The Effects of Speed on Terrestrial Locomotor Kinematics in the Common Garter Snake (*Thamnophis sirtalis*)

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ABSTRACT

THE EFFECTS OF SPEED ON TERRESTRIAL LOCOMOTOR KINEMATICS IN THE COMMON GARTER SNAKE (THAMNOPHIS SIRTALIS)

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Movement presents a unique challenge for snakes (suborder Serpentes), which utilize limbless locomotion to move in terrestrial and aquatic environments. Lateral undulation, the fastest and most commonly used type of snake locomotion, has been extensively studied in both contexts due to its prevalence in the animal kingdom. However, the effects of speed on locomotor kinematics have only been studied in aquatic conditions. During swimming, snakes are known to increase speed by increasing wavelength and amplitude while maintaining constant frequency. Additionally, amplitude in aquatic environments increases from the anterior to the posterior regions of the body. The mechanism for increasing speed in a terrestrial context is unknown, despite the fact that the majority of snakes reside in terrestrial areas. Therefore, I compared terrestrial locomotor kinematic data with existing aquatic swimming data to determine whether kinematic differences exist for increasing speed in different environments. In this study, Eastern Garter Snakes, Thamnophis sirtalis (n=4), were filmed utilizing lateral undulation at two different speeds with 120fps high-speed video. I examined speed effects on locomotion by conducting detailed comparisons of key kinematic and performance variables including wavelength, amplitude, frequency and segmental angles of the waves created during lateral undulation.

The speed effects of terrestrial locomotion were found to differ from aquatic locomotor pattern in wavelength. Mean wavelength in terrestrial trials increased
significantly as speed increased. Other variables, including frequency, amplitude, and growth of amplitude from head to tail, exhibited similar patterns to aquatic locomotion. This study provides insight into the mechanisms by which snakes generate locomotor complexity from a simple body plan.
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CHAPTER I
INTRODUCTION

Lateral undulation in limbless species has been extensively studied due to its prevalence and energetic efficiency, which can equal that of limbed locomotion (Walton et al., 1990). Limb loss in tetrapods has evolved independently in several lineages, especially within Class Reptilia, including families Pygopodidae, Anguidae, Scincidae, Suborder Serpentes and Suborder Amphisbaenia. This trend suggests a significant evolutionary advantage to limbleness in some environments (Gans, 1975). All of these taxa primarily utilize lateral undulation for locomotion, which can be effective in aquatic, terrestrial, and subterranean environments. Members of one snake genus (*Chrysopelea*) are even able to use this locomotor mode to effectively glide through the air (Socha et al., 2005). Lateral undulation has been the subject of broad interest from biomimetic engineers, many of whom use snake locomotion as a model to design robots for functions including search and rescue, exploration, and inspection (Tang et al., 2013). Previous kinematic studies have indicated that snakes in terrestrial environments utilize a highly derived and relatively complex form of lateral undulation when compared to limbless lizards, which do not utilize epaxial muscles to bend the body and cannot push the body off of a single contact point along the entire length of the body as snakes do (Moon and Gans, 1998).

Modern snakes evolved from lizards (likely varanids) about 100 million years ago (Vidal et al., 2009). The most significant shift in body form was the elongation of the body and the loss of limbs, eventually leading to the loss of the pelvic and pectoral girdles. Elongation of the body was achieved by dramatically increasing the number of vertebrae (Woltering, 2012). The evolutionary basis for this shift is still debated due to a poor fossil record resulting from the fragility and small size of snake skeletons. However, the current
prevailing theory states that the snakelike body form originally evolved to facilitate locomotion in fossorial and terrestrial habitats (Longrich et al., 2012). The originally hypothesized aquatic origin of snakes was based on morphological similarities of modern snakes to extinct marine lizards (Lee and Caldwell, 2000), but the fossil record now shows otherwise. The earliest known fossilized snake is *Coniophis precedens*, a terrestrial snake discovered in eastern Wyoming and estimated to be about 70 million years old (Longrich et al., 2012). This species lacked adaptations for aquatic locomotion, such as dorsoventrally compressed vertebrae and pachyostosism, and was likely fossorial, providing strong evidence for a terrestrial origin for snakes (Prasad and Rage, 1995; Caldwell and Lee, 1997; Longrich et al., 2012). However, because of the prevalence of swimming in modern snakes, limb loss and body elongation developed for terrestrial locomotion may have served as a preadaptation for swimming. Additionally, genetic studies have suggested that midbody Hox genes are responsible for limb development and body elongation. Hox genes control embryonic development of the body plan and mutations can cause significant changes in body form. Therefore, morphological change from a lizard-like body form to a snake-like body form may occur relatively rapidly in Squamate lineages (Cohn and Tickle, 1999). This pattern has been repeated numerous times within tetrapods, resulting in modern amphisbaenians, snakes, and several lineages of limbless lizards (Greer, 1991) (Fig. 1). Some modern lizard species, such as the striped worm lizard (*Ophiodes striatus*), appear to have a transitional body form characterized by reduced limbs and an elongate body. This species has lost the forelimbs completely but retains reduced hindlimbs and both the pectoral and pelvic girdle. It resides in terrestrial environments and is able to “swim” through tall grass more quickly than its fully limbed counterparts (Cei, 1993). Gans (1975)
suggested that elongation was the original adaptation in the transition to the serpentine form in squamates, followed by limb reduction. Elongation facilitates lateral undulation, so locomotion is hypothesized to be the driving factor for serpentine morphology (Gans, 1975). Whatever the reason for this body type shift, the prevalence of the limbless, elongate body type indicates that a lack of limbs is not a detriment to locomotion. However, the highest speeds recorded for limbless vertebrates do not nearly match attainable speeds of their limbed counterparts on flat ground (Punzo, 2007), indicating that a tradeoff may exist between top speeds in rough substrates (grass or sand) and on flat surfaces.

