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Effects of morphology, substrate use, and potential trade-offs on locomotor performance during multiple modes of snake locomotion

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ABSTRACT

Question: How do morphology, substrate usage, and biomechanical constraints (i.e. trade-offs) influence locomotor performance of multiple modes of snake locomotion?

Data studied: Nine morphological traits, substrate preferences and use, and locomotor performance (maximal speed and endurance) of four modes of locomotion (terrestrial lateral undulation, swimming, concertina, and arboreal) in five species of North American snakes.

Search method: Principal component analysis and regression models to determine whether morphological differences were associated with speed and endurance of each mode of locomotion. Linear regressions to relate time spent on terrestrial, aquatic, and arboreal substrates to performance during modes used to traverse each substrate. Determine relationships between performance of different modes to identify potential trade-offs. Each species was analysed separately.

Conclusions: Morphology significantly influenced size-relative, maximal speeds differentially across the various modes of locomotion and species, especially during modes that each species often utilizes in nature. Relationships between locomotor performance and substrate use exist, but patterns differed among species. Few trade-offs in performance were detected between modes for any species.

Keywords: arboreal, concertina, endurance, habitat use, lateral undulation, speed, swimming.

INTRODUCTION

Locomotor performance is a trait that, under most circumstances, should be selected for because individuals that are faster have extended endurance, or can manoeuvre better, are more likely to escape predators, find food, locate potential mates, and defend territories. Selection pressures should act directly on the morphological and physiological traits governing whole-animal performance as proposed by Arnold's (1983) morphology → performance → fitness paradigm, which, in turn, is influenced by a species' ecology (Garland and Losos, 1994). Because different combinations of morphological traits could result in differential performance abilities in different ecological contexts, one might expect to see

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strong relationships between morphology, locomotor performance, and the structure of frequently used habitats (Garland and Losos, 1994; Irschick, 2002, 2003; Irschick *et al.*, 2005). Moreover, the presence of trade-offs in performance among multiple, frequently used modes of locomotion can indirectly impact morphology and fitness (Irschick and Higham, 2016).

Morphological modifications are often found in animals that utilize well-defined habitats to optimize locomotion in that particular habitat. For example, in arboreal *Anolis* lizards, species with longer limbs are usually faster runners and can jump greater distances (Losos and Sinervo, 1989; Losos and Irschick, 1996). Kohlsdorf *et al.* (2001) found that species of *Tropidurus* lizards are very similar in body size and shape, but possess very different performance capabilities that are related to habitat preference. If variation in performance is related to variation in habitat use, then performance should be predictable across a gradient of habitat types because species specializing in one particular habitat likely possess adaptations that enhance movement in that habitat. For example, arboreal species should be better climbers than terrestrial species adapted to move more efficiently on terrestrial substrates, often resulting in trade-offs between types of movement (e.g. between sprinting and climbing in chameleons) (Losos *et al.*, 1993). Although these associations have been noted in lizards, the relationships among locomotor performance, morphology, and habitat use in snakes are less understood.

Because they have no limbs, snakes have evolved a variety of locomotor techniques or modes associated with moving on different substrates and media (Gans, 1986). Snakes typically move via lateral undulation when travelling on land or swimming in water (Jayne, 1985; Cundall, 1987). When climbing vertical surfaces or traversing narrow passageways, snakes utilize a slow, energetically expensive mode called concertina that involves an alternation of stop-and-go changes in momentum (Jayne, 1988a; Walton *et al.*, 1990). Snakes are also capable of arboreal locomotion, which involves a combination of lateral undulation and concertina movements with the need for simultaneous balance (Astley and Jayne, 2007; Gerald *et al.*, 2008). Morphological adaptations that enhance locomotor performance in snakes may or may not differ among modes of locomotion. Increased relative body length provides more surface area to push against the substrate, which can increase performance of several modes. However, lateral undulation is hindered in snakes with a larger number of vertebrae because of shorter epaxial muscles and increased lateral resistance present in species with more vertebrae (Ruben, 1977; Jayne, 1986).

