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## RESEARCH ARTICLE

# Locomotor kinematics on sand versus vinyl flooring in the sidewinder rattlesnake *Crotalus cerastes*

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## ABSTRACT

For terrestrial locomotion of animals and machines, physical characteristics of the substrate can strongly impact kinematics and performance. Snakes are an especially interesting system for studying substrate effects because their gait depends more on the environment than on their speed. We tested sidewinder rattlesnakes (*Crotalus cerastes*) on two surfaces: sand collected from their natural environment and vinyl tile flooring, an artificial surface often used to elicit sidewinding in laboratory settings. Of ten kinematic variables examined, two differed significantly between the substrates: the body's waveform had an average of ~17% longer wavelength on vinyl flooring (measured in body lengths), and snakes lifted their bodies an average of ~40% higher on sand (measured in body lengths). Sidewinding may also differ among substrates in ways we did not measure (e.g. ground reaction forces and energetics), leaving open clear directions for future study.

**KEY WORDS:** Biomechanics, Friction, Granular media, Locomotion, Squamates, Substrate

## INTRODUCTION

Terrestrial locomotion necessarily involves physical contact between an organism or machine and the environment. As a result, such substrate characteristics as friction, compliance, rugosity, heterogeneity, and obstacles can impact locomotor kinematics and performance (e.g. Bergmann et al., 2017; Claussen et al., 2002; Clifton et al., 2023; 2020; Collins et al., 2013; Kelley et al., 1997; Li et al., 2010; Redmann et al., 2020). Snakes are an especially interesting system for studying the effects of substrate on terrestrial locomotion because they tend to have a relatively large surface area in contact with the ground, and they can vary the length and location of the contact patch(es); moreover, they differ from limbed tetrapods in that their gait depends more on the environment than on their speed (Gray, 1946; Jayne, 2020).

Here, we investigate substrate effects on a type of snake locomotion called sidewinding. Sidewinding has a close association with sandy desert environments, probably because it allows snakes to avoid slipping while moving on granular media like sand (Cowles, 1920; Mosauer, 1932; Tingle, 2020). Several viper species have convergently evolved this unusual type of locomotion, which

involves holding some parts of the body in static contact with the ground while lifting other parts up and forward to new contact patches farther along the direction of motion (Gans and Mendelssohn, 1971; Gray, 1946; Mosauer, 1930; Mosauer and Wallis, 1928; Tingle, 2020; Tingle and Garland, 2021) (Fig. 1A). Sidewinding vipers differ in their relative use of different types of locomotion, with some employing sidewinding on nearly any surface, and others switching to lateral undulation (the gait most commonly used by snakes and other limbless reptiles) on surfaces like gravel (Gans and Mendelssohn, 1971). Many more species can sidewind facultatively, especially when strongly motivated and/or placed on granular media or smooth surfaces (Tingle, 2020). Additionally, some species also have derived morphological features that are hypothesized to enhance sidewinding, including shorter spinalis muscles (Tingle et al., 2017) and frictionally isotropic microstructure on the ventral scales (Rieser et al., 2021).


Any effect of substrate on sidewinding would be ecologically important because deserts show spatial variability in substrate, including in the size, shape and uniformity of sand grains; the prevalence of dunes (which can have varying morphologies) relative to areas that have been stabilized or semi-stabilized by plants; and the presence of hardpan or other firm surfaces, both natural and human-made, such as paved roads (e.g. Bagnold, 1941; Folk, 1978; Lancaster, 1995; 1989; 1981; Lancaster and Tchakerian, 1996; Sarré and Chancey, 1990). Sidewinding snakes likely encounter many of these different types of substrates, as they can move over large areas and have been observed on different substrate types (Dorfman et al., 2023; Kramer and Schnurrenberger, 1958; Mermod, 1970; Secor, 1994; Subach et al., 2022, 2009). Better understanding of how snakes deal with challenging terrain can also help engineers improve the performance of bio-inspired snake-like robots, which can be used for exploration and search-and-rescue missions in environments where wheeled or limbed robots may struggle to move, including on granular media like sand (Astley, 2022; Gao et al., 2008; Hopkins et al., 2009; Liljebäck et al., 2012).

Substrate effects would also have implications for laboratory studies, which often necessarily use substrates differing from those found in the study species' natural environment (Moore and Clifton, 2023). For studies of sidewinding specifically, researchers have often conducted sidewinding tests on sand that did not come from the animals' natural habitat and/or on smooth laboratory surfaces like linoleum, vinyl flooring, wood, or metal (Brain, 1960; Gasc, 1974; Gray, 1946; Jayne, 1988; Klauber, 1997; Mosauer, 1930; Scanlon, 2001). These studies have never quantified the potential effects of substrate differences on kinematics, and as a result, it is unclear to what degree our interpretation of these studies should be affected by their choice of substrate. It would therefore be very helpful to know which locomotor variables, if any, are affected by these type of substrate differences.