Snakes utilize five main locomotor modes that are employed in different environments. On smooth or loose terrain, sidewinding is preferred, in which the body is propelled sideways in a wave as described by Gray (1946). Lateral undulation, or serpentine locomotion, is preferred on terrain with projections or higher frictional coefficients and is characterized by a retrograde sinusoidal curve (Gans and Mendelssohn, 1972). Escape responses on smooth surfaces usually result in slide-pushing, a relatively irregular type of undulation used when the body slips over the substrate. This mode resembles a combination of sidewinding and lateral undulation, but is a distinct locomotor mode (Gans, 1974). Concertina, a method characterized by contraction and expansion of the body to push a snake forward using anchor points, is commonly used in areas without room to maneuver. Finally, rectilinear locomotion utilizes the ventral scales to push the body forward in a straight line. Snakes are able to combine locomotor modes in transitional terrain, especially sidewinding and lateral undulation (Gans, 1974).
The family Colubridae is the largest and most diverse group of snakes. However, it is generally acknowledged that it is a polyphyletic clade in need of reclassification (Vidal et al., 2007). Family Colubridae is a modern, relatively derived group within Suborder Serpentes (Fig. 2). Lateral undulation is the most commonly used locomotor mode by colubrids and is generally the fastest and most efficient type of snake locomotion. Propulsion is achieved through the exertion of force from the ground on the body (Gray, 1946). Several epaxial muscles, specifically the Mm. iliocostalis, multifidis, longissimus dorsi and spinalis-semispinalis, are utilized to flex the body into a wave (Gasc, 1981; Jayne, 1982). In addition to lateral motion, some of these muscles are used for torsional motion. Although vertebral torsion is restricted by spinal articulations, significant twisting can occur when considering the entire length of the body (Moon, 1999). Lateral undulation is highly effective on flat, solid substrates (Mosauer, 1932; Gans, 1985; Jayne, 1986). Recent kinematic descriptions of lateral undulation have revealed that snakes rely on frictional forces of the belly scales for movement on flat surfaces, and do not need to leverage the body against substrate irregularities to move effectively (Hu et al., 2009) as was previously hypothesized by Gray (1946) and Mosauer (1932).

Jayne (1988) compared aquatic and terrestrial locomotion in *Nerodia fasciata* and *Elaphe obsoleta* by using synchronized cinematography and electromyography. He showed that aquatic and terrestrial locomotion in snakes differs both in kinematics and motor pattern. The phase relation of epaxial flexion is uniform throughout the body in the terrestrial motor pattern. Flexion begins when the muscle is maximally convex and ends when it is maximally concave. In aquatic environments, flexion lags behind muscle activity. Additionally, snakes increased the number of active muscles toward the posterior in water, while the number
remained constant on land. Jayne (1988) concluded that the tail is a major source of propulsion in water, but is relatively unimportant for locomotion on land. This suggests that separate motor patterns may exist for lateral undulation in snakes in different environments.

There is a degree of tradeoff between aquatic and terrestrial speed in snakes (Isaac & Gregory, 2007). Aquatic specialists, such as natricine snakes, can attain a higher speed in water compared to mainly terrestrial snakes, while being limited to lower speeds on land compared to their terrestrial relatives. In species that utilize both terrestrial and aquatic environments equally, the difference in speeds is less pronounced (Isaac & Gregory, 2007). An extreme example of this tradeoff occurs in sea snakes. Shine and Shetty (2001) compared top speeds of sea snakes in aquatic and terrestrial environments, and found that they were able to achieve 60% faster speeds in water than their terrestrial relatives, but could only attain 20% of the top speed of their relatives on land. This was attributed to the morphological adaptations of the sea snakes, most notably the paddle-like tail and reduced ventral plates.

