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# Facultatively Sidewinding Snakes and the Origins of Locomotor Specialization

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**Synopsis** 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 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). 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). Western science took longer to catch on. By the early 20th century, several

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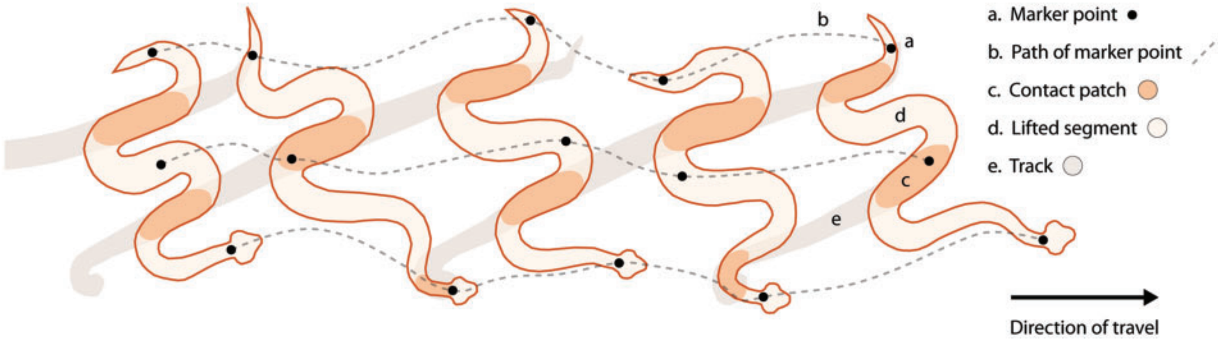

**Fig. 1** During sidewinding, a snake alternately holds some sections of its body stationary on the ground while lifting other sections up and forward in loops, eventually anchoring them to new stationary points farther along (Mosauer 1930; Gray 1946; Jayne 1986). Drawing traced from high-speed video of *Crotalus cerastes*.

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 *C. 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) 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 (1960), 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, *C. 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 in Supplementary Tables S1 – S4.

Supplementary Table S1 presents species that use sidewinding as a primary mode of locomotion when undisturbed in their natural habitats, and can therefore be considered specialized. Supplementary Table S2 presents species that do not specialize in sidewinding, but that regularly sidewind in their natural habitats. Supplementary Table S3 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. Supplementary Table S4 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 Supplementary Table S3 or S4. 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 Supplementary Table S4. 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 Supplementary Table S4 sidewind readily, or that some species in Supplementary Table S3 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; Supplementary Table S1). 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 (Supplementary Tables S2–S4). Table 1 summarizes the information in the supplementary 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 (Supplementary Fig. S1). 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, personal communication).

## 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. 2 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

**Table 1** A summary of sidewinding observations, by family

| | Specialized sidewinders (Supplementary Table S1) | Not specialized, but regularly sidewind in nature (Supplementary Table S2) | Sidewind under specific conditions (Supplementary Table S3) | Isolated or uncertain reports of sidewinding (Supplementary Table S4) |
|---|---|---|---|---|
| Boidae | – | *Candoia aspera* | – | *Boa constrictor*<br>*Eunectes murinus* |
| Colubridae | – | – | *Natrix maura*<br>*Natrix natrix*<br>*Nerodia fasciata*<br>*Nerodia rhombifer*<br>*Nerodia sipedon*<br>*Nerodia taxispilota*<br>*Opisthotropis typica*<br>*Regina septemvittata*<br>*Storeria dekayi*<br>*Thamnophis* sp. (*elegans* or *sirtalis infernalis*)<br>*Thamnophis ordinoides*<br>*Thamnophis sirtalis*<br>*Pseudoxenodon macrops* | *Phyllorhynchus decurtatus*<br>*Sonora occipitalis*<br>*Hypsiglena ochrorhynchus*<br>*Thamnophis hammondii* |
| Elapidae | – | – | *Cryptophis nigrostriatus*<br>*Denisonia devisi*<br>*Ephalophis greyae*<br>*Parasuta dwyeri*<br>*Suta punctata* | *Acanthophis antarticus*<br>*Laticauda colubrina*<br>*Naja tripudians*<br>*Suta suta* |
| Homalopsidae | – | *Bitia hydroides*<br>*Cerberus australis*<br>*Cerberus rynchops* | *Homalopsis buccata* | *Fordonia leucobalia* |
| Lamprophiidae | – | – | *Boaedon fuliginosus* | – |
| Pythonidae | – | – | *Aspidites ramsayi* | *Python bivittatus*<br>*Python curtus* |
| Tropidophiidae | – | – | *Tropidophis haetianus*<br>*Tropidophis melanurus* | – |
| Viperidae | *Crotalus cerastes*<br>*Bitis caudalis*<br>*Bitis peringueyi*<br>*Cerastes cerastes*<br>*Cerastes gasperettii*<br>*Cerastes vipera*<br>*Echis carinatus*<br>*Eristicophis macmahoni*<br>*Pseudocerastes fieldi*<br>*Pseudocerastes persicus* | *Crotalus catalinensis*<br>*Bitis cornuta*<br>*Bitis schneideri*<br>*Echis coloratus* | *Agkistrodon piscivorus*<br>*Bothrops ammodytoides*<br>*Bothrops jararaca*<br>*Echis pyramidum* | *Crotalus atrox*<br>*Crotalus helleri*<br>*Crotalus pyrrhus*<br>*Crotalus ruber*<br>*Crotalus scutulatus*<br>*Crotalus viridis*<br>*Bitis arietans*<br>*Bitis gabonica*<br>*Trimeresurus gramineus*<br>*Vipera latastei* |
| Total | 10 | 8 | 27 | 23 |

For details and citations, see Supplementary Tables S1–S4.