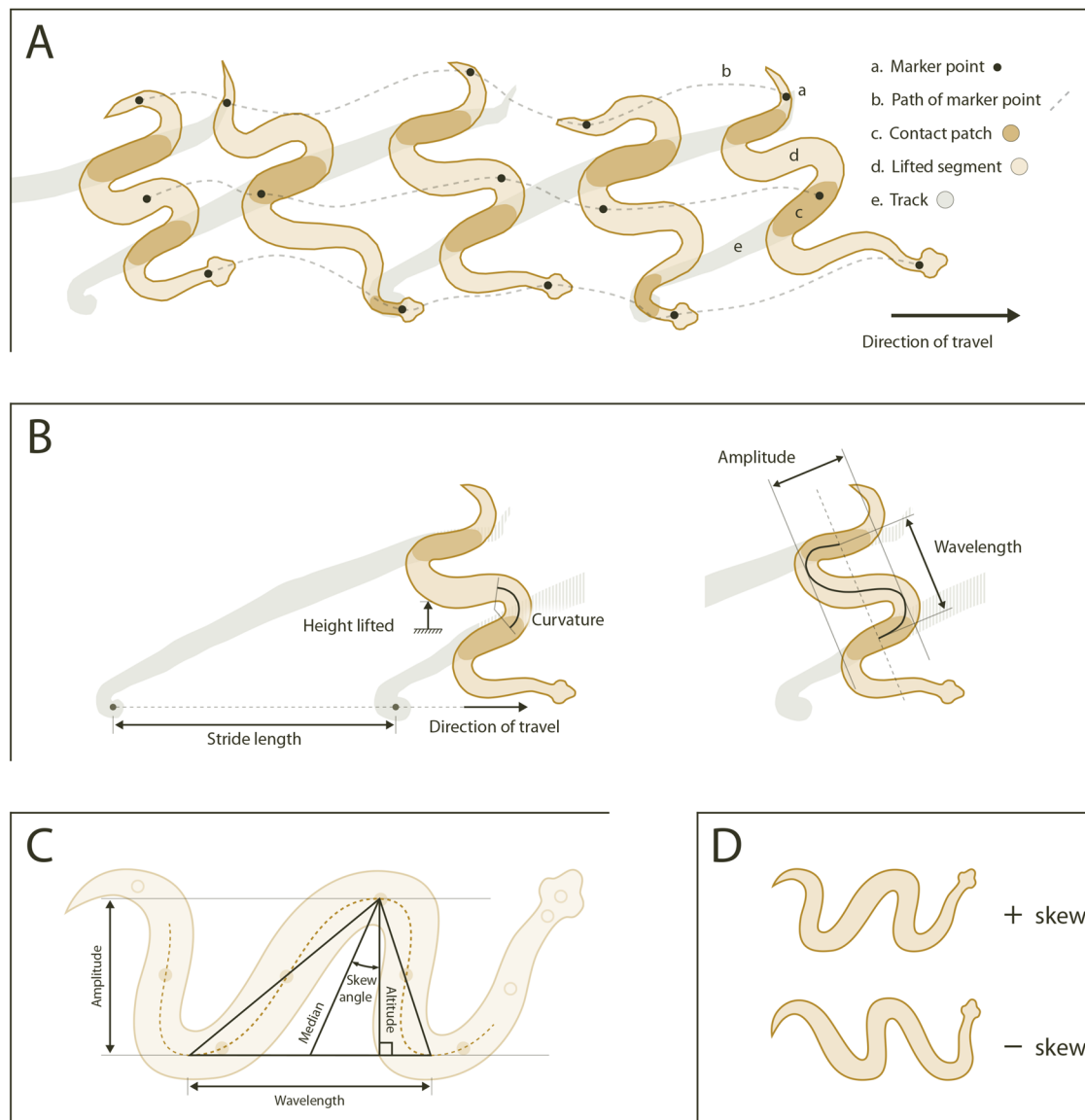
We tested sidewinder rattlesnakes (*Crotalus cerastes* Hallowell 1854) on sand from their natural habitat and on vinyl flooring to determine whether locomotor kinematics are affected. *C. cerastes* is an appropriate study species due to their strong tendency to use

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**Fig. 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. Figure and caption reproduced from Tingle et al. (2022). Panels A and B are traces from high-speed video of *C. cerastes*, modified with permission from Tingle (2020). Panels C and D are stylized.