Relative tail length has also been shown to affect speed in some species. Snakes with intermediate tail length were able to attain higher top speeds than those with either very long or very short tails (Jayne and Bennett, 1989). However, small differences in tail length were not significantly correlated with top speed. Even when the posterior two thirds of the tail was ablated, snakes only saw an average speed decrease of about 4.5% (Jayne and Bennett, 1989). Overall length, although correlated with speed (e.g. longer individuals are faster than shorter individuals in absolute terms), is not directly correlated to relative speed (Heckrotte, 1967).
Previous studies investigating snakes swimming at the surface have shown a positive correlation between speed and frequency (undulations per second at the head), while wavelength (distance covered per undulation), shows a negative correlation with speed (Jayne, 1985; Munk, 2008). Wave amplitude (maximum lateral displacement from direction of movement) has been shown to decrease with speed (Jayne, 1985). However, conflicting reports exist regarding this variable; a similar study found a positive correlation between speed and amplitude (Munk, 2008). Finally, amplitude growth from head to tail exists for all speeds observed (Jayne, 1985; Munk, 2008).

Most extant members of Colubridae reside in predominately terrestrial environments, where they must travel without a viscous medium through which they can propel themselves. Terrestrial snake lateral undulation has been well described (Mosauer, 1932; Gray and Lissmann, 1950; Gans, 1970; Jayne, 1986; Moon and Gans, 1998), but these studies have largely relied on pegs upon which snakes can propel themselves. Furthermore, Bennet at al. (1974) determined that lateral undulation kinematics are altered when pegs are placed at varying intervals as contact points for snakes. However, Hu et al. (2009) determined that these objects, albeit preferred when present, are nonessential for this locomotor mode. Snake lateral undulation across flat surfaces without pegs, which may be more ecologically relevant, has not been well studied. Additionally, the effects of speed on lateral undulation on land have not been described. Due to the described differences in aquatic and terrestrial locomotion, differences may exist in the way snakes achieve higher speeds in these environments.
I investigated lateral undulation in the common garter snake (*Thamnophis sirtalis*), a widespread, semi-aquatic generalist (Drummond, 1983) in the family Colubridae. This species was used to enable direct comparisons to aquatic lateral undulation, as Munk (2008) described swimming in *Thamnophis sirtalis*. Additionally, colubrids utilize the most derived form of lateral undulation in snakes (Moon and Gans, 1998). The goals of this study were to: 1) determine the effects of speed on kinematic variables related to locomotion in a terrestrial environment; and 2) compare terrestrial kinematics with existing aquatic undulation data (Jayne, 1985; Munk, 2008).
CHAPTER II
MATERIALS AND METHODS

Study Animals

Kinematic data were obtained from four adult wild-caught garter snakes
(*Thamnophis sirtalis*) collected from Florida in February. Snakes were housed in 38 liter
aquaria, where they were fed fish and provided water *ad libitum*. The temperature of the
room, housing the aquaria was maintained at 26°C. All individuals were female. Mean
length was 58.4cm ± 5.6cm (SVL 43cm ± 2.31cm) and mean weight was 18.3g ± 0.9g.
Snakes were marked mid-dorsally, starting at the head and again every 10% of body length
using a white paint marker, resulting in 11 total points per snake (Jayne, 1986).

Procedures

Snakes were placed in a 155 x 60 cm arena lined with artificial turf to ensure
adequate traction and filmed performing lateral undulation. Halogen lamps were used to
provide lighting and to increase the temperature of the arena to near 26°C (Fig. 3). Snakes
were encouraged to cross the arena by tapping their tails. To encourage snakes to cross the
arena using fast locomotion, the tail was briefly grabbed and released to simulate being
caught by a predator; for slow trials, the tail was simply tapped. Only escape response was
investigated in this study. Some snakes will move short distances in pursuit of prey; however,
the vast majority of prey capture is via ambush, so pursuit was not investigated. Efforts were
made to allow individuals to perform undulation without encouragement for slow trials, but
unprovoked snakes generally utilized rectilinear locomotion or did not move at all.
Therefore, all useable trials were forced rather than voluntary locomotion, which can affect
kinematics (Finkler and Claussen, 1999). Defensive responses (striking) were very uncommon. Snakes were allowed to rest without disturbances for at least three minutes between trials to avoid fatigue, and a maximum of five attempted trials per snake were performed in a single day. Each trial was only utilized if the snake did not make contact with the sides of the arena or any other obstruction, and maintained a straight trajectory for at least a single full stride. A stride was defined as a single full undulation of the head, which began at the midline of the direction of motion and ended when the head had returned to the midline for the second time (Jayne, 1985; Munk, 2008). Although this did not always encompass a full undulation of the posterior points, the maximally convex point (or point of maximum lateral displacement) was captured for each point.

