651	1.056	0.921	1.212	1
	adults	2	25	0.814	7.4E-07	-1.697	1.072	0.837	1.373	
width at 50% SVL	**all**	**1**	**72**	**0.968**	**1.1E-43**	**-1.717**	**1.141**	**1.074**	**1.211**	**1**
width at 75% SVL	**all**	**0**	**73**	**0.955**	**3.5E-39**	**-1.830**	**1.180**	**1.100**	**1.266**	**1**
neck width	**all**	**0**	**73**	**0.953**	**1.1E-38**	**-1.241**	**0.825**	**0.769**	**0.886**	**1**
head width	juveniles	1	46	0.941	**2.4E-22**	-1.026	0.873	0.788	0.968	1
	adults	0	27	0.883	1.1E-09	-1.286	0.976	0.806	1.183	
head length	**females**	**0**	**42**	**0.967**	**2.8E-25**	**-0.821**	**0.820**	**0.756**	**0.890**	**1**
	males	0	30	0.970	7.9E-19	-1.067	0.924	0.842	1.014	

RMA slopes and intercepts for log(trait) in relation to log(SVL). Bold indicates traits that scale with either positive or negative allometry (as opposed to isometry for geometric similarity). Expected slope is under geometric similarity. Note that ventral scale count and subcaudal scale count were uncorrelated with SVL, rendering it pointless to fit an RMA regression line (Sokal and Rohlf 1995, p. 544). RMA equations correspond to the solid lines shown in Fig. 2.3.

Table 2.5. Best-fitting ANCOVA models for kinematic variables.

variable		sum of squares	Df		B	F	p
centroid mean speed (cm/s)	intercept	97.36	1		-33.48	0.70	0.4107
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	241.78	1		20.55	1.74	0.1995
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	3333.64	24		-	-	-
	adjusted r^2	0.03	-		-	-	-
	AICc	207.07	-		-	-	-
centroid peak speed (cm/s)	intercept	39.81	1		-21.41	0.14	0.7081
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	219.57	1		19.59	0.79	0.3823
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	6654.14	24		-	-	-
	adjusted r^2	-0.01	-		-	-	-
	AICc	225.04	-		-	-	-

centroid mean acceleration (cm/s^2)	intercept	208.53	1		-49.00	0.25	0.6201
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	621.28	1		32.95	0.75	0.3946
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	19841.48	24		-	-	-
	adjusted r^2	-0.01	-		-	-	-
	AICc	253.45	-		-	-	-
centroid peak acceleration (cm/s^2)	intercept	2.82	1		-5.70	0.00	0.9825
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	822.89	1		37.92	0.14	0.7080
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	137451.24	24		-	-	-
	adjusted r^2	-0.04	-		-	-	-
	AICc	303.77	-		-	-	-

frequency (Hz)	intercept	0.09	1		1.00	0.32	0.5775
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	0.00	1		-0.04	0.00	0.9547
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	6.53	24		-	-	-
	adjusted r^2	-0.04	-		-	-	-
	AICc	44.95	-		-	-	-
approx wavelength (cm)	intercept	143.89	1		-41.78	46.82	0.0000
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	209.17	1		19.58	68.05	0.0000
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	70.69	23		-	-	-
	adjusted r^2	0.74	-		-	-	-
	AICc	104.08	-		-	-	-

approx amplitude (cm)	intercept	148.21	1		-42.40	138.09	0.0000
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	209.87	1		19.61	195.54	0.0000
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	24.69	23		-	-	-
	adjusted r^2	0.89	-		-	-	-
	AICc	77.77	-		-	-	-
skew angle (degrees)	intercept	280.16	1		-58.29	3.13	0.0903
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	372.00	1		26.11	4.15	0.0533
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	2060.80	23		-	-	-
	adjusted r^2	0.12	-		-	-	-
	AICc	188.39	-		-	-	-

avg height lifted (cm) markers 2-8	intercept	0.01	1		0.58	0.17	0.6867
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	0.40	1		0.88	9.22	0.0059
	body temp (°C)	0.14	1		-0.08	3.33	0.0811
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	0.99	23		-	-	-
	adjusted r^2	0.38	-		-	-	-
	AICc	-1.25	-		-	-	-
avg peak marker speed (cm/s) markers 3-7	intercept	101.82	1		-34.24	0.20	0.6549
	sex	-	-		-	-	-
	adult	-	-		-	-	-
	log(SVL)	545.25	1		30.87	1.10	0.3053
	body temp (°C)	-	-		-	-	-
	sex*adult	-	-		-	-	-
	sex*log(SVL)	-	-		-	-	-
	adult*log(SVL)	-	-		-	-	-
	sex*adult*log(SVL)	-	-		-	-	-
	residuals	11928.31	24		-	-	-
	adjusted r^2	0.00	-		-	-	-
	AICc	240.22	-		-	-	-

The best ANCOVA model for each kinematics variable (based on AICc) resulting from a comparison of models with various combinations of predictor variables and their interactions (see Methods for details).

Table 2.6. Scaling of kinematic variables (RMA)**.**

trait	sample	n	r	p	RMA intercept	RMA slope	RMA CI lower	RMA CI upper	expected slope
wavelength	all	25	0.840	1.49E-07	-2.069	1.155	0.916	1.456	1
amplitude	juveniles	16	0.775	4.27E-04	-2.149	1.185	0.831	1.690	**1**
	adults	**9**	**0.980**	**3.88E-06**	**-3.088**	**1.505**	**1.259**	**1.799**	
height lifted	all	26	0.581	0.002	-1.894	0.728	0.520	1.020	1

RMA slopes and intercepts for log(trait) in relation to log(SVL). Bold indicates traits that scale with either positive or negative allometry (as opposed to isometry for geometric similarity). Expected slope is under geometric similarity. The table omits traits that were not significantly correlated with SVL (Table 2.5). RMA equations correspond to the solid lines shown in Fig. 2.4.

Figure 2.1. Sidewinding kinematics. A. Sidewinding snakes move in a direction oblique to their body axis, propagating waves that have a horizontal as well as a vertical component. At any given time, some sections of the body remain in static contact with the ground while other sections are lifted up and forward to a new contact patch. B. The shape of a sidewinder's body can be described using common wave properties, including peak-to-peak amplitude and wavelength. Stride length is the distance between successive tracks in the direction of travel. Because the body axis is oblique to the direction of travel, both amplitude and wavelength contribute to stride length, and their relative contributions are determined by other aspects of the wave's shape, such as skew angle. C. Wavelength is the distance between successive maxima (crests) or successive minima (troughs). If we draw a triangle between two minima and the maximum in between them (or two maxima and the minimum in between them), then skew angle is the angle between the triangle's median and any line perpendicular to the line connecting the minima (or the maxima). Amplitude is the triangle's altitude, which equals the median times the cosine of the skew angle. D. Positive skew angle indicates that waves are tilted towards the head, whereas negative skew angle indicates a tail-wards tilt. Panels A and B are traces from high-speed video of *Crotalus cerastes*, modified with permission from Tingle 2020. Panels C and D are stylized.

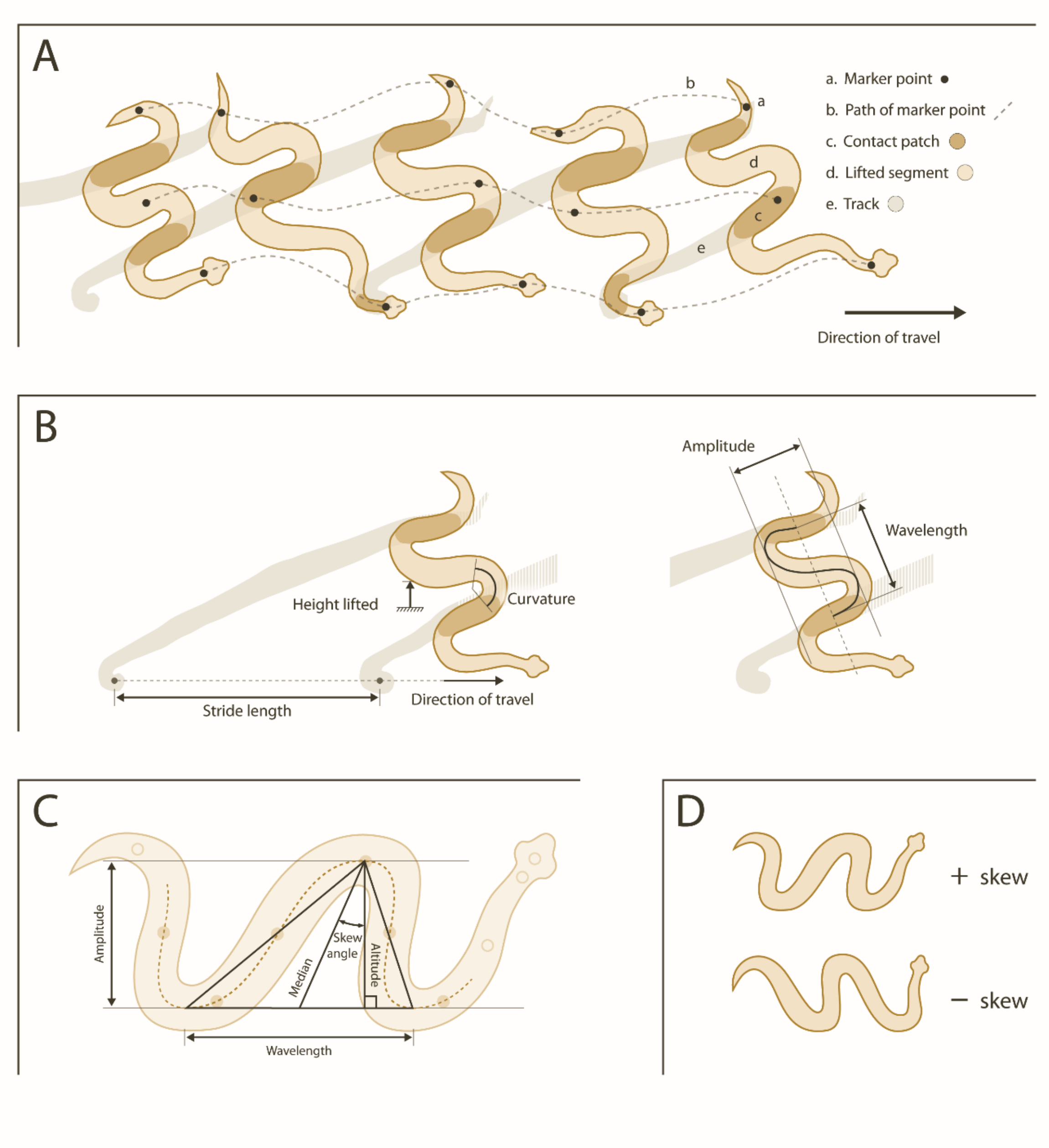

A
a
b
c
d
e
a. Marker point ●
b. Path of marker point
c. Contact patch
d. Lifted segment
e. Track
Direction of travel
B
Height lifted
Curvature
Stride length
Direction of travel
Amplitude
Wavelength
C
Amplitude
Skew angle
Median
Altitude
Wavelength
D
+ skew
− skew

Figure 2.2. Path model of hypothesized relationships among morphological traits (rectangles), kinematic variables (ovals), and performance (hexagon). By convention, causal relationships are represented as one-headed arrows (here in red) and correlations as two-headed arrows. Adjacent numbers are estimates and standard errors from Ωnyx (Onyx), in addition to p values from likelihood ratio tests. Correlations required for model fitting are shown as dotted gray two-headed arrows without estimates or p values.