sidewinding over other types of locomotion on a wide variety of surfaces (Klauber, 1997; Tingle, 2020) and because we can readily access free-living individuals in the field. We chose sand from their natural habitat and vinyl flooring as our test substrates because, 1) they represent a natural surface and an artificial one that has often been used in laboratory studies, such that the results of this study can help contextualize the ecological relevance of results from laboratory studies and inform the design of future studies, and 2) their very different properties increase the likelihood that we would detect any kinematic differences that might arise from sidewinding on different substrates, as opposed to testing snakes on substrates that differ more subtly from

each other. Sand shifts around beneath an animal, behaving somewhat like a solid and somewhat like a fluid (Duran, 2000). Vinyl flooring, on the other hand, is firm but has a low frictional coefficient, such that a snake's skin can easily slide across it. Given that sand and vinyl differ substantially, with one shifting under pressure and the other solid but smooth, we expected that successful locomotion (i.e. forward progress) would require different kinematics on the two surfaces.

## RESULTS

Of the ten kinematic variables we examined, with body length as a covariate, two of them differed significantly between substrates:

wavelength was longer on vinyl flooring, and sidewinders lifted their bodies higher on sand (Table 1, Fig. 2). Wavelength averaged 0.217 body lengths on sand (range: 0.123-0.297) versus 0.259 body lengths on vinyl (range: 0.223-0.328), a difference of 17.6%. Height lifted averaged 0.027 body lengths on sand (range: 0.014-0.043) versus 0.018 body lengths on vinyl (range: 0.009-0.033), a difference of 40%. Wavelength, amplitude, height lifted, and skew angle increased significantly with snout-vent length (Table 1, Fig. 2). Results from the paired *t*-tests for the four individuals tested on both substrates partially agreed with our main results from the ANCOVA analysis (Fig. 3 presents data for only those four individuals). As for the ANCOVA, wavelength was significantly longer on vinyl ( $t(3)=6.751$ ,  $P=0.007$ ), but the difference between substrates for height lifted was not significant in the paired *t*-test ( $t(3)=-1.938$ ,  $P=0.148$ ).

## DISCUSSION

Previous studies have found kinematic differences on sand versus solid substrates for many kinds of locomotion. For example, eels differ in their kinematics and performance when moving terrestrially on sand versus pebble substrates (Mehta et al., 2020;