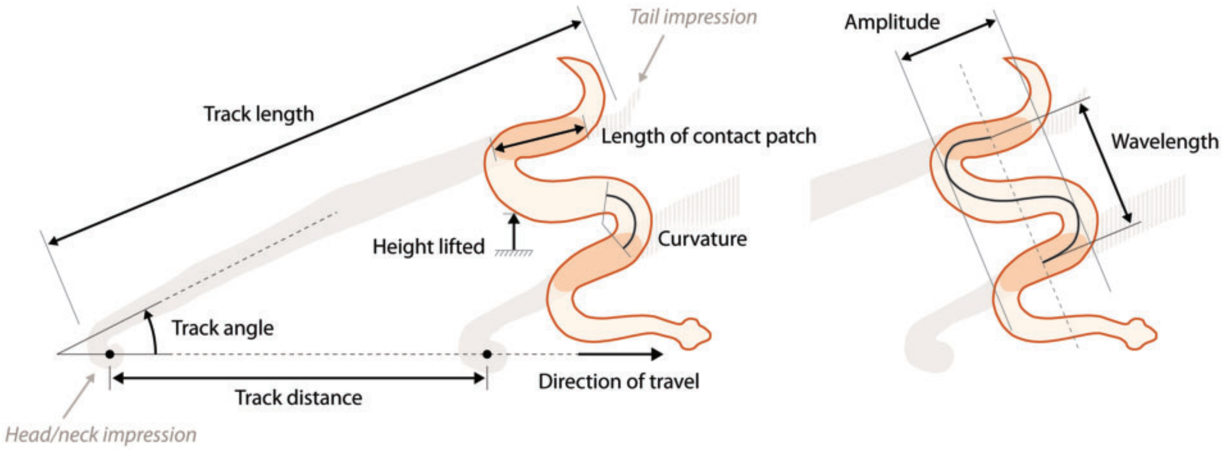

**Fig. 2** This diagram shows some metrics that vary among sidewinding species.

study that quantified vertebral flexion during sidewinding (Jayne 1988), water snakes (*Nerodia fasciata*) had slightly lower maximal vertebral flexion than did sidewinder rattlesnakes (*C. 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 et al. (1992) found that sidewinder rattlesnakes, *C. 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*, *N. 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 (personal observation). Although individual snakes do not always use the same frequency, different sidewinding species (both specialized and facultative) could tend toward 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 (*C. 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 *N. 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.

**Table 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) |

### 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 *C. 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 *B. 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 (personal observation).

### 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 traveled over the course of one sidewinding cycle. This distance was significantly smaller in *N. fasciata* than in *C. cerastes* or *C. 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 (personal observation). 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 (personal observation). On the 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 (personal observation; 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 (personal observation). 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 (personal observation; see also description of facultative sidewinding by *Natrix maura* in Gasc 1974, details in Supplementary Table S3). 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 (personal observation; see also Secor et al. [1992], who tested *C. 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 (personal observation; 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 (personal observation; Ditmars 1908; Bergman 1951; Helmcke et al. 1962; Scanlon 2001; details in Supplementary Tables S3 and S4). 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

**Table 3** Reported maximum speeds of specialized sidewinding snakes

| Species | Speed (km/h) | Notes | Source |
|---|---|---|---|
| *Bitis caudalis* | 5.5 | No details on conditions for eliciting speed; two individuals (apparently), unknown number of trials | Hoffmann (1988) |
| *Crotalus cerastes* | 3.3 | Burst speed trials on sand, with unknown ambient temperature; several individuals, several trials each | Mosauer (1935) |
|  | 3.7 | 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 | No details on conditions for eliciting speed; unclear how many individuals were tested/observed | Mendelssohn (1965) |
| *Pseudocerastes fieldi* | 1.3 | Trials on a serpentarium floor at 30°C ambient temperature; two individuals, apparently one trial each | Mendelssohn (1965) |

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, when 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, *C. 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; Jayne 1986, 1988; Klauber 1997; Scanlon 2001; details in Supplementary Table S3). 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 Supplementary Table S2). 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 *B. 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 *C. 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 *C. 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 *C. cerastes* can sustain sidewinding for 33 to >180 min at 0.5 km/h, and 9–52 min at 0.7 km/h (Secor et al. 1992). The paucity of data invites further, careful studies of these 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 with 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 *C. cerastes* traveled an annual mean of 173 m per night over the course of 3 years, with one individual traveling 1269.2 m in a night (Brown and Lillywhite 1992). Another 3-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 *C. cerastes* more than 3 km before finding the animal (Kramer and Schnurrenberger 1958). Three individuals of *C. 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. 2006; although see Brattstrom et al. [2016] for an observation of two Western diamondback rattlesnakes [*C. atrox*] moving 3.28 km over the course of 4 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, *C. 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 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 with 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 backward fashion, retreating while maintaining eye contact with an aggressor (personal observation; Brendan Schembri, personal communication, details in Supplementary Table S3). 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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## Supplementary data

Supplementary data are available at *ICB* online.

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