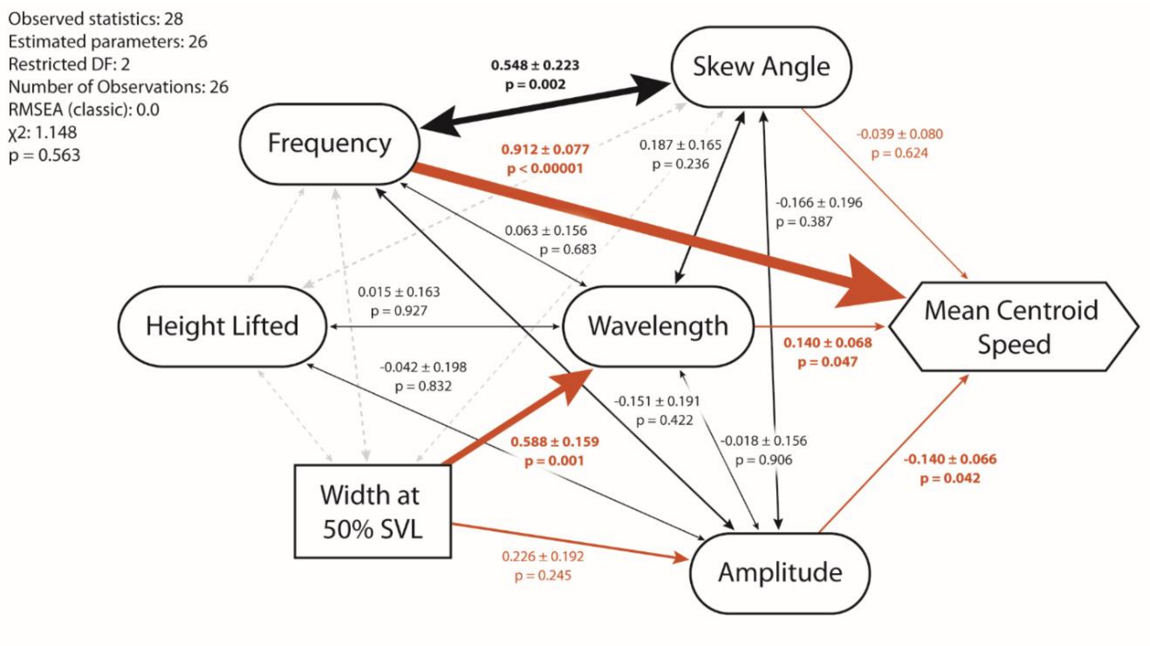


Figure 2.3. Scaling of morphometric traits. Dashed lines have a slope equal to the expectation under isometry and pass through the mean value of (x,y) for all specimens. Solid lines represent RMAs for subgroups determined to be statistically distinct (Tables 2.3 and 2.4). Note that in many cases the lines for distinct subgroups are quite similar. These plots and corresponding analyses do not include outliers (see text).

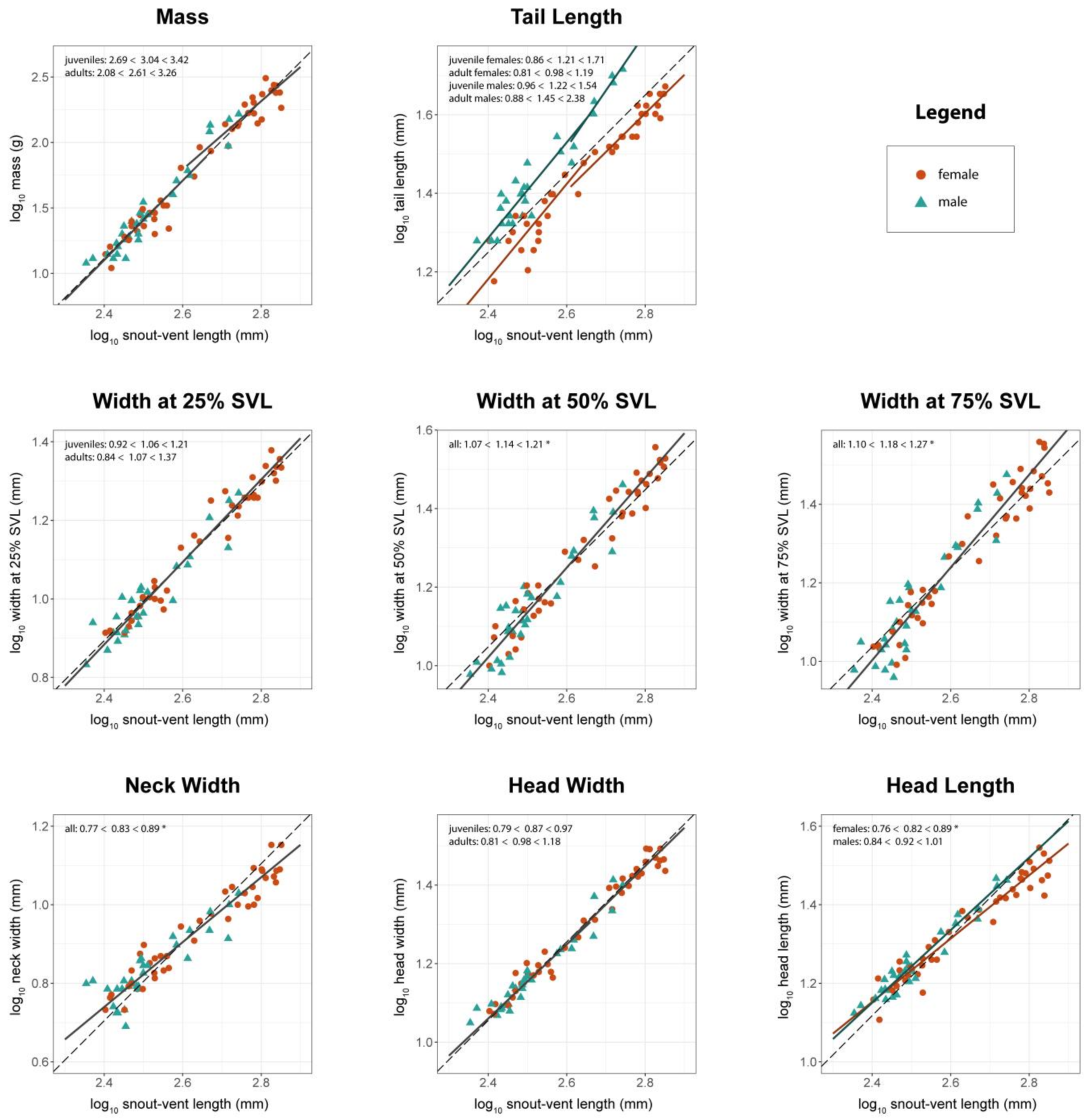
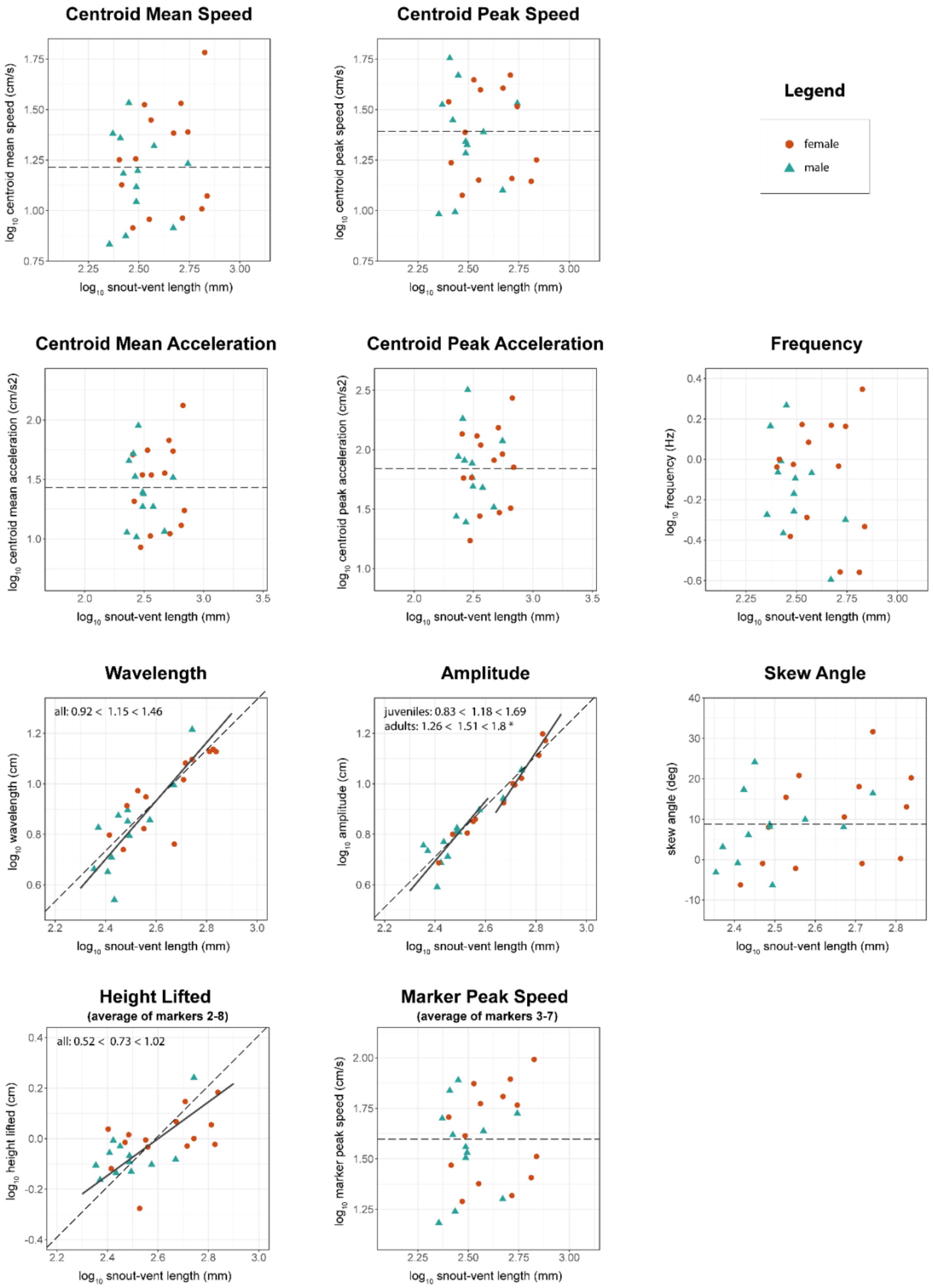


Figure 2.4. Scaling of kinematic variables. Dashed lines have a slope equal to the expectation under isometry (geometric similarity) and pass through the mean value of (x,y) for all specimens. Solid lines represent RMAs for subgroups determined to be statistically distinct (Tables 2.5 and 2.6). No outliers were identified for kinematic variables.