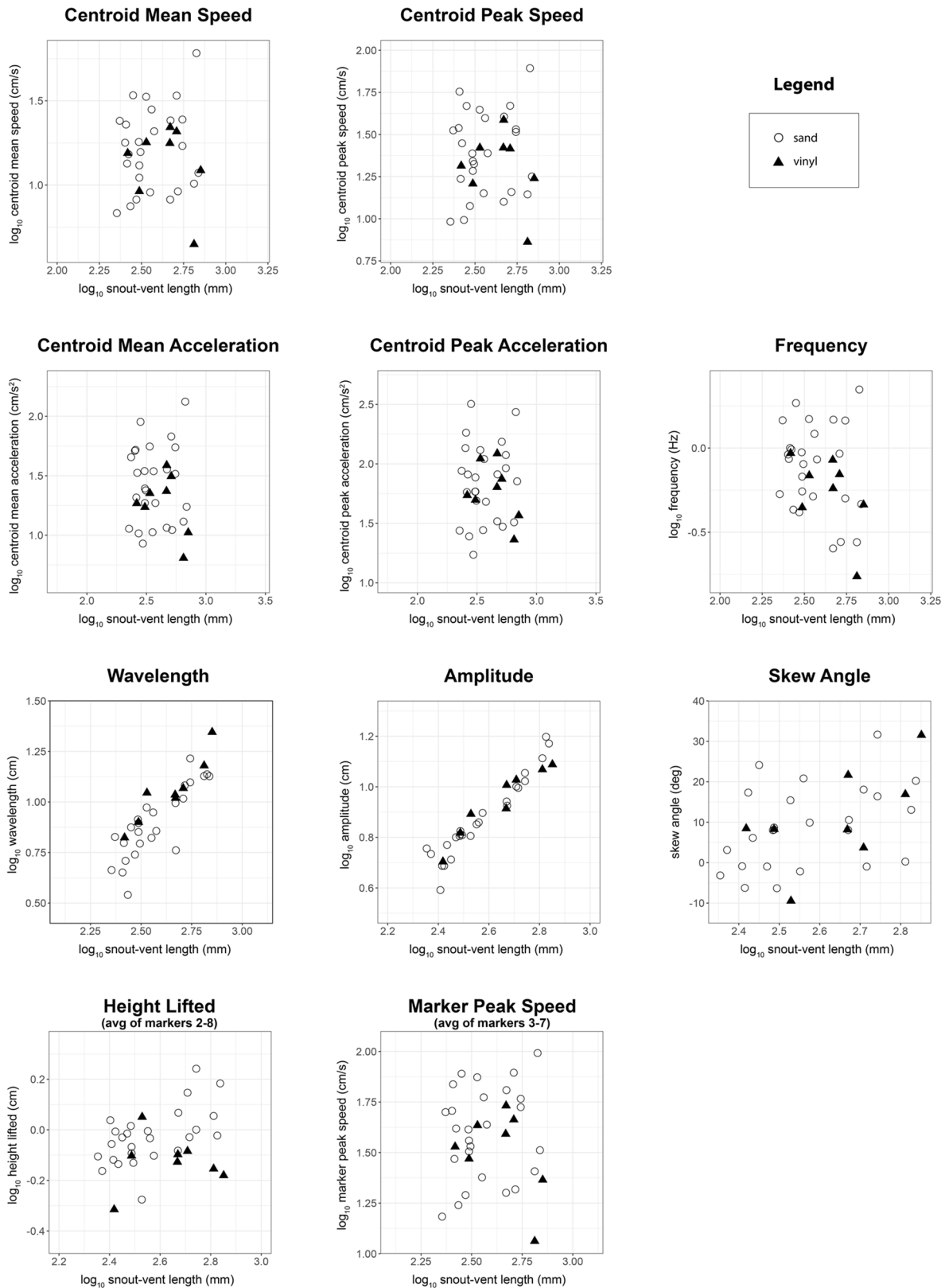
Redmann et al., 2020), box turtles have shorter strides and lower speeds on sand than on Styrofoam (Claussen et al., 2002), human athletes use different ankle and hip joint kinematics during squat jumps on rigid versus sand surfaces (Giatsis et al., 2004), and a cursorial gecko species was shown to change its body angle and duty factor during transitions from firm to sand surfaces (Naylor and Higham, 2022). On the other hand, one experiment showed that kangaroo rats could hop at  $1.8 \text{ m s}^{-2}$  on either sand or a solid surface without changing any of the kinematic variables that were measured (hop period, hop length, duty cycle) (Hall et al., 2022). Even within granular media, variation in physical characteristics can affect locomotion. For example, sand particle size may affect running in some lizards (Bergmann et al., 2017), skinks do not burrow as deeply in wet sand as in dry sand (Sharpe et al., 2015), and mudskippers change their locomotor behavior on mud versus dry sand (Naylor and Kawano, 2022).

Our results add not only to the literature on kinematic differences between sand and solid surfaces, but also to a growing body of literature on the ways sidewinding snakes and robots can modulate their kinematics to overcome locomotor challenges. Previous studies have focused on ascending slopes (Hatton and Choset, 2010;