**Digitization**

A RedLake Motionscope M3 digital high-speed video camera was used to record a dorsal view at 120 frames per second. A lateral view was not necessary, as the majority of terrestrial movement exists in the horizontal plane (Jayne, 1986). Strides ranged from about 30-70 frames depending on speed. Video sequences recorded were scaled by digitizing a cube of known dimensions in MaxTRAQ 3D (Innovision Systems, Columbiaville, MI, US) prior to each filming session. Mid-dorsal points were tracked through every frame using the autotracking function, which recognizes and tracks designated points. Output was given as a set of 2D coordinates for each of the digitized points. Coordinates were subsequently converted into distances. To account for directional variation among trials, tracking outputs produced were normalized to occur about a horizontal line using Microsoft Excel (Microsoft Corporation, Redmond, WA, USA). Segmental excursion angles were measured between
each point; angle 1 represents the excursion angle between points 1 and 3, angle 2 represents the excursion angle between points 2 and 4, etc. (Fig. 4). The direction of motion was calculated as the average position of the head on the y-axis through a full undulation. Amplitude, or the maximum lateral displacement from the direction of motion, was also measured for each point. Distance covered in a single stride was measured as wavelength, and frequency was calculated for each trial as the number of undulations per second at the head. Speed was measured and normalized for length by calculating total body lengths per second to account for differences in body size among individuals.

**Analysis**

A total of forty trials were collected, and the best fast trials (n=19) and slow trials (n=17) were chosen for analysis based on consistency of direction and speed. No fewer than 4 trials were collected from each snake for each speed. All statistical tests were performed using NCSS software (NCSS, LLC, Kaysville, UT, USA). The effect of snout-vent length (SVL) on locomotor kinematics was tested using multivariate analysis of variance. Trials were then placed into two categories: slow (<50% max speed observed; \( \bar{x} = 0.41 \pm 0.17 \) body lengths per second (BL/sec)) and fast (>50% max speed observed; \( \bar{x} = 0.98 \pm 0.19 \) BL/sec) locomotion. The distribution of speeds observed in trials is shown in Fig. 5. Only two categories were used due to the relatively large movement variations observed among trials, even at similar speeds, which combined with a relatively small sample size could have diluted real differences between fast and slow locomotion in a regression analysis. Speed effects have been previously studied using categories of speed by Gillis (1996). Jayne (1985) noted that regression data do not necessarily represent complex
wave kinematics accurately. Results were analyzed using Hotelling's $T^2$ test to determine whether overall locomotor differences occurred between speeds. Paired t-tests were used for individual variable comparisons using $\alpha=0.05$. The null hypothesis for every test was that no kinematic differences exist between fast and slow locomotion.
CHAPTER III

RESULTS

Tail markings were left out of quantitative analysis due to extreme variability in movement (Fig. 6). Snakes appeared to have little control of tail movement during locomotion. Wavelength and frequency were calculated for the head only. A full undulation of the head did not correspond to a full undulation of following points. Results from other variables were calculated for all points, as the body does not perfectly follow the pathway of the head. Each individual produced both fast and slow trials, and there was little variation of top speed among individuals. Snout-vent length was found not to significantly affect kinematics (Wilks’ $\lambda=0.53$, $p=0.07$).

Amplitude

Mean amplitude at the head (point 1) was found to be significantly greater in slow trials ($\overline{x}=0.074 \pm 0.024$ body lengths (BL)) than in fast trials ($\overline{x}=0.043 \pm 0.053$ BL; $t=2.34$, $p=0.025$) (Fig. 7). Significant amplitude differences were not observed in the posterior seven points, although points 2 and 3 were nearly significant ($p=.056$ and $p=.058$, respectively) and may increase in significance with a larger sample size. Both fast and slow trials showed a significant increase in amplitude from head to tail ($p= <0.001$), with the largest increases occurring at the anterior three points. Amplitude increased twofold (average 2.08x) from point 1 ($\overline{x}=0.074 \pm 0.024$ BL) to point 8 ($\overline{x}=0.154 \pm 0.048$ BL) in slow trials, and more than threefold (average 3.43x) in fast trials (Point 1: $\overline{x}=0.043 \pm 0.023$ BL; p8: $\overline{x}=0.149 \pm 0.039$ BL).
Wavelength and Frequency

Mean undulation wavelength was not significantly different between fast and slow trials. Slow locomotion produced a mean undulation wavelength of 15.70 cm ± 4.1 cm, while fast locomotion was measured at 18.57 cm ± 4.4 cm (t=2.03, p=0.0502; Fig. 8). Frequency exhibited a significant positive correlation with speed. In fast locomotion, frequency was greater (\(\bar{x}=3.26\ \text{Hz} \pm 1.25\ \text{Hz}\)) when compared to frequency in slow locomotion (\(\bar{x}=1.88\ \text{Hz} \pm 1.22\ \text{Hz}\), t=3.35, p=0.002; Fig. 9).