Centroid Mean Speed
log10 centroid mean speed (cm/s)
Centroid Peak Speed
log10 centroid peak speed (cm/s)
Legend
female
male
Centroid Mean Acceleration
log10 centroid mean acceleration (cm/s2)
Centroid Peak Acceleration
log10 centroid peak acceleration (cm/s2)
Frequency
log10 frequency (Hz)
Wavelength
all: 0.92 < 1.15 < 1.46
log10 wavelength (cm)
Amplitude
juveniles: 0.83 < 1.18 < 1.69
adults: 1.26 < 1.51 < 1.8 *
log10 amplitude (cm)
Skew Angle
skew angle (deg)
Height Lifted
(average of markers 2-8)
all: 0.52 < 0.73 < 1.02
log10 height lifted (cm)
Marker Peak Speed
(average of markers 3-7)
log10 marker peak speed (cm/s)
log10 snout-vent length (mm)

Chapter 3

Morphological evolution in relationship to sidewinding, arboreality, and precipitation in snakes of the family Viperidae

Abstract

Compared with other squamates, snakes have received relatively little ecomorphological investigation. We examined morphometric and meristic characters of vipers, in which both sidewinding locomotion and arboreality have evolved multiple times. We used phylogenetic comparative methods that account for intraspecific variation (measurement error models) to determine how morphology varied in relation to body size, sidewinding, arboreality, and mean annual precipitation (which we chose over other climate variables through model comparison). Some traits scaled isometrically; however, head dimensions were negatively allometric. Although we expected sidewinding specialists to have different body proportions and more vertebrae than non-sidewinding species, they did not differ significantly for any trait after correction for multiple comparisons. This result suggests that the mechanisms enabling sidewinding involve musculoskeletal morphology and/or motor control, that viper morphology is inherently conducive to sidewinding ("pre-adapted"), or that behavior has evolved faster than morphology. With body size as a covariate, arboreal vipers had long tails, narrow bodies, and lateral compression, consistent with previous findings for other arboreal snakes, plus reduced posterior body tapering. Species from wetter environments tended to have longer tails, wider heads, and reduced anterior tapering. This study adds to the growing evidence

that, despite superficial simplicity, snakes have evolved various morphological specializations in relation to behavior and ecology.

Introduction

Locomotor behaviors and related morphologies should often be under relatively strong selection (Garland and Losos 1994; Dickinson et al. 2000; Irschick et al. 2008); therefore, locomotion is ideal for studies of ecological morphology (or "ecomorphology"), a field that examines how an animal's physical form relates to its external environment, generally with the goal of finding evidence for evolutionary adaptation (Van der Klaauw 1948). In addition to locomotion, many other factors can influence an animal's morphology, such as habitat specialization and body size. Moreover, the factors that influence the evolutionary trajectory of morphology may interact. For example, a small-bodied lineage that evolves to specialize on arboreal habitats may do so in ways that differ greatly from those that occur in a large-bodied lineage, as demonstrated by differential use of leaping vs. swinging in small and large arboreal primates (Fleagle and Mittermeier 1980). Further, specialization for certain types of habitats may be facilitated by the evolution of different modes of locomotion (e.g. digging facilitates use of underground habitats).

An organism's body plan constrains the type(s) of locomotion it can perform. For example, limbless terrestrial vertebrates interact with the environment in a fundamentally different way than their limbed relatives do. Lacking hands and feet to provide traction, they rely entirely on the trunk musculature and vertebral column for propulsion (Gasc 1974; Jayne 1988a, 1988b). Although a limbless body plan might impose constraints, elongation with concurrent limb reduction has evolved more than 25 times in Squamate reptiles (Gans 1975; Wiens et al. 2006). Many limbless tetrapods are primarily burrowers, but snakes have radiated into a wide variety of niches on six continents and have developed many ways of moving without limbs. They effectively use subterranean, terrestrial, arboreal, and aquatic environments (Greene 1997), and they can use many distinct types of movement (Jayne 2020). Most snakes, like all limbless tetrapods, generally use lateral undulation on land (Gans 1962). However, some environments elicit other types of locomotion that not all species can perform adequately, including a specialized gait termed "sidewinding" (Gans 1962; Tingle 2020).

In the present study, we examined whether body size, sidewinding locomotion, arboreality, and/or climate (specifically, mean annual precipitation) could predict interspecific variation in body shape and scalation in vipers. Sidewinding locomotion and arboreal habitats both seem likely to pose special demands on the body. By including precipitation in our study, we can tease apart whether any morphological differences relate more to ecological specialization (arboreality and/or sidewinding) or to broader-scale environmental characteristics.

Sidewinding locomotion has evolved in several distantly-related viper species and in a few other snake species (Tingle 2020). This type of locomotion might allow desert-dwelling species to deal with the difficulties of shifting sand, and/or to move quickly so that they can minimize the amount of time spent in dangerous open areas (e.g. see Cowles 1920, 1956; Gans and Mendelssohn 1971). During sidewinding, the snake alternately lifts some regions of its body up and forward while other regions remain in static contact with the ground. Given the relative uncommonness of this mode of locomotion, we expected that sidewinding species would show clear evidence of morphological differences from non-sidewinding snakes, i.e., coadaptation of morphology with sidewinding behavior. However, only one previous study has directly tested this hypothesis, finding shorter spinalis muscles in sidewinding species (Tingle et al. 2017), while another study found highly derived ventral scale microstructure in two genera of distantly related sidewinding specialists (*Crotalus cerastes* and *Cerastes* spp.) that, according to mathematical modelling, should aid sidewinding, thus suggesting adaptation (Rieser et al. 2021).

Arboreality has evolved many more times than has sidewinding, including several independent origins in vipers (Alencar et al. 2017; Harrington et al. 2018). Animals living in trees face special challenges, such as the need to grip branches and maintain balance on narrow surfaces (Cartmill 1985). Although snakes do not have limbs or claws that could be modified for climbing, some species that regularly move through trees have been shown to exhibit elements of trunk and tail morphology that are presumed to aid their movement, such as slender, laterally compressed bodies, relatively long tails, and long spinalis muscles (Henderson and Binder 1980; Jayne 1982; Vitt and Vangilder 1983; Guyer and Donnelly 1990; Lillywhite and Henderson 1993; Martins et al. 2001; Pizzatto et al. 2007a, 2007b; França et al. 2008; Alencar 2010; Tingle et al. 2017). Arboreal vipers show some convergence with arboreal snakes in other clades, including slender bodies and relatively long tails (Alencar et al. 2017), but it is unknown whether they show specialization with regard to other body shape traits or scalation.

Here, we combined tests of specific hypotheses with exploratory data analysis to study the evolution of body shape in vipers. Given that ours is the first study to quantify body shape in sidewinding species, we chose to explore many body measurements and indices representing body shape. We had ideas for some important traits to examine based on previous observations and (bio)mechanical principles: (1) anecdotally, sidewinding species may have relatively wide, flat bodies (Gray 1968, pp. 180–181), which would increase contact with the ground, possibly reducing slippage; (2) sidewinding species may have relatively short tails, as the tail seems not to contribute to force production during sidewinding (Jayne 1988b); and (3) more vertebrae would increase flexibility (Jayne 1982), which could be important for forming tight bends in the body during sidewinding.

Unlike sidewinding, arboreality has been the focus of several previous studies; therefore, we had clearer expectations with respect to the morphology of arboreal species. As noted above, Alencar et al. (2017) found slender bodies and relatively long tails in arboreal vipers. We expected that arboreal vipers might show several additional specializations to their habitat, unexplored by Alencar and colleagues. In particular, we tested the following hypotheses: (1) that arboreal vipers would be laterally compressed in cross-section, convergent with arboreal snakes in other clades (Lillywhite and Henderson 1993; Pizzatto et al. 2007a, 2007b); (2) that the bodies of arboreal species would taper more sharply in the front, thus shifting their center of mass backwards (Peters 1960; Cadle and Greene 1993), which could aid in gap-bridging; and (3) that arboreal species would have more vertebrae, which would increase flexibility, facilitating complex motions.

To determine whether body shape differences were related to specialized behavior (sidewinding or use of arboreal habitats) or to some other environmental characteristic, we also examined whether body shape varied with climate. For example, Scanlon (2001) suggested that sidewinding snakes are generally smaller than other species in their clades.

However, such a trend could result from limited food ability in deserts rather than from the demands of sidewinding locomotion. By examining the potential influence of one or more variables related to climate, we could tease apart these potential causes of morphological differences. Because body size and phylogenetic history also influence morphology, we additionally examined scaling relationships and phylogenetic signal in the traits that we measured.

Methods

Our study included 86 geographically diverse species from across the viper phylogeny. For each species in the study, we measured the following parameters with either digital calipers or measuring tape: snout-vent length (SVL); tail length; neck width immediately behind the quadrates; head width at the corners of the mouth; ventral head length, measured from the tip of the snout to the anterior edge of the first true ventral scale as defined by Dowling (1951); dorsal head length, measured from the tip of the snout along the body axis to a line connecting the distal ends of the two quadrates at jaw articulation (this measurement likely correlates with mandible length); body width, height, and girth (circumference) at 25%, 50%, and 75% of SVL; number of ventral scales, according to the convention put forth by Dowling (1951); number of subcaudal scales; and number of dorsal scale rows. We collected measurements from museum specimens, as it would be unfeasible to collect measurements from a large sample size of live vipers, and impossible for us to obtain access to live specimens for many of these species. We did not use body measurements affected by large gut contents, gravidity, damage, or obvious deformation in our analyses. We measured several individuals of most species (mean: 8.3; range: 1-51) for a total sample of 716 adult specimens. Additionally, although we collected measurements for some juvenile specimens, we conducted analyses on data from adult specimens only (we determined adulthood based on specimens having reached a snout-vent length consistent with published adult size ranges for their species). In some cases, catalogs contained out-of-date species identifications, so we changed species IDs according to the most current literature.

From these measurements, we calculated several indices describing body shape. The average body width to height ratio from measurements at 25%, 50%, and 75% SVL describe whether the body is flattened or laterally compressed in cross-section. We calculated an index to describe anterior tapering by dividing the body width measurement at 50% SVL by the body width measurement at 25% SVL and an index to describe posterior tapering by dividing the body width measurement at 50% SVL by the body width measurement at 75% SVL.