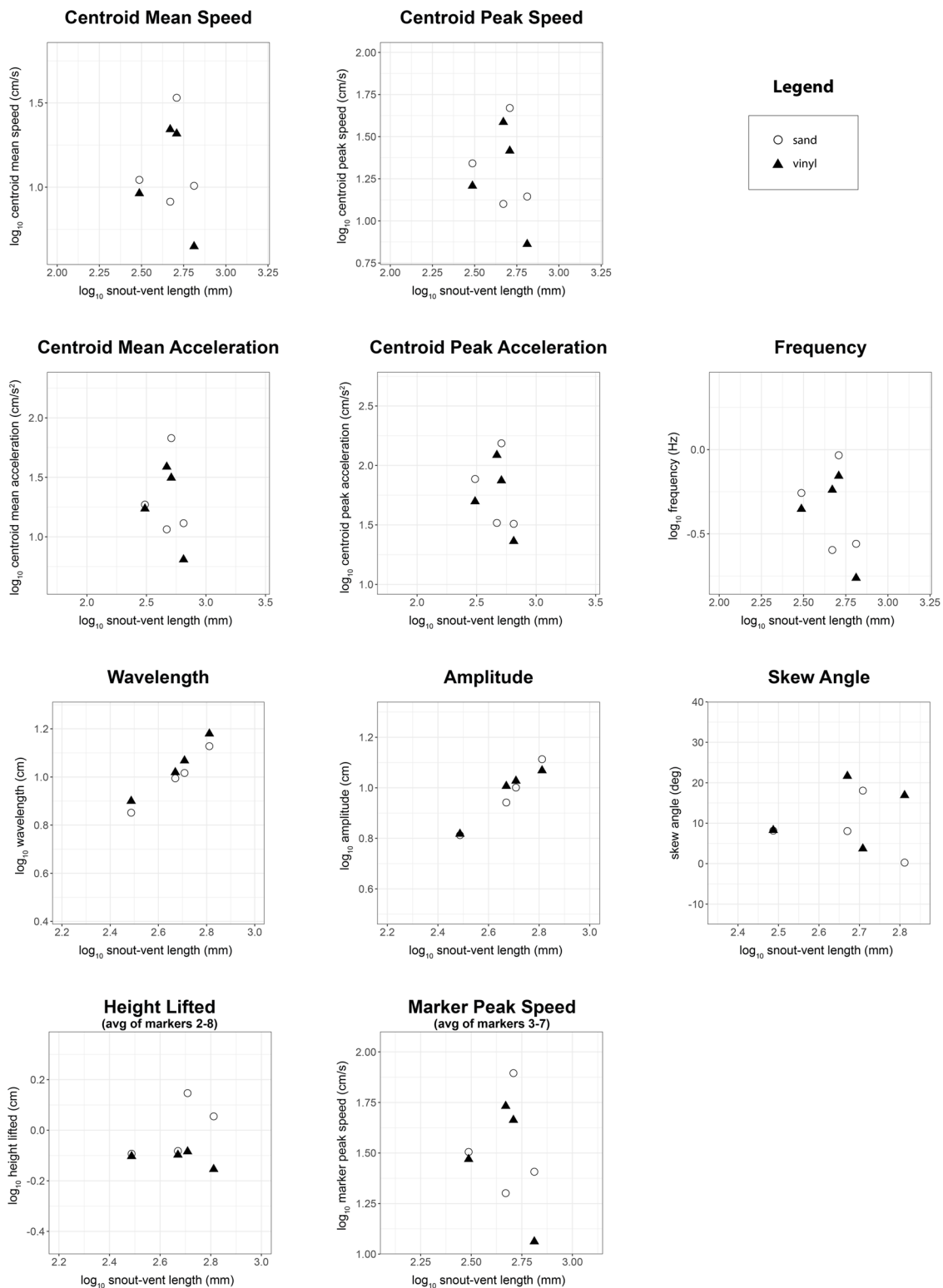
**Table 1. ANCOVA results showing the effects of snout-vent length and substrate type on ten kinematic variables**

Kinematic variable		Sum of squares	d.f.	$\beta$	SE	<i>F</i>	<i>p</i>
log(centroid mean speed) $r^2$ : 0.030; adjusted $r^2$ : -0.033	Intercept	0.062	1	0.772	0.755	1.046	0.314
	Substrate type	0.052	1	0.095	0.101	0.877	0.356
	SVL	0.014	1	0.136	0.284	0.230	0.635
	Residuals	1.840	31				
log(centroid peak speed) $r^2$ : 0.026; adjusted $r^2$ : -0.037	Intercept	0.124	1	1.091	0.754	2.093	0.158
	Substrate type	0.048	1	0.091	0.101	0.812	0.375
	SVL	0.005	1	0.082	0.284	0.084	0.774
	Residuals	1.839	31				
log(centroid mean acceleration) $r^2$ : 0.052; adjusted $r^2$ : -0.008	Intercept	0.187	1	1.341	0.969	1.914	0.176
	Substrate type	0.154	1	0.163	0.130	1.576	0.219
	SVL	0.001	1	-0.028	0.364	0.006	0.940
	Residuals	3.034	31				
log(centroid peak acceleration) $r^2$ : 0.010; adjusted $r^2$ : -0.054	Intercept	0.319	1	1.749	0.978	3.200	0.083
	Substrate type	0.030	1	0.072	0.131	0.298	0.589
	SVL	0.000	1	0.008	0.368	0.001	0.982
	Residuals	3.089	31				
log(frequency) $r^2$ : 118; adjusted $r^2$ : 0.061	Intercept	0.072	1	0.829	0.774	1.147	0.292
	Substrate type	0.075	1	0.113	0.104	1.196	0.283
	SVL	0.126	1	-0.413	0.291	2.020	0.165
	Residuals	1.935	31				
log(wavelength) $r^2$ : 0.770; adjusted $r^2$ : 0.755	Intercept	0.227	1	-1.504	0.283	28.176	0.000
	<b>Substrate type</b>	<b>0.041</b>	<b>1</b>	<b>-0.084</b>	<b>0.037</b>	<b>5.023</b>	<b>0.033</b>
	<b>SVL</b>	<b>0.665</b>	<b>1</b>	<b>0.967</b>	<b>0.107</b>	<b>82.432</b>	<b>4.1E-10</b>
	Residuals	0.242	30				
log(amplitude) $r^2$ : 0.917; adjusted $r^2$ : 0.911	Intercept	0.255	1	-1.592	0.143	124.337	0.000
	Substrate type	0.000	1	0.004	0.019	0.052	0.821
	<b>SVL</b>	<b>0.653</b>	<b>1</b>	<b>0.958</b>	<b>0.054</b>	<b>318.478</b>	<b>1.6E-17</b>
	Residuals	0.061	30				
skew angle $r^2$ : 0.213; adjusted $r^2$ : 0.161	Intercept	533.142	1	-72.829	30.356	5.756	0.023
	Substrate type	0.005	1	-0.030	4.000	0.000	0.994
	<b>SVL</b>	<b>718.000</b>	<b>1</b>	<b>31.776</b>	<b>11.413</b>	<b>7.752</b>	<b>0.009</b>
	Residuals	2778.748	30				
log(height lifted) avg of markers 2-8 $r^2$ : 0.327; adjusted $r^2$ : 0.284	Intercept	0.107	1	-1.016	0.302	11.341	0.002
	<b>Substrate type</b>	<b>0.092</b>	<b>1</b>	<b>0.126</b>	<b>0.040</b>	<b>9.670</b>	<b>0.004</b>
	<b>SVL</b>	<b>0.083</b>	<b>1</b>	<b>0.336</b>	<b>0.113</b>	<b>8.808</b>	<b>0.006</b>
	Residuals	0.294	31		NA		
log(marker peak speed) avg of markers 3-7 $r^2$ : 0.033; adjusted $r^2$ : -0.029	Intercept	0.179	1	1.312	0.705	3.463	0.072
	Substrate type	0.055	1	0.097	0.094	1.063	0.311
	SVL	0.004	1	0.073	0.265	0.077	0.784
	Residuals	1.606	31				