Previous studies that have assessed performance of different modes of locomotion have mostly compared the performance of terrestrial lateral undulation with that of swimming. Shine and Shetty (2001) found that aquatic and terrestrial speeds of marine and terrestrial snakes (Elapidae) mirrored the use of those habitats, and also that snakes which performed well during one mode performed more poorly in the other. The aquatic snake *Natrix maura* is a faster swimmer but moves more slowly on land compared with the semi-aquatic *Natrix natrix* (Isaac and Gregory, 2007). Bonnet *et al.* (2005) found that variation in climbing ability on a typical reef cliff by sea snakes reflected how frequently each species and sex climbed in nature. After comparing pairs of arboreal and terrestrial species, Rozar (2010) concluded that arboreal species exhibit superior arboreal performance than terrestrial species and vice versa. To my knowledge, no study has examined the relationships among morphological characteristics and habitat use on performance of multiple modes of snake locomotion.

I set out to accomplish three things. First, examine the relationships between morphological traits and locomotor performance (speed and endurance) during four modes of limbless locomotion in five snake species (families Colubridae and Natricidae). Second,

assess the linkages between individual variation in habitat use and performance during different modes of locomotion. Third, investigate potential trade-offs in performance among modes of locomotion within species to test the hypothesis that adaptations that enhance some modes of locomotion conflict with those of other modes. Additionally, I sought to provide insight as to how the combination of both morphology and habitat use might potentially exacerbate or mitigate differences in locomotor performance among modes.

MATERIALS AND METHODS

Study species

I studied five species of North American snakes that vary in their patterns of habitat usage (Wright and Wright, 1957; Ernst and Ernst, 2003; Powell *et al.*, 2016). Three of the species (*Pantherophis guttatus*, *Pantherophis alleghaniensis*, and *Pituophis catenifer*) belong to the family Colubridae, and hence are more closely related to each other than to the other two species (*Thamnophis sauritus* and *Nerodia sipedon*), which belong to the family Natricidae. Although none of the species used in this study would be considered habitat specialists, all five differ from each other in the proportions of time they spend exhibiting terrestrial, fossorial, aquatic, and arboreal behaviours in nature [though this has yet to be formally measured (Powell *et al.*, 2016)].

Cornsnakes (*Pantherophis guttatus*) live in many habitat types, but are mostly a terrestrial species frequently found climbing trees (Powell *et al.*, 2016; G.W. Gerald, personal observation) and in or near water (Ernst and Ernst, 2003). Yellow ratsnakes (*Pantherophis alleghaniensis*) live in a variety of wooded habitats where they frequently display arboreal habits and forage on squirrels, birds, and bird eggs; therefore, this species is described by numerous sources as being semi-arboreal (Wright and Wright, 1957; Tennant, 1997; Powell *et al.*, 2016). Bullsnakes (*Pituophis catenifer*) occupy a large variety of terrestrial habitats and spend a large proportion of their time underground (Ernst and Ernst, 2003; Rodriguez-Robles, 2003). Ribbon snakes (*Thamnophis sauritus*) possess long, thin bodies and relatively long tails (up to 38.8% of their total body length). They are most often found on the banks of waterways where they forage (mostly on fishes and amphibians) and bask in low-lying vegetation (Carpenter, 1952; Wright and Wright, 1957; Ernst and Ernst, 2003). Consequently, Powell *et al.* (2016) and Rossman *et al.* (1996) consider this species to be both semi-aquatic and semi-arboreal. Northern watersnakes (*Nerodia sipedon*) are found in or near almost any type of freshwater habitat throughout its geographical range and have been described many times as being excellent swimmers (Finkler and Claussen, 1999; Ernst and Ernst, 2003; Powell *et al.*, 2016).

I gathered data on morphology and locomotor performance from twelve individuals from each of the five aforementioned species. Because body size can have a marked influence on locomotor performance (see Jayne and Bennett, 1990; Wisco *et al.*, 1997), I used individuals across different species that were relatively similar in body length (i.e. snout–vent length, SVL; Table 1). However, interspecific variation in body mass was large (Table 1). I chose to use snakes that were more similar in body length rather than mass because length is likely to be a more important determinant of locomotor performance across various modes of locomotion compared with mass (G.W. Gerald, unpublished data). Relatively longer snakes can use more push points in a given area to enhance performance during most modes of locomotion (Jayne, 1985, 1986; Cundall, 1987; Gerald *et al.*, 2008).