We coded both sidewinding and arboreality as 0-1 indicator (a.k.a. dummy) variables in which 1 indicated specialization. We followed Tingle's (2020) coding for sidewinding specialization, with two exceptions: *Echis pyramidum* and *Bitis schneideri*. Tingle (2020) categorized *Echis carinatus* as the only specialized sidewinder in its genus based mainly on the work of Gans and Mendelssohn (1971). However, *E. carinatus* has been split into multiple species, and Gans and Mendelssohn's *"Echis carinatus* subspecies" from Kenya is now considered to be *E. pyramidum* (Pook et al. 2009), so we categorized *E. pyramidum* as a sidewinder. Tingle (2020) placed *B. schneideri* in the second rather than the most specialized category for sidewinding due to differences among populations: although some populations of *B. schneideri* use sidewinding as a primary mode of locomotion, other populations seem never to use sidewinding despite living in sandy habitats. For this study, we have decided to count *B. schneideri* among the sidewinding species. We used various literature accounts to determine specialization for arboreality (Pitman 1938; Campbell and Lamar 1989; Gloyd and Conant 1990; Campbell 1998; Grismer 2002; Orlov et al. 2002; Spawls et al. 2002; Mallow et al. 2003; Stebbins 2003; Vogel 2006). Specialization for sidewinding locomotion is estimated to have five independent origins in vipers (Tingle 2020), all of which are included in our dataset (Fig. 3.1). Arboreality probably has seven independent origins in vipers (Harrington et al. 2018), of which we have captured four (Fig. 3.1).

In addition to sidewinding and arboreality, we examined the relationship between climate and morphology. We used GPS coordinates associated with specimens in our sample to obtain climate data from the WorldClim database (Fick and Hijmans 2017). For some specimens, coordinates were obtained directly from VertNet.org. For others, VertNet.org did not list coordinates, but it did list locality information, allowing us to obtain approximate GPS coordinates. Some specimens did not have locality information, or had locality information that was not precise enough to meaningfully approximate GPS coordinates. For those specimens, we left latitude and longitude, as well as climate data, as not assessed (NA). For two species (*Bothrops barnetti* and *Montivipera latifii*), none of the specimens we measured had locality data. Therefore, we obtained range information from the IUCN and Reptile Database websites, and then chose GPS coordinates representing a point in the middle of their ranges.

Climate variables obtained from WorldClim included the following: average maximum temperature of the hottest month in °C (T_{max}), average minimum temperature of the coldest month in °C (T_{min}), mean annual precipitation (which we recorded in meters), and precipitation seasonality (coefficient of variation). We square-root transformed precipitation to reduce negative skewness. We also calculated two indices representing climate: the aridity index of Emberger (1942, 1955), (precipitation in mm * 100) / $((T_{max}+T_{min})(T_{max}-T_{min}))$ which has subsequently been used in several other ecophysiological studies within and among species (e.g. Tieleman et al. 2003; Oufiero et al. 2011; Wishingrad and Thomson 2020).; and the desert index of McNab and Morrison (1963), T_{max} / precipitation in cm, subsequently used by MacMillen and Garland (1989).

Prior to analysis, we $\log_{10}$-transformed linear measurements and scale counts, but not body shape indices, for individual specimens. We then aggregated climatic and morphological data by species, calculating a mean and a standard error for each trait of interest so that we could account for within-species variation (which includes measurement error) in our analyses. Ives et al. (2007) showed that when it is not accounted for, within-species variation can lead to bias and excessive uncertainty in parameter estimates. Several other studies have also emphasized the importance of the accounting for within-species variation (Felsenstein 2008; Freckleton 2011; Hardy and Pavoine 2012; Johnson et al. 2014).

Several species in our sample were represented by a single adult individual (*Agkistrodon taylori*, *Bothrops barnetti*, *Crotalus ehecatl*, *C. mictlantecuhtli*, *C. simus*, *C. triseriatus*, *Daboia siamensis*, *O. convictus*, and *Trimeresurus gramineus*), so we could not directly calculate a standard error for these species. Therefore, we regressed standard error on sample size for each trait of interest and then used the slope and intercept to calculate the expected standard error for N = 1. In general, species with larger sample sizes have lower standard errors for a given trait. Accordingly, our approach for dealing with singleton species assigns relatively high errors to those species, accounting for our uncertainty of the true trait means for those species. Methods accounting for within-species variation give lower weight to species with greater errors. Thus, our method appropriately gives less weight to the species for which we measured only one individual. Additionally, for some species, all specimens were collected from the same locality, and therefore had the same GPS coordinates. As a result, they had a standard error of 0 for climate variables, which is clearly inappropriate. Therefore, we replaced those 0s with the expected standard error for N = 1.

As a result of their shared evolutionary history, species typically do not represent statistically independent samples (Felsenstein 1985; Harvey and Pagel 1991; Rezende and Diniz-Filho 2012). Therefore, we conducted phylogenetic regressions to explore whether morphological traits relate to sidewinding, arboreality, and climate. We used a type of Ornstein-Uhlenbeck model of trait evolution that incorporates intraspecific variation, using the MATLAB program MERegPHYSIGv2.m (Ives et al. 2007; Johnson et al. 2014). We chose MERegPHYSIGv2 to conduct our analyses because it can handle measurement error in addition to multiple independent variables, including categorical variables, and it can perform simulations to provide confidence intervals for model coefficients. The program is available from TG upon request.

Predictors for SVL included sidewinding, arboreality, and the square root of precipitation. For other traits, predictors included sidewinding, arboreality, the square root of precipitation, and SVL. Although sidewinding species all occur in arid or semi-arid environments, the correlation between sidewinding and precipitation was only -0.52, which is low enough to eliminate concerns regarding multicollinearity (Slinker and Glantz 1985). We chose the square root of precipitation over the other possible climate variables by model selection. MERegPHYSIGv2 can handle four predictor variables, so we compared models including sidewinding + arboreality + SVL + one of our potential climate variables or the absolute value of latitude. In all cases, the model with precipitation had higher log likelihood than the other options. Therefore, we present the results of models including precipitation.

We used the partial regression coefficient and associated 95% confidence interval for SVL from simulations performed in MERegPHYSIGv2 to examine scaling relationships. We corrected for multiple comparisons with adaptive FDR, implemented in SAS Procedure MULTTEST. Based on analysis of the 59 P values, those ≤ 0.02 would still be considered significant.

We used the phylogeny from Alencar et al. (2016) as the basis of our analyses, adding eleven additional species: *Ovophis convictus*, *O. makazayazaya*, *Cerrophidion wilsoni*, *Crotalus tlaloci*, *Crotalus ehecatl*, *C. mictlantecuhtli*, *C. stephensi*, *C. pyrrhus* , *Sistrurus tergeminus*, *Daboia russelii*, and *Causus maculatus*. Figure 3.1 shows our final tree.

For comparison with previous studies of ecomorphological traits, we estimated phylogenetic signal for each trait using the program PHYSIG_LL.m in MATLAB (Blomberg et al. 2003), available from TG upon request. Prior to conducting the analysis for phylogenetic signal, we corrected traits for body size according to the methods of Blomberg et al. (2003), by regressing log(trait) on log(SVL) using phylogenetic generalized least square in REGRESSIONv2.m, and then using that slope to calculate log(trait/$\mathrm{SVL}^{\mathrm{slope}}$).

Results

All traits showed statistically significant phylogenetic signal, with the K values for subcaudal scale count (1.221) and dorsal scale row count (1.262) being substantially larger than 1 (Table 3.1). Thus, related species tended to resemble each other, generally less than expected under purely Brownian motion evolution, but occasionally more so.

Tail length as well as mid-body width, height, and girth scaled isometrically with SVL (i.e., slopes not significantly different from one for $\log_{10}$-transformed variables); however, neck width and all head measurements scaled with negative allomety (Table 3.2; Fig. 3.2). All three scale counts increased significantly with body size (Table 3.2; Fig. 3.2).

Snout-vent length did not vary in relation to locomotor specialization or precipitation (Table 3.2). Adjusting for variation in SVL and after correcting for multiple comparisons, sidewinding specialists did not differ significantly from non-sidewinding species for any measured trait (Table 3.2). Arboreal snakes, however, had relatively long tails, narrow mid-body width, a low body width/height ratio, and a low posterior tapering index compared to other species. They also had high subcaudal scale counts, and this effect remained when we replaced SVL with tail length as a predictor variable in the model, indicating that arboreal vipers have high subcaudal counts even relative to their tail length (results not shown). Ventral scale counts did not differ between arboreal and terrestrial species. Precipitation was positively related to head width, but negatively related to anterior tapering index (Table 3.2).

Discussion

Phylogenetic signal

All traits showed statistically significant phylogenetic signal (Table 3.1). Values for the K statistic ranged from 0.410 to 1.262, with a mean of 0.724. All of these values are within the range reported by Blomberg et al. (2003) for morphological traits, and the mean is similar to their value of 0.71.

Allometry and scaling

All head measurements scaled with negative allometry, which agrees with a previous study that reported head length allometry in 30 snake species from four families (Phillips and Shine 2006). Allometric scaling of head dimensions could have functional ramifications for prey ingestion, as snakes are gape-limited predators whose ability to ingest large prey increases with relative head size (Pough and Groves 1983; Forsman and Lindell 1993). Negative interspecific allometry in head dimensions could allow smaller species to eat disproportionately large prey for their body size. However, macrostomatan snakes have achieved their prodigious gape through complex morphological changes, and several traits can contribute to gape size differences among species, including the properties of multiple skeletal elements as well as soft tissues (Gans 1961; Arnold 1983; Cundall and Irish 2008; Hampton and Moon 2013). Therefore, although head size allometry may have implications for gape size allometry, the two probably do not correspond exactly.

Geometric similarity predicts that any linear scale dimension should vary in direct proportion to body length. If the scales are the same size relative to body size, then the number of scales should not vary with body size (i.e., geometric similarity equates to an allometric slope of zero for scale counts). However, one would not expect geometric similarity for ventral or subcaudal scale counts in snakes because they correspond 1:1 with the vertebrae in vipers (Charas 1669; Tyson 1682; Alexander and Gans 1966), and several studies have shown that larger snake species tend to have more vertebrae (Lindell 1994; Head and Polly 2007; Lee et al. 2016). We found that all three scale counts increased with body size, meaning that they show significant positive allometry, i.e., slopes greater than zero (Table 3.2; Fig. 3.2). We are not aware of any previous studies that examine allometry of dorsal scale row counts in snakes. Opposite to our findings for snakes, Oufiero et al. (2011) found negative allometry for dorsal scale row count in *Sceloporus* lizards.

The adaptive significance of positive allometry in scale counts, if any, remains obscure. This allometry could result from developmental differences among species that do not necessarily reflect selection on the number of body segments per se. Ventral and subcaudal scales with their corresponding vertebrae arise from the segmentation of embryos into somites (Richardson et al. 1998). The number and size of somites corresponds to the rate of axial growth (Tam 1981). Thus, any change in axial growth rates, which are themselves likely often under selection, could lead to changes in the numbers of scales, vertebrae, and associated muscle segments.