Excursion Angles

Excursion angles for a single undulation did not differ significantly between fast and slow trials for any point along the body (Fig. 10). However, angles did increase significantly from head to tail. For fast trials, mean excursion angles increased from 75.8° ± 16.9° for angle 1 to 158.1° ± 48.9° for angle 8 (t= -6.94, p= <0.001). For slow trials, the mean excursion angle increased from 83.1° ± 15.6° for angle 1 to 149.5° ± 36.1° at angle 8 (t= -6.98, p=<0.001). The greatest increases occurred in the anterior portion of the body for both fast and slow speeds. The increase from point 1 (\(\bar{x}= 75.8° \pm 16.9°\)) to point 2 (\(\bar{x}= 108.1° \pm 17.8°\)) in fast trials was highly significant (t= -5.75, p= <0.001), as was the increase from point 1 (\(\bar{x}= 83.1° \pm 15.6°\)) to point 2 (\(\bar{x}=120.5° \pm 19.6°\)) in slow trials (t= -6.17, p= <0.001). The increase for fast trials from point 2 (108.1° ± 17.8°) to point 3 (\(\bar{x}= 122.1° \pm 15.4°\)) was also significant (t= -2.60, p= 0.007), as was the increase for slow trials from point 2 (\(\bar{x}= 120.5° \pm 19.6°\)) to point 3 (\(\bar{x}= 131.5° \pm 17.5°\); t= -1.73, p= 0.047).
Overall

Overall movements (combination of wavelengths, frequencies, amplitudes, and excursion angles) that were statistically compared with Hotelling’s $T^2$ statistic were found to be significantly different between fast and slow locomotion for the anterior two points (Point 1: $t=9.95$, $p=0.04$; Point 2: $t=10.6$, $p=0.03$). No significant differences were found for the posterior six points.
CHAPTER IV
DISCUSSION

Our results demonstrate that the effects of speed on snake locomotion are dissimilar in terrestrial and aquatic environments. However, the extent of dissimilarities is unknown due to conflicting data from studies of aquatic locomotion. Munk (2008) and Jayne (1985) showed that while swimming, amplitude increases from head to tail and wavelength decreases with increased speed. However, conflicting results exist regarding amplitude. Jayne (1985) found a decrease in amplitude with increasing speed in Elaphe guttata and Nerodia fasciata, two semi-aquatic colubrids, while Munk (2008) found a positive correlation between amplitude and speed in Thamnophis sirtalis. We found that during terrestrial locomotion, mean amplitude was greater at slow speeds than at fast speeds at the head, similar to the findings of Jayne (1985) for aquatic locomotion (Fig. 7). Nevertheless, comparisons with Munk (2008) may be more applicable due to use of the same model organism. This strategy may be used in order to direct more energy in the forward rather than lateral direction, resulting in higher speeds that may be useful for avoiding predation (Greene, 1988). Amplitudes observed were generally lower in Munk’s (2008) aquatic trials than in our terrestrial trials when comparing similar speeds.

Speed was higher in aquatic trials (max= 1.9 BL/sec, $\bar{x}= 1.16$ BL/sec; Munk, 2008) than terrestrial trials (max= 1.24 BL/sec, $\bar{x}= 0.72$ BL/sec). We observed an insignificant effect of speed on wavelength in our trials. However, because of the close proximity of the p-value for this variable ($p=0.0502$) to our $\alpha$ of .05, this may be a real effect that would be pushed into statistical significance with a larger sample size. Snakes covered an average of
18% more distance in a single stride during fast trials than during slow trials (Fig. 8). Overall wavelength for all speeds was lower than those observed in water (Munk, 2008).

A positive correlation between frequency and speed was observed in terrestrial trials, which is the same pattern observed in aquatic studies (Jayne, 1985; Munk, 2008). The number of undulations per second was an average of 1.73 times higher at fast speed than slow speed (Fig. 9); each stride required less time to complete. At similar speeds, aquatic frequencies observed by Munk (2008) were lower than our observed terrestrial frequencies.

The mechanism of action utilized by snakes for increasing speed in terrestrial environments can be summarized as follows: snakes increase the speed of strides (undulations) and decrease the amplitude at the head, while amplitude significantly increases from anterior to posterior. Wavelength may be increased with speed, but further study is required to determine wavelength patterns. Additionally, the excursion angles of the vertebral column do not vary among speeds, but do increase from anterior to posterior. The primary difference observed between speed regulation techniques in water and on land is amplitude at the head, which is decreased on land to increase speed but increased in water to increase speed (Munk, 2008).