Table 1. Morphological measurements for five species of snakes used in the present study (mean values with standard deviations in parentheses; $N = 12$ per species)

	Pantherophis guttatus	*Pantherophis alleghaniensis*	*Pituophis catenifer*	*Thamnophis sauritus*	*Nerodia sipedon*
Mass (g)	28.1 (14.8)	56.6 (22.6)	73.0 (46.4)	11.4 (3.3)	119.1 (40.2)
Snout–vent length (cm)	45.0 (6.8)	61.0 (10.1)	52.8 (9.6)	37.8 (3.9)	54.0 (6.8)
Tail length (cm)	7.9 (1.8)	13.7 (3.0)	7.9 (2.0)	16.6 (4.8)	15.2 (3.3)
Cross-sectional area (mm^2)	108.2 (44.3)	154.2 (42.3)	226.9 (77.7)	57.6 (15.9)	351.4 (114.1)
Ventral scale width (cm)	1.5 (0.1)	1.4 (0.1)	1.9 (0.2)	1.2 (0.1)	2.0 (0.2)
Neck circumference (cm)	3.1 (0.2)	4.0 (0.4)	4.6 (0.4)	2.3 (0.1)	7.5 (0.6)
Mid-body circumference (cm)	5.9 (0.6)	4.8 (0.3)	6.3 (0.7)	4.6 (0.2)	8.4 (1.3)
Tail base circumference (cm)	2.2 (0.1)	2.1 (0.2)	4.0 (0.2)	1.8 (0.1)	5.1 (0.70)
Number of vertebrae	231.2 (6.8)	251.2 (20.1)	221.3 (6.9)	174.9 (3.7)	141.2 (3.8)

Husbandry

I acquired all *Pantherophis guttatus*, *P. alleghaniensis*, and *Thamnophis sauritus* from a commercial supplier (Glades Herp Inc., Bushnell, FL) that were either captive bred (*P. guttatus*) or wild-collected and kept in captivity before being used for this study (*P. alleghaniensis* and *T. sauritus*). I acquired all *Pituophis catenifer* from various private collectors; all were either captive-raised or wild-collected and kept in captivity for a short period of time before I obtained them. I hand-collected all *Nerodia sipedon* from several streams in Butler Co., Ohio. Therefore, previous conditions experienced by all snakes used in this study likely varied.

All snakes were housed in plastic bins ($54 \times 21 \times 9$ cm) within a custom-made rack system in an environmental chamber (25 ± 0.5°C) set to a 12 : 12 hour light : dark photoperiod. I fed all snakes approximately the same amount of food relative to body mass per week. Three species (*P. guttatus*, *P. alleghaniensis*, *Pit. catenifer*) were fed pre-killed mice (*Mus musculus*) of the appropriate size (width of the mouse was approximately equal to the maximum width of the snake), once per week. Every three days, I fed *T. sauritus* two live fathead minnows (*Pimethales promelas*) and fed *N. sipedon* crayfish (*Procambarus clarkii*) or *Pim. promelas*. I conducted no trials for two days following feeding. All individuals were acclimated for at least two weeks prior to the start of experimental trials.

Morphological measurements

I collected morphological data for each individual prior to conducting the locomotor trials (Table 1). I measured body mass to the nearest 0.1 g and snout–vent length (SVL) and tail length to the nearest 0.1 cm. I calculated cross-sectional area using measurements of body width and height. Using a tape measure, I measured body circumference at the neck (1 cm posterior to the back of the skull), mid-body, and tail base (at the cloaca) to the nearest 0.1 cm. Using digital callipers, I determined all length and width measurements to the nearest 0.1 cm. Because vertebrae are important sites for the attachment of epaxial musculature and the number of them can influence lateral bending, I counted the number

of pre-caudal ventral scales as an indicator of the number of vertebrae (Kerfoot, 1970; Jayne, 1986; Cundall, 1987; Arnold and Bennett, 1988).

Substrate use

I measured the time each individual spent using terrestrial, arboreal, and aquatic substrates in captivity. I did this for each species to make sure that published accounts of habits and habitat usages reflected behaviours of individuals used in the present study. I put each individual in a Neodesha cage ($57 \times 27 \times 26$ cm) containing opportunities for snakes to exhibit terrestrial, arboreal, and aquatic behaviours. Cages possessed a substrate consisting of terrarium carpet, a large water dish ($24 \times 20 \times 5$ cm), and a cylindrical perch (6 cm diameter) that was positioned horizontally 18 cm above the substrate. The perch was wrapped in burlap carpet to prevent slipping and to facilitate movement (Gerald *et al.*, 2008). The cage was placed in an environmental chamber set at 25 ± 0.5°C with a 12 : 12 hour light : dark photoperiod. Although the chamber was lit with fluorescent bulbs, red incandescent bulbs placed approximately 1 m from the cage illuminated the cage for videotaping during the dark hours. Snakes could easily move among the three habitats within the cage. Snakes remained completely undisturbed during these experiments.