No apparent morphological adaptations in sidewinding vipers

We did not find evidence of morphological specialization in sidewinding vipers. This apparent lack of morphological differentiation between sidewinding specialists and terrestrial generalists might be explained in various ways, which are not mutually exclusive. First, our analyses may have lacked statistical power. This seems unlikely, given that our dataset contains five independent origins of sidewinding specialization and only four independent origins of specialization for arboreality, yet we detected several morphological differences between arboreal and terrestrial vipers. Second, the viper body plan may be preadapted (sensu Futuyma and Kirkpatrick 2017) for sidewinding, in which case their morphology need not change (much) after the sidewinding behavior evolves. For example, Gray (1968, pp. 180–181) observed that sidewinding species may tend to have stout, flattened bodies, and large, wide heads, but these traits generally characterize the family Viperidae (Pough and Groves 1983; Feldman and Meiri 2013). Although some non-vipers can approximate sidewinding under certain conditions, the highly specialized sidewinders are all vipers (Tingle 2020). Third, body shape may not affect sidewinding locomotion. Finally, specialization for sidewinding may have evolved recently enough that the morphology has not yet caught up to the behavior. Comparative evidence is consistent with the idea that behavioral traits may generally evolve more rapidly than do morphological traits (Blomberg et al. 2003). Thus, organisms often evolve increased expression of a behavior, or even novel behaviors, with little if any accompanying change in overt morphology, which causes an ecomorphological mismatch until the morphology evolves to better support the altered behavior (Lister 2014; Diogo 2017).

Apparent morphological adaptations to arboreality

Arboreal vipers in our study had relatively long tails (Table 3.2, Fig. 3.2), consistent with a previous study on arboreal vipers (Alencar et al. 2017). Long tails characterize arboreal snakes in many clades (Vitt and Vangilder 1983; Martins et al. 2001; Pizzatto et al. 2007b, 2007a; Alencar 2010; Lawing et al. 2012; Sheehy et al. 2016). When they cross gaps, snakes often resist the torque that they experience at the edge of the perch by putting part of their body or tail underneath the perch, or even by wrapping the tail around it (Jayne and Riley 2007; Byrnes and Jayne 2012). Juveniles of one arboreal viper (*Trimeresurus albolabris*) can perform defensive strikes over 50% of their body length, holding onto branches with their prehensile tails (Herrel et al. 2011). Thus, the tail may play an important role in preventing snakes from pitching downward during cantilevering maneuvers and strikes by providing a counterweight for the body and/or by actually grasping a perch in the case of prehensile tails. In cases where the tail acts as a counterweight, longer tails are presumably more effective than shorter ones because they presumably have greater total mass and also because they increase the length of the moment arm for the counter-torque that prevents the body from pitching downward. Another plausible explanation for long tails in arboreal snakes relates to non-locomotor demands of arboreality. Sheehy et al. (2016), suggested that a relatively long tail, which is composed of stiffer tissues than the body and therefore better prevents blood pooling, could help to offset cardiovascular stress resulting from gravity when the snake is climbing in an upright position.

Arboreal vipers had significantly lower mid-body width than did terrestrial generalists (Table 3.2, Fig. 3.2). This result matches the findings of previous studies, including one on vipers and the rest in other snake clades, that found higher elongation ratios (length divided by width) (Vitt and Vangilder 1983; Martins et al. 2001; Pizzatto et al. 2007a; Alencar et al. 2017) or lower body mass relative to length (Guyer and Donnelly 1990; Feldman and Meiri 2013) in arboreal species. Slender bodies may aid arboreal snakes in several ways, probably leading to strong selection. Gravity acting on the mass of unsupported parts of a snake's body causes torque, which can lead to downward bending (Byrnes and Jayne 2012; Hoefer and Jayne 2013). Thus, we expect that more massive snakes experience greater torque while cantilevering across gaps (shown experimentally by Hoefer and Jayne 2013), which might limit them to crossing relatively shorter gaps than a more slender snake of a similar size might cross. Juvenile rat snakes (*Pantherophis obsoletus*), which have lower body mass relative to their body length than adults, had significantly higher cantilever performance in one experiment (Lillywhite et al. 2000). We expect that if the slenderer viper species in our study were tested in a similar experiment, they would show better cantilevering performance than the stockier species.

An alternate explanation for why arboreal snakes have more slender bodies hinges on the idea that stockier snakes of a given length may have a disadvantage not in gap-bridging performance, but in the diameter of branches that will support their weight without bending (Lillywhite and Henderson 1993). Branches of very small diameters predominate in some arboreal habitats (Mattingly and Jayne 2004), and the greater tendency for these narrower branches to bend under applied weight has consequences for locomotion (Byrnes and Jayne 2010). Slender bodies likely allow arboreal snakes to effectively move along branches with smaller diameters than heavy snakes would be able to negotiate without excessive bending or breaking (Lillywhite and Henderson 1993). This advantage should persist whether the snakes crawl along a single narrow twig or whether they distribute their weight over many narrow twigs. Hoefer and Jayne (2013) pointed out that Brown Tree Snakes (*Boiga irregularis*) in Guam were repeatedly found with their weight supported by tiny stems measuring only 2-3 mm in diameter, despite the relatively large size of the snakes considered in terms of body length. A slender form could also improve crypsis in environments where slender branches predominate (Lillywhite and Henderson 1993). The Rough Green Snake (*Opheodrys aestivus*) spends most of its time on branches well under 1 cm in diameter (Goldsmith 1984), and two arboreal snakes of the genus *Uromacer* use branches of 1 cm or less in diameter, with the smaller species using branches averaging only 5 mm across (Henderson et al. 1981).

Lateral compression characterizes arboreal species in several snake clades (Pizzatto et al. 2007b, 2007a). Our study is the first to show evidence for lateral compression in arboreal vipers (Table 3.2, Fig. 3.3). Some species may also actively compress themselves laterally during climbing – Lillywhite et al. (2000) observed this phenomenon in some boas. Jayne et al. (2015) also commented on this ability of snakes to actively change their cross-sectional shape. External lateral compression may relate to vertebral differences in arboreal species, such as the higher length/width ratio of the vertebrae (Lawing et al. 2012) and the lesser lateral projection of the prezygapophyses (Johnson 1955). Additionally, some species, especially among the boas and vipers, have this body shape because the ribs are directed markedly downward (Johnson 1955). Lillywhite and Henderson (1993) suggest that lateral compression would increase arboreal snakes' ability to grasp certain objects "due to the increased contact area for static friction;" however, this hypothesis assumes that the snakes wrap laterally around objects and that increased body surface area would improve grasping ability. We could find no supporting evidence for either assumption in the literature. If we consider a snake's body projecting from a branch across a gap as a beam attached on one end to a wall, then we can explain lateral compression with Euler Bernoulli beam theory. This theory describes a beam's vertical deflection, which depends in part on the beam's material properties and cross-sectional shape. A laterally compressed cross-section leads to a stiffer beam and therefore reduces bending, a desirable outcome for a snake that needs to cross a gap. This explanation relies on the assumption that snakes behave reasonably similarly to beams, an assumption that we have not tested.

We found that arboreal viper species do not taper more in the front of the body than terrestrial species do, but they taper significantly less posteriorly, with some arboreal species having wider measurements towards the back of the body than at mid-body (Table 3.2, Fig. 3.3). Thus, arboreal species have generally shifted their center of mass towards the back of the body. Apparently, ours is the first study to test for such a morphological configuration in snakes. Cadle and Greene (1993) listed “center of gravity shifted posteriorly” as a characteristic of arboreal snakes, and Peters (1960) observed several modifications for arboreality including an “abrupt narrowing of the body immediately posterior to the head” in snakes of the subfamily Dipsadinae. However, neither these authors nor the references they cite provide empirical evidence for these observations. Therefore, it is unclear whether a more posterior center of gravity characterizes arboreal snakes in other clades, and if so, whether other arboreal snakes achieve this shift via increased tapering of the anterior body or decreased tapering of the posterior body. Intuitively, a caudally shifted center of mass would benefit arboreal snakes as they extend the front part of their bodies unsupported across gaps, so we would expect to see similar tapering patterns in other clades.

We did not find evidence for increased numbers of body vertebrae in arboreal vipers, but we did find increased numbers of tail vertebrae, even when controlling for their relatively long tails. Previous studies have shown mixed results with respect to the relationship between arboreality and number of body vertebrae – Jayne (1982) found that arboreal snakes had relatively more body vertebrae, whereas Lindell (1994) found no difference between arboreal and terrestrial species. Hampton (2011) found that arboreal vipers had more total vertebrae (body + tail vertebrae) relative to their total body length, but it is unclear whether this trend resulted from increases in the number of both body and tail vertebrae, or whether higher tail vertebrae alone may have driven this trend. A previous study showed that vipers with prehensile tails have more tail vertebrae, and all arboreal viper clades have evolved prehensile tails (Hampton 2011).

Relationship between precipitation and morphology

Viper species from locations with higher precipitation had longer tails. One previous study found evidence for longer tails in snake species that live in leaf litter (Guyer and Donnelly 1990). In principle, the leaf litter niche should be tied to precipitation: low-precipitation biomes such as deserts and grasslands do not have leaf litter, whereas high-precipitation biomes, such as temperate deciduous forests and rainforests do. Unfortunately, we do not have information on substrate use for most of the species in our sample, and the potential function of long tails in leaf-litter species remains untested. One testable hypothesis relates to defensive signaling. Many snake species vibrate the tail when disturbed (Greene 1988), which generates noise most effectively in dry plant matter, and may therefore be more beneficial to leaf-litter species than to species dwelling on other substrates, such as rocks or sand. Additionally, several viper species use their tails to lure prey (Heatwole and Davison 1976), and a few species can even constrict prey with the tail (Greene 1977; Murphy 1977). Future studies could investigate whether these behaviors are more common in some habitats than in others.

An alternate explanation involves the effect of environmental variation on developing embryos. Some studies have shown that temperature during gestation or incubation can affect the number of body vertebrae and other phenotypic traits in snakes (e.g. Fox 1948; Osgood 1978; Lourdais et al. 2004), although Arnold and Peterson (2002) found that manipulating temperature during gestation of the garter snake *Thamnophis elegans* led to differences in the number of scale abnormalities but not in the number of scales. Thus, direct environmental effects on development are possible. However, the present study does not employ a common garden approach (i.e., all animals raised under common conditions), as is true for all broad-based comparative studies (cf Garland and Adolph 1991, 1994; Rezende and Diniz-Filho 2012), so it is not possible to infer whether developmental effects may be involved in the relationship between tail length and precipitation.