These differences may exist because of the methods of propulsion utilized in different environments. Physical disparities exist between air and water, which can strongly affect the structure and function of organisms (Dejours et al., 1987). Aquatic environments increase the buoyancy of an organism, thus reducing gravitational load, but also increasing drag (Lillywhite, 1987). Additionally, water yields to some degree when force is exerted on it, while terrestrial substrates are largely unaffected by the exertion of force. To achieve
movement in terrestrial environments, organisms must overcome higher gravitational forces, a major obstacle to terrestrial locomotion (Martinez et al., 1998). Moreover, they must rely solely on the ventral surface of the body for propulsion, while the entire body can be used in water. In water, the retrograde wave of the snake propels the body forward by simultaneously pushing against a uniform and viscous medium regardless of speed, while fast terrestrial locomotion relies on pushing against the ground only at certain points along the body (Gans, 1984; Hu, 2009). Parts of the body not engaged in pushing are slightly lifted off the ground to reduce friction, leading to a dramatic increase of efficiency and top speed. Snakes may use torsional movements to achieve this body elevation during terrestrial fast locomotion (Moon, 1999). However, during slow locomotion, the body is either not lifted at all or lifted to a much lesser degree (Gans, 1984; Jayne, 1985; Hu, 2009). This body lifting behavior appears to be unique to snakes among limbless tetrapods. Another locomotor difference between aquatic and terrestrial locomotion is the role of the tail. Jayne (1985) hypothesized that most propulsion is generated in the posterior section of the body due to observed increases in amplitude toward the rear in aquatic environments. Although this pattern exists terrestrially as well, propulsion does not likely originate from the posterior in this context based on results from previous kinematic studies in which the posterior muscles were relatively inactive on land (Jayne, 1985; Gillis and Blob, 2001; Hu, 2009). Energetic costs also differ by environment. To increase speed on in terrestrial environments, the energetic cost follows a largely linear increase. However, in aquatic environments, increasing speed requires an exponential increase of energy (Goldspink, 1977). Due to these described differences between terrestrial and aquatic locomotion, I predict that different muscular mechanisms are used to increase speed in aquatic and terrestrial environments.
In natural environments, the heterogeneity of most terrain likely precludes the smooth, uniform movements observed in our tests. However, because Bennet et al. (1974) showed that utilizing pegs in the arena could alter kinematics, a flat surface was used to remove any experimental effects. Direct comparisons between our results and results from previous studies investigating terrestrial lateral undulation are not useful due to the large effect of peg spacing on kinematics and the lack of data representing the variables studied here. Additionally, locomotor performance can be affected by the frictional properties of the substrate even within a single locomotor mode (Kelley et al., 1997; Abdel-Aal et al., 2011). However, the substrate used in our experiments provided sufficient friction to avoid excessive slipping, which is likely the cause of kinematic differences due to substrate variation (Kelley et al., 1997).

Another potential source of variation in locomotor performance is the environment that the snakes were exposed to most often as juveniles. Aubret et al. (2007) demonstrated that snakes exposed to more aquatic conditions during development were able to achieve significantly higher aquatic speeds, but lower land speeds than their counterparts that were raised in terrestrial environments. As our study animals were wild-caught, their exposure to different environments during development is unknown. Kinematics may vary depending on amount of exposure to land. Additionally, snakes raised in aquatic environments are able to maintain slightly higher body temperatures for longer periods than snakes raised in terrestrial environments (Aubret and Michniewicz, 2010). Temperature is known to affect locomotor performance in snakes ( Heckrotte, 1967; Finkler and Claussen, 1999). Therefore, the arena temperature used in our study was made to closely approximate the water temperature in Jayne’s (1985) investigation of snake swimming kinematics in order to enable a more direct
comparison. Although the environmental conditions of development of the study animals in both ours and Jayne’s studies is unknown, small (<1°C) variations of body temperature observed by Aubret and Michniewicz (2010) due to this plasticity do not have a large effect on performance. Future studies could compare snakes captive-raised in both aquatic and terrestrial environments to determine the effects of adaptive plasticity on locomotor kinematics.

Sex has been demonstrated to affect performance in some types of snake locomotion (Bonnet et al., 2005; Jayne and Bennett, 1990). Specifically, sex can affect endurance in snakes performing lateral undulation (Jayne and Bennett, 1990). This is hypothesized to be caused by differences in mass. Many snakes species exhibit sexual dimorphism; female snakes are typically heavier when compared to male snakes of the same species at similar lengths (Shine, 1994). However, this variation did not likely affect our results, as we only investigated burst speeds, which have been demonstrated to not be affected by sex (Jayne and Bennett, 1990).