Each individual ($n = 12$ per species; total $n = 60$) was videotaped over a 24-hour period following 24 hours of acclimation. I recorded observations of substrate use with a Videolabs Flexcam (Videolabs, Inc., Minneapolis, MN). For each individual, I measured time spent on the terrestrial substrate, in the water, and on the perch. Therefore, I am assuming that the distribution of use of substrates is a good reflection of an individual's natural habitat distribution.

Locomotor performance

I measured maximal speeds and endurance for all twelve individuals of each species. I conducted all trials at 25 ± 0.5°C for four modes of limbless movement: terrestrial lateral undulation, concertina, arboreal, and swimming. For all speed trials, I videotaped the dorsal view of the snake using a Sony DCR-TRV460 Digital8 (New York, NY) while encouraging it to move at maximal speed (Fig. 1). For all modes, I defined maximal speed as the fastest of three successive movements across a 50-cm segment of the substrate, which I measured by analysing the video. The protocol used to elicit maximal speed consisted of lightly tapping the tail of the snake with a painter's brush or with a finger (see Gerald and Claussen, 2007). I converted all speeds to size-relative speeds ($SVL \cdot s^{-1}$) for subsequent analyses. To measure endurance, I stimulated snakes to move continuously at maximal speed until exhaustion. I measured endurance times to the nearest second with a digital stopwatch. I defined exhaustion as the state when a snake would no longer move forward after at least five attempts to stimulate movement. Between individuals, I cleaned all tracks with ethanol. I randomized the sequence of individuals and modes tested using a repeated-measures design with at least two days between trials for a given individual.

For terrestrial lateral undulation (LU), I used a track (3.0×0.75 m) containing a terrarium carpet substrate. This set-up allowed me to gather data on maximal speed and endurance (Fig. 1). The carpet substrate provided numerous small projections that snakes need to produce force along the lateral body surfaces that characterize lateral undulation (Jayne, 1986). I used a raceway (7.25 m long) around the perimeter of the rectangular track

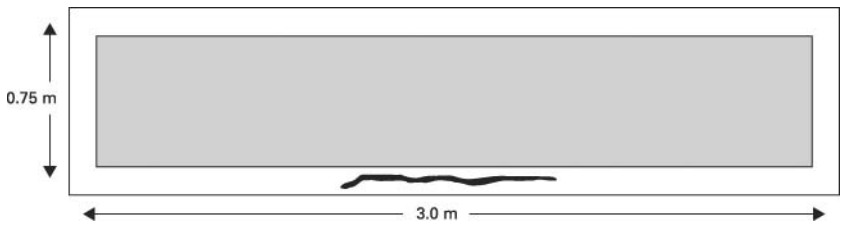

Fig. 1. Diagram of the rectangular track used to measure speed and endurance of terrestrial lateral undulation and concertina locomotion. Speeds were measured by chasing snakes down one long side of the track. Endurance was measured by chasing snakes around the periphery of the track until exhaustion. Interior walls made of plywood were movable to adjust the width of the track. Substrates were changed and width adjusted to elicit the different modes of locomotion.

(Fig. 1) to measure LU performance. I adjusted track width to at least 30 cm using plywood walls positioned to create a rectangular, unused portion in the middle of the track (Fig. 1). I measured LU speeds by videotaping snakes moving on one linear section of the track (2.5 m). To measure endurance, I stimulated snakes to move at maximal speed around the perimeter of the rectangular track until exhaustion.

The track used to assess LU was also used to measure concertina (Conc) performance (Fig. 1). However, to stimulate concertina locomotion, I adjusted the width of the track for each individual to 2.5 times its maximum body width. This width permitted comparisons of concertina performance among snakes differing in body size (Gerald and Claussen, 2007). I used smooth Plexiglas® as the substrate for the concertina trials to promote use of the side walls for the force generation that defines this mode of locomotion. I measured concertina speed and endurance as described above for lateral undulation.