In addition to longer tails, vipers from wetter environments also had significantly wider heads. Because larger heads enable snakes to swallow larger prey (Pough and Groves 1983; Shine 1991; Forsman and Lindell 1993), we speculate that head width differences in wetter vs. drier habitats reflect differences in prey availability. One study on a Mediterranean viper species found that individuals from drier environments include a higher proportion of lizards in their diet, whereas those from wetter environments mainly consume mammals (Santos et al. 2008), a pattern that corresponds to increased abundance of small mammals in the wetter parts of the region (Barbosa and Benzal 1996). In general, even small mammals are larger in body size than lizards (e.g. Pough 1980). Interspecific dietary differences may similarly track climate-related patterns of prey relative abundance, which may lead to selection on head morphology in gape-limited predators such as snakes. Previous studies examining head size and prey type in snakes have provided mixed results.

In pit vipers of the genus *Bothrops*, juveniles, but not adults, have significantly larger heads in species specializing on mammals (Martins et al. 2002). Results of one study suggest that boids specializing on mammals may have longer heads, compared to generalists (Pizzatto et al. 2007b). As discussed above, external head dimensions do not provide a full picture of gape size, since many traits contribute to gape (Gans 1961; Arnold 1983; Cundall and Irish 2008; Hampton and Moon 2013). Detailed studies of skull and soft tissue anatomy, as well as functional studies, could therefore provide further insight into the relationships between environmental characteristics, diet, and swallowing performance.

Conclusions and Future Directions

Although vipers have superficially simple morphology, they have evolved along several axes with respect to ecology and behavior. Here, we show that several body shape and scalation traits vary in relation to specialization for arboreal habits and/or precipitation. Contrary to our expectations, sidewinding species did not exhibit statistically significant specialization in body shape or number of vertebrae. Given that many viper species, including some close relatives of sidewinding specialists, do not sidewind even under duress on low-traction surfaces (Marvi et al. 2014), some factor likely prevents them from expressing this behavior. If external body characteristics do not enable or prevent sidewinding, then perhaps it relies on particular configurations of the underlying musculoskeletal system, such as reduced spinalis muscle lengths (Tingle et al. 2017) or aspects of motor control. The statistically supported differences between arboreal and non-arboreal vipers, mostly consistent with patterns found in other snake clades, suggest that we have chosen functionally relevant measurements and that these cases provide examples of coadaptation (correlated responses to multivariate natural selection) between behavior/habitat selection and morphology.

The present study provides several leads for future work on adaptive ecomorphological variation in snakes. In particular, functional studies could test various hypotheses regarding the reasons for those patterns. For example, do slender bodies aid crypsis in arboreal snakes? Do long tails improve climbing or cantilever performance? What prevents some species from sidewinding proficiently? Previous studies have provided insight into the relationships between habitat, morphology, functional performance, and diversification in various clades (for some examples, see: Gomes et al. 2009; Price et al. 2011, 2012; Crumière et al. 2016; Alencar et al. 2017; Ceccarelli et al. 2019; Yuan et al. 2019). Because snakes move in fundamentally different ways from aquatic vertebrates or limbed terrestrial vertebrates, answers to outstanding questions about snake locomotion would improve our general understanding of the relationships between locomotor adaptation and functional diversification.

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Table 3.1. Phylogenetic signal of SVL and size-corrected traits estimated using PHYSIG_LL in MATLAB (Blomberg et al. 2003).

Trait	**Expected MSE_0/MSE**	**Observed MSE_0/MSE**	**K**	**MSE**	**MSE_{star}**	**P**	**Maximum likelihood**	**Maximum $likelihood_{star}$**
snout-vent length, log transformed	2.117	1.375	0.650	0.0871	0.1189	<0.001	0.650	-29.957
tail length, size corrected	2.117	1.906	0.901	0.0604	0.1020	<0.001	-0.838	-0.838
neck width, size corrected	2.117	1.357	0.641	0.0295	0.0400	<0.001	29.981	16.856
head width, size corrected	2.117	1.345	0.635	0.0264	0.0355	<0.001	34.725	22.024
head length (ventral), size corrected	2.117	1.277	0.603	0.0182	0.0206	<0.001	50.822	45.502
head length (dorsal), size corrected	2.117	1.171	0.553	0.0123	0.0144	<0.001	67.557	60.794
mid-body width, size corrected	2.117	1.580	0.746	0.0411	0.0599	<0.001	15.681	-0.511
mid-body height, size corrected	2.117	1.195	0.628	0.0407	0.0487	<0.001	16.105	8.432
mid-body girth, size corrected	2.117	1.557	0.736	0.0325	0.0449	<0.001	25.816	11.870
ventral scale count, size corrected	2.117	1.563	0.739	0.0076	0.0118	<0.001	88.564	69.431
subcaudal scale count, size corrected	2.117	2.585	1.221	0.0566	0.1335	<0.001	1.943	-34.947
dorsal row count, size corrected	2.117	2.671	1.262	0.0104	0.0275	<0.001	74.644	33.026
body width / height, size corrected	2.117	1.124	0.531	0.0227	0.0255	<0.001	41.198	36.268
anterior tapering, size corrected	2.117	0.868	0.410	0.0121	0.0102	0.015	68.269	75.613
posterior tapering, size corrected	2.117	1.279	0.604	0.0073	0.0087	<0.001	89.856	82.315

We log transformed SVL prior to analysis. Following Blomberg et al. (2003), we corrected all other traits for body size by regressing the trait on SVL using phylogenetic generalized least squares (no branch length transformations), then using the estimated slope to calculate $\log(trait/SVL^{slope})$. MSE_0/MSE represents the ratio of the mean squared error of the species data on a star phylogeny to the mean squared error of the species data calculated using the variance-covariance matrix from the phylogenetic tree. Expected MSE_0/MSE under Brownian motion depends on the size and shape of the phylogenetic tree. The K statistic (observed MSE_0/MSE divided by expected MSE_0/MSE) indicates the amount of phylogenetic signal. Values < 1 indicate less phylogenetic signal than expected under Brownian motion evolution along the specified tree, whereas $K > 1$ indicates more than expected. Significance levels (P values) are based on randomization tests as described in Blomberg et al. (2003), which test the null hypothesis of no phylogenetic signal.

Table 3.2. Phylogenetic regression models accounting for measurement error (within-species variation (Johnson et al. 2014)).

Snout-Vent Length

d = 0.476

	$B_{estimate}$	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	0.010	-0.096	0.012	0.117	0.824
Arboreal	-0.119	-0.248	-0.120	0.015	0.070
sqrt(Precipitation)	**0.107**	**0.014**	**0.107**	**0.195**	**0.020**
log(SVL)	-	-	-	-	-

Tail Length

d = 0.965

	$B_{estimate}$	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	-0.053	-0.132	-0.052	0.024	0.192
Arboreal	**0.192**	**0.080**	**0.192**	**0.299**	**<0.002**
sqrt(Precipitation)	0.025	-0.043	0.026	0.092	0.418
log(SVL)	**1.095**	**1.032**	**1.096**	**1.162**	**<0.002**§

Neck Width

d = 1.813

	$B_{estimate}$	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	0.006	-0.046	0.006	0.056	0.812
Arboreal	-0.085	-0.172	-0.084	0.001	0.052
sqrt(Precipitation)	-0.012	-0.059	-0.013	0.028	0.556
log(SVL)	**0.867**	**0.824**	**0.868**	**0.913**	**<0.002**§

Head Width

d = 1.615

	$B_{estimate}$	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	-0.003	-0.056	-0.002	0.049	0.914
Arboreal	0.019	-0.071	0.020	0.105	0.658
sqrt(Precipitation)	-0.003	-0.049	-0.002	0.042	0.902
log(SVL)	**0.844**	**0.801**	**0.843**	**0.885**	**<0.002**§

Head Length (Ventral)

d = 1.493

	$B_{estimate}$	**B_{lower}**	**B_{mean}**	**B_{upper}**	**P**
Sidewinding	-0.039	-0.088	-0.040	0.006	0.100
Arboreal	-0.013	-0.083	-0.013	0.055	0.682
sqrt(Precipitation)	-0.001	-0.031	-0.001	0.029	0.952
log(SVL)	**0.801**	**0.771**	**0.802**	**0.832**	**<0.002**§

Head Length (Dorsal)

d = 1.657

	$B_{estimate}$	**B_{lower}**	**B_{mean}**	**B_{upper}**	**P**
Sidewinding	-0.030	-0.071	-0.030	0.006	0.128
Arboreal	-0.006	-0.067	-0.006	0.053	0.836
sqrt(Precipitation)	**0.033**	**0.009**	**0.033**	**0.057**	**0.002**
log(SVL)	**0.795**	**0.771**	**0.795**	**0.818**	**<0.002**§

Mid-Body Width

d = 1.690

	$B_{estimate}$	**B_{lower}**	**B_{mean}**	**B_{upper}**	**P**
Sidewinding	0.015	-0.043	0.015	0.070	0.614
Arboreal	**-0.154**	**-0.251**	**-0.157**	**-0.064**	**<0.002**
sqrt(Precipitation)	-0.013	-0.063	-0.013	0.036	0.606
log(SVL)	0.965	0.915	0.965	1.017	0.172§

Mid-Body Height

d = 2.000

	$B_{estimate}$	**B_{lower}**	**B_{mean}**	**B_{upper}**	**P**
Sidewinding	0.032	-0.033	0.033	0.098	0.308
Arboreal	-0.056	-0.161	-0.056	0.052	0.278
sqrt(Precipitation)	-0.008	-0.062	-0.009	0.043	0.726
log(SVL)	0.950	0.900	0.952	1.005	0.072§

Mid-Body Girth

d = 1.608

	B_{estimate}	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	0.019	-0.042	0.018	0.074	0.552
Arboreal	-0.072	-0.172	-0.073	0.019	0.114
sqrt(Precipitation)	-0.040	-0.092	-0.040	0.011	0.120
log(SVL)	1.018	0.971	1.018	1.065	0.5[§]

Ventral Scale Count

d = 1.128

	B_{estimate}	B_{lower}	B_{mean}	B_{upper}	P
Sidewinding	0.014	-0.017	0.014	0.046	0.346
Arboreal	0.031	-0.016	0.031	0.079	0.184
sqrt(Precipitation)	-0.018	-0.041	-0.019	0.003	0.088
log(SVL)	**0.247**	**0.226**	**0.247**	**0.271**	**<0.002**

Body measurements, scale counts, and body shape indices were analyzed in relation to sidewinding locomotion (dummy variable in which 1 indicates sidewinding), arboreality (dummy variable in which 1 indicates arboreal), and square root precipitation. We also included log snout-vent length (SVL) as a predictor variable for all other measurements and scale counts. Prior to conducting the analysis, we log-transformed measurements and scale counts for individual specimens, then computed means and standard errors for each species. Estimated effects are partial regression coefficients (B_{estimate}) along with their 95% confidence intervals and p values based on parametric bootstrapping (B_{lower} and B_{upper}; B_{mean} is the mean coefficient for the simulated datasets) (Johnson et al. 2014). The parameter d represents the Ornstein-Uhlenbeck branch length transformation: a value of 1 indicates the original branch lengths, a value of 0 indicates a star phylogeny, values between 0 and 1 indicate a tree that is less hierarchical than the original tree, and values greater than 1 indicated a more hierarchical tree than the original (by a more hierarchical tree, we mean one in which the internal nodes are nodes pushed up towards tips and away from the root). Bold text indicates cases where sidewinding, arboreality, or precipitation showed a significant relationship with a given morphological trait, or when a trait scaled with isometry rather than allometry.