For each variable, the ANCOVA model included substrate (sand or vinyl floor tiles) as a categorical predictor variable and snout-vent length (SVL) as a continuous covariate. SVL was  $\log_{10}$  transformed, as were all kinematic variables except skew angle (which cannot be log transformed because it can have negative values).



**Fig. 2. Comparison of sidewinding kinematics on sand versus vinyl floor tiles with the full sample used in the main analysis.** Scatterplots showing kinematic variables plotted against  $\log_{10}$  snout-vent length (SVL). Kinematic variables are  $\log_{10}$  transformed except for skew angle, which cannot be log transformed because it is signed. Open circles represent sand trials ( $n=25$  snakes for wavelength, amplitude, and skew angle;  $n=26$  for all other variables), whereas filled triangles represent vinyl trials ( $n=8$ ). ANCOVA results indicate that SVL is significantly related to wavelength, amplitude, height lifted, and skew angle (Table 1). Substrate significantly affected wavelength and height lifted (Table 1). Wavelength averaged 0.217 body lengths on sand (range: 0.123-0.297) versus 0.259 body lengths on vinyl flooring (range: 0.223-0.328), a difference of 17.6%. Height lifted averaged 0.027 body lengths on sand (range: 0.014-0.043) versus 0.018 body lengths on vinyl (range: 0.009-0.033), a difference of 40%.



**Fig. 3. Comparison of sidewinding kinematics on sand versus vinyl floor tiles, showing only four individuals tested on both substrates.** Scatterplots showing kinematic variables plotted against  $\log_{10}$  SVL. Kinematic variables are  $\log_{10}$  transformed except for skew angle, which cannot be log transformed because it is signed. Open circles represent sand trials ( $n=4$ ), whereas filled triangles represent vinyl trials ( $n=4$ ).

Marvi et al., 2014), turning (Astley et al., 2015; Gong et al., 2012), and negotiating obstacles (Astley et al., 2020). As other workers have noted, a more thorough understanding of locomotor control in biological sidewinders can help engineers more effectively coordinate the motion of snake-like robots to achieve a greater

range of functions (Astley et al., 2020; 2015; Gong et al., 2016; Marvi et al., 2014).

We provide the first evidence that sidewinding snakes adjust their kinematics at least subtly between substrates. Sidewinders may lift their bodies higher on sand than on vinyl in response to the sand

shifting beneath them and/or to clear the ridges of sand that pile up on the edges of their tracks. Speculating why wavelength might be longer on vinyl is more difficult, given that it may change in tandem with other parameters that we were not able to measure.