I assessed arboreal (Arb) locomotion on two horizontal, artificial perches (6 cm diameter) that were round in cross-section. Perches were wrapped in rough-textured burlap carpet to provide push-off points, and positioned together directly across from each other end-to-end to produce a 2-m long perch (described in Gerald *et al.*, 2008). Snakes were positioned on one end of the perch and stimulated to move, as previously described, at maximum speed along the perch three times in succession. Arboreal endurance was not measured because the design of the perches did not permit the uninterrupted movements needed to quantify endurance.

To assess swimming (Swim) speeds, I used a linear trough ($220 \times 20 \times 0.15$ cm) marked at 0.5-m intervals and filled with aged water equilibrated to room temperature. To determine maximum swimming speed, I put each snake at one end of the trough and stimulated it to swim the length of the track three times in succession. Maximum swimming speed was defined as: (the time it took to swim 1.5 m)/1.5 m. I determined swimming endurance by stimulating snakes to swim continuously around a circular swimming pool (1.3 m diameter). I prodded snakes to swim around the pool until they remained motionless (typically on the water's surface) following at least five attempts to encourage swimming. I replaced all water between testing of different individuals.

Statistical analyses

I used the residuals of the linear regressions between log snout–vent length (SVL) and each morphological variable to remove the effect of body size. I pooled, among species, log transformations of the residuals for each variable and used them to conduct a principal

component analysis (PCA) to: (1) describe the covariation among morphological variables, and (2) use PC scores for each individual to quantify the relationship between morphology and performance. I conducted linear regressions between the first two PC axes and size-relative performance measurements for each mode of locomotion of each species. I ascertained this relationship for each species separately because species cannot be treated as statistically independent in that they share evolutionary histories (Felsenstein, 1985). Statistical analyses that correct for phylogeny (e.g. Garland *et al.*, 1993) were not utilized for this study because the number of species ($n = 5$) did not provide sufficient statistical power.

Within a species, I examined differences in size-relative speeds and endurance among modes using repeated-measures analyses of variance (ANOVA) with Tukey's tests for *post hoc* comparisons. I used χ^2 analyses to assess the differences in time spent on terrestrial, arboreal, and aquatic substrates among species. Using linear regressions despite the small sample size ($n = 5$), I examined the relationship between time spent on a given substrate and speed of mode of locomotion used on that substrate among species. I calculated partial correlation coefficients between time spent on different substrates and locomotor performance. This was done separately for each mode of locomotion and species. I also used partial correlations to assess potential relationships in performance among modes of locomotion to identify any trade-offs. As before, I conducted this at the intraspecific level because of problems associated with making interspecific comparisons without phylogenetic corrections. However, size-relative performance measures were depicted together to facilitate qualitative comparisons. All analyses were conducted using Microsoft® Excel 2011/XLSTAT (Addinsoft, Inc., Brooklyn, NY).

RESULTS

Morphology and locomotor performance

Owing to differences in body shape, body mass varied much more (means 11.4–119.1 g) than SVL (means 37.8–61.0 cm) among the five species in this study (Table 1). The first three axes of the PCA of the nine morphological variables explained 84.0% of the total variation. The first component (PC1) explained 43.8% of the variation with high positive loadings for SVL, cross-sectional area, and mid-body circumference, and a high negative loading for 'number of vertebrae' (Table 2). Therefore, PC1 describes body shapes that are relatively longer with a larger mid-body circumference containing fewer vertebrae. The second component (PC2) explained 21.0% with high positive loadings for 'number of vertebrae' and 'ventral scale width.'

Size-relative speeds were positively correlated with the PC1 axis for one or two modes for each of the five species (Table 3). However, size-relative speeds were negatively correlated with the PC2 axis for lateral undulation in *Pit. catenifer* (Table 3). Only two speeds were positively related to the PC2 axis (swimming for *Pit. catenifer* and arboreal for *N. sipedon*). Endurance times were not significantly correlated with either PC axis for any mode or species.