§ For linear measurements, we used 1 rather than 0 as the null expectation under isometry.
¶ P-values over 0.02 were non-significant after correction for multiple comparisons by the adaptive FDR procedure.

Figure 3.1. Phylogeny used for statistical analyses. Tip labels indicate locomotor specialization, the square root of precipitation (m), and $\log_{10}$ snout-vent length (mm). Note that both sidewinding and arboreality are estimated to have evolved multiple times. Branch lengths are proportional to estimated divergence times. Data for this figure were visualized using the R package ggtree (Yu et al. 2017).

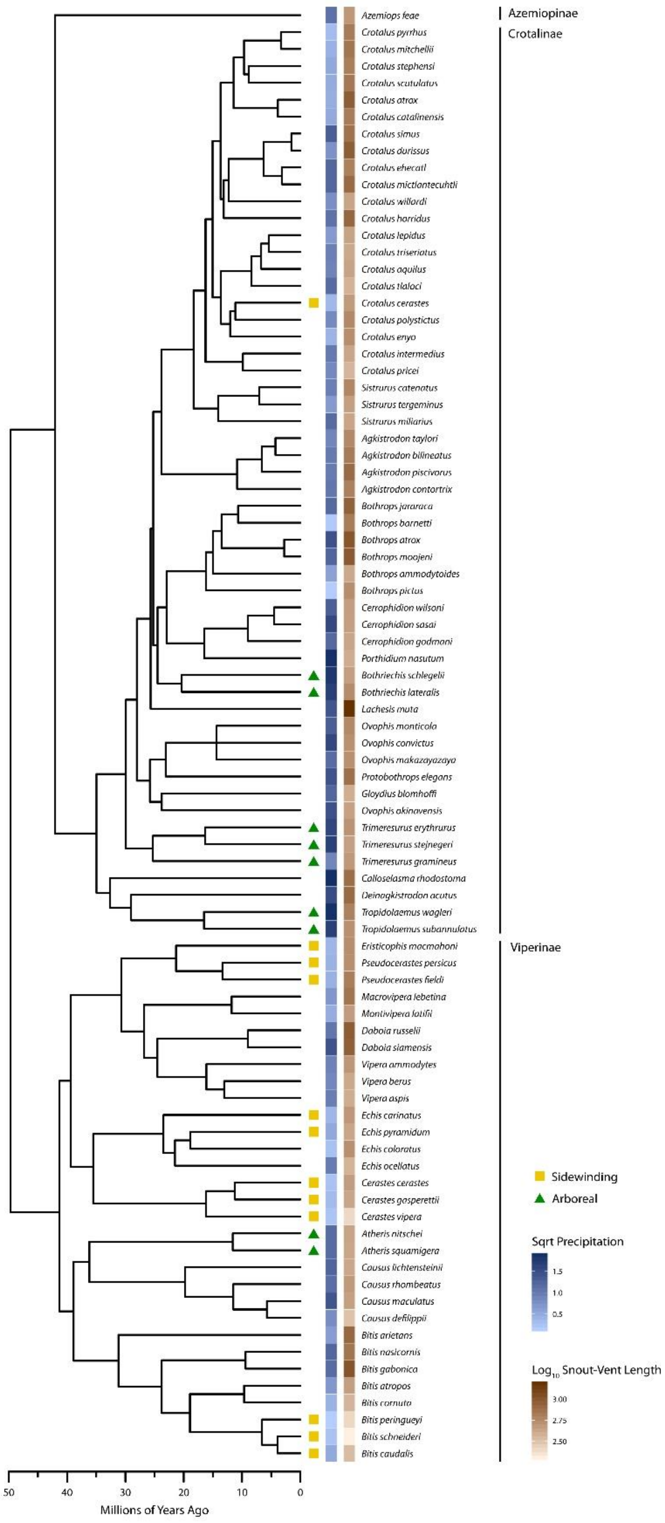

Azemiops feae
Azemiopinae
Crotalus pyrrhus
Crotalinae
Crotalus mitchellii
Crotalus stephensi
Crotalus scutulatus
Crotalus atrox
Crotalus catalinensis
Crotalus simus
Crotalus durissus
Crotalus ehecatl
Crotalus mictlantecuhtli
Crotalus willardi
Crotalus horridus
Crotalus lepidus
Crotalus triseriatus
Crotalus aquilus
Crotalus tlaloci
Crotalus cerastes
Crotalus polystictus
Crotalus enyo
Crotalus intermedius
Crotalus pricei
Sistrurus catenatus
Sistrurus tergeminus
Sistrurus miliarius
Agkistrodon taylori
Agkistrodon bilineatus
Agkistrodon piscivorus
Agkistrodon contortrix
Bothrops jararaca
Bothrops barnetti
Bothrops atrox
Bothrops moojeni
Bothrops ammodytoides
Bothrops pictus
Cerrophidion wilsoni
Cerrophidion sasai
Cerrophidion godmani
Porthidium nasutum
Bothriechis schlegelii
Bothriechis lateralis
Lachesis muta
Ovophis monticola
Ovophis convictus
Ovophis makazayazaya
Protobothrops elegans
Gloydius blomhoffi
Ovophis okinavensis
Trimeresurus erythrurus
Trimeresurus stejnegeri
Trimeresurus gramineus
Calloselasma rhodostoma
Deinagkistrodon acutus
Tropidolaemus wagleri
Tropidolaemus subannulatus
Eristicophis macmahoni
Viperinae
Pseudocerastes persicus
Pseudocerastes fieldi
Macrovipera lebetina
Montivipera latifii
Daboia russelii
Daboia siamensis
Vipera ammodytes
Vipera berus
Vipera aspis
Echis carinatus
Echis pyramidum
Echis coloratus
Echis ocellatus
Cerastes cerastes
Cerastes gasperettii
Cerastes vipera
Atheris nitschei
Atheris squamigera
Causus lichtensteinii
Causus rhombeatus
Causus maculatus
Causus defilippii
Bitis arietans
Bitis nasicornis
Bitis gabonica
Bitis atropos
Bitis cornuta
Bitis peringueyi
Bitis schneideri
Bitis caudalis
Sidewinding
Arboreal
Sqrt Precipitation
1.5
1.0
0.5
Log10 Snout-Vent Length
3.00
2.75
2.50
50
40
30
20
10
0
Millions of Years Ago

Figure 3.2. Scaling and effects of locomotor and habitat specialization. Linear measurements were recorded in mm and all traits and were log transformed prior to the analysis. Dashed black lines have a slope equal to isometry (1 for linear measurements and 0 for scale counts) and go through the mean value of (x, y). Solid black line segments have slope equal to the estimated partial regression coefficient for SVL from the models shown in Table 3.2 and pass through the phylogenetic mean of (x,y), computed in the MATLAB program RegressionV2.m (Lavin et al. 2008). The estimated slopes along with 95% confidence intervals (from parametric bootstrapping in the MATLAB program MERegPHYSIGv2.m (Johnson et al. 2014) are labelled on the plots. All traits that depart significantly from isometry after correcting for multiple comparisons are noted with an asterisk. Sidewinding specialists do not differ from non-sidewinding species, but arboreal specialists differ from terrestrial species for several traits (Table 3.2).

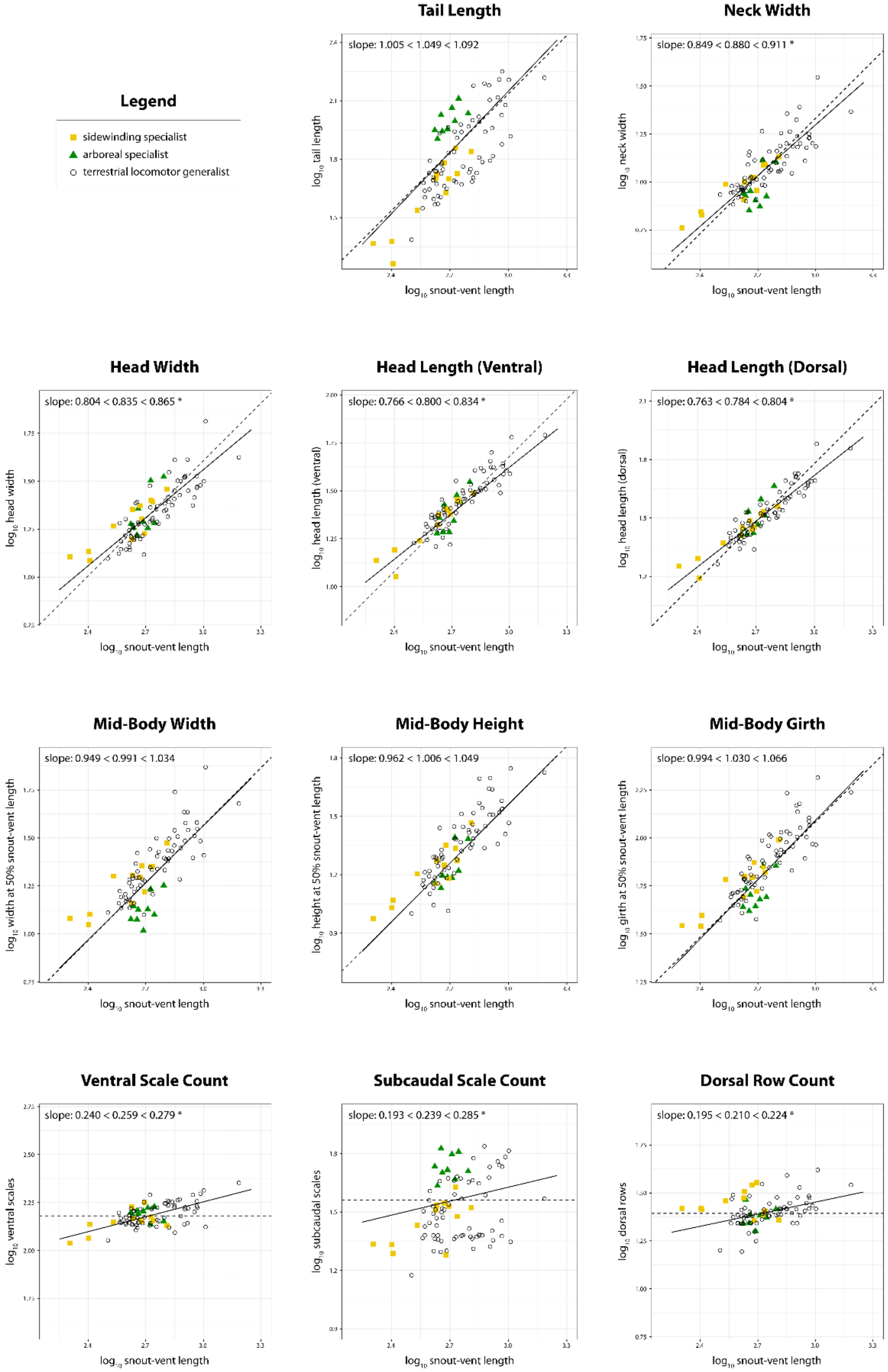
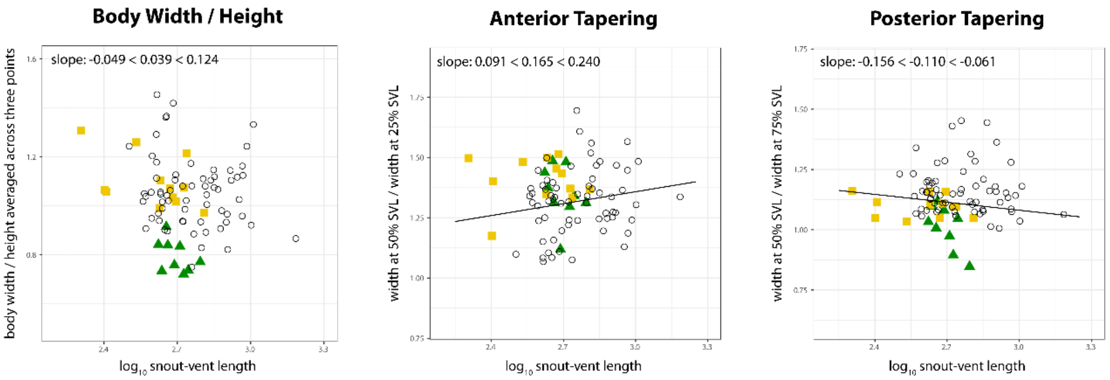