The pattern of increasing frequency with increased speed is common among anguilliform animals during swimming (Gillis, 1998). Most osteichthyan fishes exhibit some of these patterns, but are poor models for comparison to snakes. This is primarily because they utilize a retrograde sinusoidal curve for locomotion (the body can only perform one half of a wave at a time) and they do not possess a tail or significant elongation of the body. Eels, however, rely heavily on lateral undulation for locomotion and perform similar movements to snakes due to their similar morphology. Moreover, some species occasionally move across land for short periods (Scott and Scott, 1988). In a comparative study of aquatic and
terrestrial locomotion in eels, patterns of increased frequencies, constant amplitudes and amplitude growth with increasing speed were exhibited in both environments. However, unlike snakes, the anterior portion of the eels exhibits very little lateral movement during swimming, while lateral movement is much more pronounced on land. This suggests that eels use a separate motor pattern for increasing speed in different environments (Gillis, 1998). This method of utilizing different motor patterns for moving in water and on land is common. Taxa as diverse as toads, turtles, and rats employ a similar strategy (Gillis, 2001). The prevalence of this pattern suggests that snakes may also use this strategy.

Reilly and Delancey (1997) showed that a simple speed increase of femoral retraction was the major factor for increased speed in the limbed lizard *Sceloporis clarkii*, and the same pattern was observed in limbed salamanders and tuataras by Ashley-Ross (1994). Both authors hypothesized that this is a common technique among sprawling vertebrates for increasing speed. However, several more derived species of lizards have much more complex locomotor kinematics with respect to increasing speed. *Dipsosaurus dorsalis*, a generalized iguanian lizard, exhibits an increase in stride length and stride frequency in the hindlimb with increasing speed, as well as reduced duration of foot contact with the ground (duty factor) (Fieler, 1998). In addition, many lizards use bipedal locomotion for traveling at high speed, a highly specialized locomotor type that requires specialized morphology (Snyder, 1962). Although lizards exhibit lateral bending during locomotion, less than 5% of the total mechanical energy used for locomotion is used for lateral movement. Lateral movement primarily results as a byproduct of the movement of the limbs (Farley and Ko, 1997). The epaxial muscles, while heavily relied upon for lateral bending in snakes, are primarily utilized for stabilizing the trunk against vertical ground reaction forces in lizards,
and are not responsible for a significant amount of lateral bending (Ritter, 1995). Additionally, although snakes utilize body lifting during locomotion, limbless lizards do not use this technique during fast terrestrial lateral undulation, and appear unable to do so (Gans and Gasc, 1990).

Snakes must direct much more energy than lizards into lateral movements for locomotion (Jayne, 1988). Therefore, the degree of epaxial muscle flexion may greatly affect speed. Terrestrial speed regulation may be achieved by a simple modulation of the degree of flexion of the epaxial muscles rather than an entirely different motor pattern. Snakes may use a single motor pattern for increasing speed in both aquatic and terrestrial environments, and kinematic differences observed may be solely a product of mechanical feedback imposed by the environment rather evidence of a separate motor pattern. An organism performing identical muscular movements will exhibit different kinematics and propulsive impulses in different environments due to large variances in environmental properties (Aerts and Nauwelaerts, 2009), i.e. water is 800 times denser and 50 times more viscous than air (Denny, 1993). This paradigm is exemplified in frogs. Investigations of frog locomotion have determined that frogs may utilize the same behavior for both jumping and swimming, and that the kinematic differences observed are likely due to feedback from the medium. The way in which the medium reacts to force being exerted upon it is responsible for observed kinematic differences rather than motor pattern variation (Peters et al., 1996). Future studies could compare electromyographic data to determine which muscles are used and the degree of muscle flexion during terrestrial speed modulation in snakes. Kinematic descriptions alone are insufficient to determine whether a separate motor pattern exists for increasing speed in different environments.
The means of predator avoidance also differs by environment. In water, a snake will often simply dive under the surface to escape potential predators, while on land, a snake has to move away or fight back if no cover is available. During the filming of snakes, it was observed that individuals moving quickly rarely performed more than a single undulation in any direction during a single trial, often drastically changing course with seemingly little regard for their destination, making it difficult to obtain more than one stride per trial. Heckrotte (1967) has also observed this behavior in *Thamnophis sirtalis*. This could suggest that threatened snakes intentionally change direction as a means of predator avoidance, a common escape technique that impedes the ability of a predator to predict the location of potential prey. Because of the relative infrequency of prey pursuit in snakes (Greene, 1997), it is likely that fast locomotion evolved primarily as a predator avoidance strategy; however, some highly derived modern snakes now use fast locomotion for catching prey as well as predator escape (Greene, 1997). Snakes are a common prey item, and are preyed upon by arthropods, mammals, other reptiles (including snakes), and especially birds (Greene, 1988).