Given the results of previous studies and the mechanical differences between sand and vinyl flooring, we were surprised to find that only wavelength and height lifted differed, and that they differed relatively subtly, with overlapping distributions in the values for the two substrates (Table 1, Fig. 2). We speculate that morphological adaptations of sidewinder rattlesnakes (*C. cerastes*) might improve the robustness of their locomotion, allowing them to maintain similar kinematics in the face of substrate differences. To give one example of a morphological trait presumed to be an adaptation, *C. cerastes* and some other sidewinding species have a microstructure on the skin of their ventral surface that differs from that of most other snakes (Rieser et al., 2021). This derived microstructure causes their ventral skin to be frictionally isotropic (i.e. to have the same friction coefficient in every direction), which was shown by mathematical modelling to enhance sidewinding performance at the cost of lateral undulation by reducing slipping within the track (Rieser et al., 2021). Species that lack morphological adaptations for sidewinding might face greater challenges controlling their movement, affecting their kinematics. One previous study quantitatively compared sidewinding kinematics in *C. cerastes* and two species that can sidewind facultatively but are not known (or suspected) to have morphological specializations for sidewinding, *Cerberus rynchops* and *Nerodia fasciata* (Jayne, 1986). At times, these two species could be observed to slide within their tracks while otherwise exhibiting an asymmetric movement pattern characteristic of sidewinding (Jayne, 1986). It would be interesting to pursue the question of whether morphological specialization (or lack thereof) affects the magnitude of kinematic change on differing substrates.

Sidewinding locomotion may differ among surfaces in ways we did not quantify. For example, we could not measure slipping, and our method for quantifying the body's waveform could not capture all details of body shape (e.g. local curvatures, the length of regions of static contact with the ground). Perhaps more importantly, we measured only kinematics, and not forces or energetics. The different nature of slipping on sand versus vinyl could have important consequences for ground reaction forces. Additionally, locomotion can be particularly intensive on a shifting surface like 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). Therefore, energy expenditure (along with cost of transport) might be expected to differ on shifting versus smooth surfaces. We expect that future studies may also demonstrate differences in ground reaction forces and/or energy use on shifting versus firm substrates. Future studies could also determine whether sand characteristics or other naturally varying aspects of the substrate affect cost of transport, speed, stability, or other biologically relevant performance metrics. Any effects would be consequential for our understanding of free-living animals' habitat use and activity patterns, while informing future experiments on snake locomotion and control of snake-like robots.

## MATERIALS AND METHODS

### Data collection

Our sample consisted of juvenile and adult sidewinder rattlesnakes (*Crotalus cerastes* Hallowell 1854) collected in June and July 2016 at the Barry M. Goldwater Range near Yuma, Arizona, USA. Research procedures were approved by the San Diego State Institutional Animal Care and Use

Committee (permit number 16-08-014C), and animals were collected under Arizona State Scientific Collecting Permit SP506470. Within approximately 1 day of capture, we anesthetized the snakes with isoflurane via inhalation, measured snake snout-vent length (SVL) with a measuring tape, and painted ten markers along the body following the protocol described in Tingle et al. (2022). Snake sex and SVL can be found in [Supplementary Dataset 1](#), and additional morphological data collected from the same specimens for a different study (Tingle et al., 2022) can be downloaded from the Dryad data repository (Tingle et al., 2022).

After allowing the snakes to recover from anesthesia for about a day, we conducted locomotor trials on sand and on vinyl flooring. After reducing our sample to trials that did not suffer from video calibration or other issues, the final sample consisted of trials for 26 snakes tested on sand and eight tested on vinyl, with four of those individuals overlapping between the trial types (see below for details on data processing and statistical analysis). The sand trials were previously used for a different study that focused on scaling and relations of morphology with locomotor kinematics (Tingle et al., 2022). The testing arena for sand trials consisted of a shallow 1.2×1.2 m square box containing a 2 cm layer of sand, which was collected on the Barry M. Goldwater Range very near to where the sidewinders were found. We raked and smoothed the sand between trials. The vinyl testing arena consisted of a 1.2×1.2 m area covered in 30.5×30.5 cm squares of 1/8" standard Excelon vinyl composition tiles (model number 51858), a common flooring in labs (note that such flooring is often colloquially referred to as linoleum, but linoleum is a different material that appears superficially similar). This arena size provided enough space for the snakes, which measured 0.23 to 0.69 m SVL, to complete several sidewinding cycles per trial. Substrate temperatures during testing ranged from 20.4 to 27.2°C, within the range recorded during field observations of active sidewinders (Cowles and Bogert, 1944; Moore, 1978; Signore et al., 2022).