Legend
sidewinding specialist
arboreal specialist
terrestrial locomotor generalist
Tail Length
slope: 1.005 < 1.049 < 1.092
log10 tail length
log10 snout-vent length
Neck Width
slope: 0.849 < 0.880 < 0.911 *
log10 neck width
log10 snout-vent length
Head Width
slope: 0.804 < 0.835 < 0.865 *
log10 head width
log10 snout-vent length
Head Length (Ventral)
slope: 0.766 < 0.800 < 0.834 *
log10 head length (ventral)
log10 snout-vent length
Head Length (Dorsal)
slope: 0.763 < 0.784 < 0.804 *
log10 head length (dorsal)
log10 snout-vent length
Mid-Body Width
slope: 0.949 < 0.991 < 1.034
log10 width at 50% snout-vent length
log10 snout-vent length
Mid-Body Height
slope: 0.962 < 1.006 < 1.049
log10 height at 50% snout-vent length
log10 snout-vent length
Mid-Body Girth
slope: 0.994 < 1.030 < 1.066
log10 girth at 50% snout-vent length
log10 snout-vent length
Ventral Scale Count
slope: 0.240 < 0.259 < 0.279 *
log10 ventral scales
log10 snout-vent length
Subcaudal Scale Count
slope: 0.193 < 0.239 < 0.285 *
log10 subcaudal scales
log10 snout-vent length
Dorsal Row Count
slope: 0.195 < 0.210 < 0.224 *
log10 dorsal rows
log10 snout-vent length
2.4
2.7
3.0
3.3

Figure 3.3. Variation of body shape indices with respect to locomotor and habitat specialization. These body shape indices are all ratios calculated from raw measurements, and they are not $\log_{10}$-transformed. As in Figures 3.1 and 3.2, yellow squares indicate sidewinding specialists, green triangles indicate arboreal specialists, and black circles indicate terrestrial locomotor generalists. Solid black line segments are shown for the two indices that show a significant correlation with SVL. These line segments have slope equal to the estimated partial regression coefficient for SVL from the models shown in Table 3.2 and pass through the phylogenetic mean of (x,y), computed in the MATLAB program RegressionV2.m (Lavin et al. 2008). The estimated slopes along with 95% confidence intervals (from parametric bootstrapping in the MATLAB program MERegPHYSIGv2.m (Johnson et al. 2014) are labelled on the plots. Sidewinding specialists do not differ from terrestrial generalists for any body shape indices. Arboreal specialists have lower body width / height ratio than terrestrial generalists, indicating a laterally compressed shape in cross-section, and they show less tapering towards the back of their bodies.



Concluding remarks

Even though many land-dwelling animals have independently evolved body plans that lack walking, running, swimming, or flight (Alexander 2003). Limbless animals move fundamentally differently than do limbed ones, relying entirely on the vertebral column, ribs, and trunk musculature for propulsion (Gasc 1974; Jayne 1988). Snakes have evolved numerous distinct types of locomotion, though not all species can perform all of these (Gans 1962; Jayne 2020). Over the last half century or so, researchers have begun to study the biomechanics, energetics, and muscular mechanisms of snake locomotion (e.g. Gans 1962; Jayne 1986, 1988; Walton et al. 1990; Marvi et al. 2014; Astley 2020). However, many details of life without limbs remain a mystery. In this dissertation, I have used several approaches to advance our knowledge of sidewinding, an unusual locomotor mode apparently restricted to a subset of snake species.

I make three major contributions in Chapter 1 (Tingle 2020): the first comprehensive literature review of sidewinding; a thorough compilation of every species observed to sidewind or approximate sidewinding, along with assessments of proficiency and the conditions eliciting sidewinding; and an ancestral state reconstruction of specialized sidewinding in vipers, the family that includes the best-known and most proficient sidewinding species. The review demonstrates many gaps in our knowledge that merit further study. Previous studies indicate variation in many aspects of sidewinding biomechanics, but for the most part this variation has neither been quantified nor compared within and among species. Additionally, performance implications of biomechanics variation have not been thoroughly examined. Not only do we lack a thorough understanding of sidewinding biomechanics, but we also do not have an excellent understanding of the evolution of sidewinding. Adaptation to shifting substrates (especially sand, but also mud) seems to be the main explanation for sidewinding, but sidewinding may confer other adaptive advantages. Once a species evolves sidewinding behavior, it seems likely that they would also evolve morphological specializations to enhance sidewinding, but this idea deserves further exploration. My ancestral state reconstruction for Chapter 1 indicated five independent origins of specialized sidewinding in vipers. Therefore, vipers provide a suitable system in which to explore correlated evolution of sidewinding behavior and morphology at the interspecific level.

I took a biomechanics approach to Chapter 2, using high-speed video data to characterize the kinematics of sidewinding within a single species and then exploring the factors influencing sidewinder morphology, kinematics, and performance. Despite sexual dimorphism in several morphological traits, I found no evidence for sexual dimorphism of sidewinding kinematics. Additionally, body width scaled with positive allometry, indicating that larger snakes had disproportionately wide bodies, and in adult sidewinders (but not juveniles), larger individuals also had disproportionately higher wave amplitude. Path analysis supported several hypothesized causal relationships among morphological, kinematic, and performance variables. Snakes with wider bodies had longer wavelengths, indicating that they didn’t curve their bodies as tightly during sidewinding. Sidewinders achieved higher speeds primarily through increased frequency and not through increased stride length (displacement per sidewinding cycle). Frequency may be an inherently better way to sidewind faster because increasing stride length beyond a certain point might lead to a decrease in stability. Finally, the path analysis supported a relationship between skew angle of the body's waveform and frequency, a result that warrants further investigation into the physical and/or physiological basis of the relationship.

I took a macroevolutionary approach to Chapter 3, using phylogenetic comparative methods to explore whether vipers specialized for sidewinding differ from non-sidewinding-specialists in their body shape or vertebral count (Tingle and Garland 2021). I also looked for evidence of morphological evolution related to arboreality (specialization for life in the trees) or climatic differences. Although I found no statistical evidence for specialized morphology in sidewinding specialists, arboreal species differ from terrestrial species in numerous ways, and precipitation predicts several morphological traits.

Several possible explanations could account for the lack of body shape or vertebral count differences in sidewinding vs. non-sidewinding vipers. The behavior may have evolved recently enough that morphology has not had time to catch up (the "behavior evolves first" hypothesis; Blomberg et al. 2003; Rhodes and Kawecki 2009). Today's deserts, home to the sidewinding specialists, formed more recently than did the Earth's forests, home to most arboreal specialists. Forests had appeared by 385 Myr ago (Stein et al. 2007), and tropical forests resembling modern ones spread throughout the world during the Paleocene, 66-60 Myr ago (Morley 2000, pp. 262–263). Snakes appear in the fossil record 167 Myr ago (Caldwell et al. 2015), so arboreal species could have taken advantage of these forests. By contrast, Asia's interior became arid and began accumulating wind-blown sediments only 22 Myr ago (Guo et al. 2002). The oldest evidence for sandy desert conditions in the Sahara region of northern Africa dates to 7 Myr ago, with the geologic record indicating that desert conditions have alternated with more humid conditions since that time (Schuster et al. 2006). Deserts covered southern Africa during the Last Glacial Maximum, 21-18,000 years ago (Partridge et al. 1999). The oldest dunes in southern Africa's Namib Sand Sea are only 5,700 years old (Bristow et al. 2007), although the Namib Desert is much older than these dune sands indicate, with conflicting models placing it at 16 or 65 Myr old (Ward and Corbett 1990). Sand deposits began to form in the Mojave Desert of North America much more recently, approximately 15-20,000 years ago (Wells et al. 1987; Clarke 1994).

Despite the plausibility of the "behavior evolves first" hypothesis given Earth's geologic history, it seems unlikely to explain the lack of body shape or vertebral count specializations in sidewinding vipers. Other studies show that sidewinding specialists have shorter spinalis muscles and derived ventral scale morphology (Jayne 1982; Tingle et al. 2017; Rieser et al. 2021). Alternately, vipers may be pre-adapted for sidewinding in terms of their body shape and/or vertebral count, such that they do not need to evolve further modifications to enhance sidewinding. Another possibility is that body shape and vertebral count simply don't matter for sidewinding. Functional studies could provide data to distinguish among these possibilities. For example, morphology could be experimentally manipulated prior to locomotor testing to determine the effect of different morphology on kinematics and performance. A different option would be to use snake-like robots to explore phenotypes not seen in real snakes.

Taken together, this dissertation's three chapters represent a considerable fraction of current knowledge on sidewinding. They help to establish sidewinding as an excellent system for studying a variety of questions at the interface of multiple fields, including biomechanics, functional morphology, evolutionary biology, physiology, ecology, and animal behavior. More generally, this dissertation extends our understanding of biological diversity and evolutionary adaptation in an elongate, limbless vertebrate body plan. Ultimately, we cannot understand the fantastic variety of life without working to understand drivers of functional diversification in many different types of organisms.

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