Fleeing, or locomotor escape, is the most commonly used defensive tactic used by snakes once identified by a predator as a potential prey item (Martins, 1996). Faster top speeds would aid the effectiveness of this escape response, which may explain the tradeoff between top speeds in terrestrial and aquatic environments discussed earlier (Isaac and Gregory, 2007). Snakes may use slow lateral undulation primarily for migratory or foraging purposes in terrestrial environments when intermediate speed is preferred. It may also be utilized in competing for a female upon leaving the communal wintering den, when relatively fast but highly controlled locomotion is useful (Shine, 2000).
There is a wide disparity of top speeds among snake species, with highest speeds attained by members of the families Viperidae and Colubridae, while the slowest species include members of the families Boidae and Pythonidae. Ruben (1977) hypothesized that the relative length of major axial muscle units is largely responsible for this disparity. The long muscle units of colubrids allow travel with lesser lateral resistance, resulting in faster speeds. However, lateral flexibility is limited in snakes with long axial muscle units. This limited lateral flexibility results in limited constriction ability. Conversely, the short muscle units found in boas and pythons result in high flexibility and increased constriction ability, but severely limit speed. This is consistent with their life history strategies as relatively sedentary predators that rely heavily on ambush and constriction techniques for killing prey (Greene, 1997). This suggests a tradeoff between top speed and constriction ability. Garter snakes, all of which are relatively fast organisms that utilize fast lateral undulation to chase and capture prey, possess relatively long axial muscle units (Arnold, 1988). Therefore, snakes with relatively shorter axial muscle units may exhibit different kinematic patterns while modulating speed. Future studies could compare the effects of axial muscle unit length on speed modulation techniques to gain insight into the locomotor consequences of these anatomical differences.

This study clarifies how snakes increase speed in terrestrial environments, as well as differences in speed modulation techniques between aquatic and terrestrial locomotion. Significant speed modulation differences were found to exist between terrestrial and aquatic environments. Lateral displacement (amplitude) at the head was found to decrease with speed in terrestrial environments, contrary to results from previous aquatic studies on the same species. Undulation frequency was found to significantly increase with speed, similar
to patterns observed in aquatic speed modulation. Other variables exhibited similar patterns for speed regulation in both environments as well. It remains unknown whether separate motor patterns are employed for speed regulation in these different environments; environmental differences may account for kinematic differences observed, as is the case with several other organisms, most notably frogs. Synchronized cinematography and electromyography are recommended for future studies to determine whether observed differences are due to motor pattern variation or environmental feedback.
REFERENCES


Figure 1. Phylogeny of Order Squamata (adapted from Vidal and Hedges, 2005). Boxed family names indicate limblessness of at least some members. Not all limbless squamate families are included.
Figure 2. Phylogeny of Suborder Serpentes (adapted from Lee and Scanlon, 2002).
Figure 3. Diagram of filming system.
Figure 4. Marked and digitized *Thamnophis sirtalis* in filming arena showing representations of measured variables. Point 1 corresponds to the head and points 2-11 occur sequentially from anterior to posterior every 10% of body length. White bands directly posterior to the head were used to distinguish individuals.
Figure 5. Histogram of speeds observed in trials. Results are shown in body lengths per second to account for size differences. Most slow trials were between 0.51 and 0.6 body lengths/second, while most fast trials were between 0.91 and 1.1 body lengths/second.
Figure 6. Amplitude of axial bending during all fast trials (n=19). Point 1 corresponds to the head, remaining points occur sequentially along the body. Results are shown as units of body length to account for size differences. Points 9 and 10 were omitted from analysis due to high variability.
Figure 7. Mean amplitude of axial bending comparing fast and slow locomotion. Point 1 corresponds to the head, and points occur sequentially along the body. Results are shown as units of body length to account for size differences. Mean amplitude at point 1 was significantly higher in slow trials ($\bar{x}=0.074 \pm 0.024$ BL) than in fast trials ($\bar{x}=0.043 \pm 0.023$ BL; $p=0.025$, $t=2.34$). Amplitude increased twofold (average 2.08x) from point 1 ($\bar{x}=0.074 \pm 0.024$ BL) to point 8 ($\bar{x}=0.154 \pm 0.048$ BL) in slow trials, and more than threefold (average 3.43x) in fast trials ($p1: \bar{x}=0.043 \pm 0.023$ BL; $p8: \bar{x}=0.149 \pm 0.039$ BL).
Figure 8. Mean undulation wavelength exhibited in a single stride comparing fast and slow terrestrial locomotion. Wavelength results were calculated from the head point and presented as units of body length to account for size differences. Mean wavelength during fast locomotion (18.57 cm ± 4.4 cm) was significantly higher than for slow locomotion (15.70 cm ± 4.1 cm; t=2.03, p=0.0502).
Figure 9. Mean undulation frequency exhibited in a single stride comparing fast and slow terrestrial locomotion. Wavelength results were calculated from the head point. Fast ($\bar{x}=3.26$ Hz ± 1.25 Hz) and slow ($\bar{x}=1.88$ Hz ± 1.22 Hz) locomotion were significantly different ($t=3.35$, $p=0.002$).
Figure 10. Mean excursion angle comparing fast and slow terrestrial locomotion. Angle 1 corresponds to point 2, and denotes the change in angle between point 1 and point 3 in a single stride. This pattern is constant along the body. No significant differences existed between fast and slow locomotion for any point.