For both trial types, snakes were placed gently into the arena, and if they did not begin moving on their own, they were given the minimum motivation required for them to move, which involved waving snake tongs behind them and/or tapping the tongs on either the substrate or the snake's tail. Trials were recorded with two high-speed cameras (Edgertronic Model SC1; San Jose, CA, USA) positioned approximately 1.5-2 m away from the testing arenas, with one camera on a tall tripod, well above the arena, and the other on a short tripod, close to arena-level. For each individual, we recorded three trials that included at least 2-3 full cycles of sidewinding.

### Data processing

Videos were calibrated and digitized using the MATLAB programs DLTcal5 and DLTdv5 (Hedrick, 2008) to produce 3D coordinates of the ten painted marker points. Our calibration object consisted of several metal rods fixed to each other and to a metal base plate, with markers at regular known intervals. Calibration residuals were <2 pixels. After digitizing, we processed the data and extracted kinematic variables with two custom MATLAB programs, described in detail in our previous paper (Tingle et al., 2022). Briefly, we used the X, Y, and Z coordinates output from DLTdv5 to calculate displacement for all ten markers, which we then smoothed in MATLAB using a 3-pass fourth order Savitzky-Golay filter with a uniform weight distribution. Velocity and acceleration were calculated from smoothed displacement and then smoothed using a single-pass fourth order Savitzky-Golay filter with a uniform weight distribution. After smoothing, we extracted several kinematic variables, including peak speed of individual marker points, mean and peak speed of the centroid of the ten painted markers, mean and peak acceleration of the centroid, frequency of the sidewinding cycles, wavelength and amplitude of the body's waveform, skew angle of the wave, and the height to which the body was lifted (Fig. 1B-D provides diagrams and explanations of kinematic variables).

### Statistical analysis

For each snake, we chose one representative trial based on the following criteria: 1) ruled out trials with obvious issues, like excessively poor video quality or calibration problems, 2) we ruled out trials where the snake did not perform steady-state sidewinding (i.e. trials where the snake stopped or

turned); 3) we ruled out trials where our MATLAB program was unable to compute all the variables of interest from the digitizing output, which sometimes occurred if not enough sidewinding cycles were recorded; however, for one individual on sand, all trials lacked some variables, so we chose the trial with the fewest variables lacking; 4) of the remaining trials, we chose the one that captured the greatest number of sidewinding cycles. We originally planned to test for differences in kinematics on vinyl versus sand using a paired design. However, of the ten snakes tested on vinyl, we could not use trials for two of those due to calibration issues, and for four of the eight remaining individuals, their corresponding sand trials were not useable due to calibration issues. Therefore, we compared the eight vinyl trials to the 26 sand trials from our previous study (Tingle et al., 2022). Those sand trials included 22 individuals that were not tested on vinyl, and four individuals that were. For the present study, we used ANCOVAs with type III sums of squares (package *car*; Fox and Weisberg, 2019) to test whether any of the ten kinematic variables differed between the two substrates, with snout-vent length as the covariate. We previously found no significant effect of temperature, sex, or age class on any of the kinematic variables considered (Tingle et al., 2022), so we did not include them as predictors in the current model. As described previously (Tingle et al., 2022), we  $\log_{10}$  transformed all traits prior to conducting the ANCOVAs except for skew angle, which cannot be log transformed because it is signed. We examined standardized residuals to check for outliers, and we found none using the criterion that outliers would have standardized residuals exceeding  $\sim 3$  in magnitude. Residuals were normally distributed, and Levene's test confirmed homogeneity of variance between substrates for all variables.

In addition to our main ANCOVA analysis, we conducted two-tailed paired *t*-tests for the four individuals that were tested on both substrates. Although a sample size of four individuals is at best marginal for such an analysis, we present it for completeness. All statistical analyses were implemented in R 4.2.1 (R Core Team, 2022). Data for trials used in our analysis are provided in [Supplementary Dataset 1](#).

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: J.L.T.; Methodology: J.L.T., B.M.S., T.G. Jr.; Software: J.L.T., B.M.S.; Validation: J.L.T., B.M.S., T.G. Jr.; Formal analysis: J.L.T., B.M.S., T.G. Jr.; Investigation: J.L.T.; Resources: J.L.T., B.M.S.; Data curation: J.L.T., B.M.S.; Writing - original draft: J.L.T.; Writing - review & editing: J.L.T., B.M.S., T.G. Jr.; Visualization: J.L.T., B.M.S.; Supervision: J.L.T.; Project administration: J.L.T.; Funding acquisition: J.L.T.

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#### Data availability

Data on snake sex, snout-vent length, and kinematics for all trials used in our analysis are provided as [Dataset 1](#). Additional morphological data collected from the same specimens for a different study (Tingle et al., 2022) can be downloaded from the Dryad data repository (Tingle et al., 2022).

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