Performance comparisons among modes of locomotion

Species were not compared statistically to each other because of the previously mentioned issues related to non-independence. In all species studied, swimming speeds were fastest, followed by lateral undulation (LU) speeds ($P < 0.001$; Table 4). There were no differences

Table 2. Matrix showing the percentage variance and the factor loadings of principal components analysis using nine morphological size-relative traits

	PC1	PC2	PC3
% Variance	43.8	21.0	19.2
Mass	0.58	0.47	0.25
Snout–vent length	0.94	−0.18	−0.08
Tail length	0.12	0.35	−0.03
Cross-sectional area	0.91	0.10	0.44
Ventral scale width	0.10	0.40	0.68
Neck circumference	0.09	−0.10	0.49
Mid-body circumference	0.84	0.11	0.15
Tail base circumference	0.24	−0.05	−0.10
Number of vertebrae	−0.44	0.66	0.08

Table 3. Summary regression coefficients comparing size-relative maximal speeds and PC axes 1 and 2 for four locomotor modes for five different snake species and for all individuals of all species combined ignoring phylogeny ($N = 12$ per species)

Species	Mode of locomotion	PC1	PC2
Pantherophis guttatus	Lateral undulation	0.72	0.09
	Concertina	1.24**	−0.06
	Arboreal	1.18**	−1.02
	Swimming	0.33	0.48
Pantherophis alleghaniensis	Lateral undulation	0.21	−0.11
	Concertina	0.83	0.57
	Arboreal	1.87**	0.04
	Swimming	0.58*	−0.52
Pituophis catenifer	Lateral undulation	0.45	−0.55**
	Concertina	1.10**	−0.38
	Arboreal	0.29	−0.10
	Swimming	0.44	0.77*
Thamnophis sauritus	Lateral undulation	0.95**	−0.06
	Concertina	0.76	0.44
	Arboreal	0.20	−0.04
	Swimming	1.72**	−0.17
Nerodia sipedon	Lateral undulation	0.88**	−0.08
	Concertina	0.18	−0.10
	Arboreal	0.21	0.84**
	Swimming	1.08*	−0.06
All snakes	Lateral undulation	0.70	−0.11
	Concertina	0.91*	0.08
	Arboreal	0.84*	0.34
	Swimming	1.05**	0.22

*$P < 0.05$; **$P < 0.001$.

Table 4. Summary of percentage time spent using different substrates and locomotor performance (speed and endurance) for four modes of limbless locomotion for five species of colubrid snakes (mean values with standard deviations in parentheses)

Species	Habitat niche	% Time			Mode	Performance		
		Terrestrial	Arboreal	Aquatic		Maximal speed ($m \cdot s^{-1}$)	Size-relative maximal speed ($SVL \cdot s^{-1}$)	Endurance (s)
Pg	Generalist	89.0 (2.1)	8.2 (1.5)	2.8 (0.7)	LU	0.191 (0.02)	0.482 (0.02)	921 (201)
					Conc	0.051 (0.03)	0.110 (0.05)	887 (281)
					Arb	0.021 (0.02)	0.059 (0.04)	NA
					Swim	0.486 (0.13)	1.007 (0.17)	894 (187)
Pa	Semi-arboreal	64.3 (4.3)	35.7 (4.3)	0.0	LU	0.470 (0.09)	0.634 (0.08)	891 (199)
					Conc	0.076 (0.03)	0.118 (0.03)	908 (145)
					Arb	0.059 (0.02)	0.114 (0.04)	NA
					Swim	0.627 (0.10)	0.997 (0.12)	842 (129)
Pc	Terrestrial	98.0 (1.9)	1.5 (1.1)	0.5 (0.8)	LU	0.258 (0.07)	0.586 (0.03)	1648 (150)
					Conc	0.094 (0.02)	0.179 (0.02)	1311 (124)
					Arb	0.020 (0.01)	0.042 (0.01)	NA
					Swim	0.557 (0.13)	1.080 (0.16)	709 (77)
Ts	Semi-arboreal, semi-aquatic	53.6 (2.8)	45.3 (2.6)	1.1 (0.1)	LU	0.521 (0.09)	1.281 (0.12)	825 (195)
					Conc	0.052 (0.02)	0.013 (0.01)	843 (136)
					Arb	0.024 (0.01)	0.070 (0.02)	NA
					Swim	0.498 (0.14)	1.315 (0.18)	705 (158)
Ns	Semi-aquatic	78.2 (2.5)	2.4 (0.6)	19.4 (1.9)	LU	0.520 (0.10)	0.807 (0.14)	1207 (371)
					Conc	0.098 (0.02)	0.125 (0.03)	688 (280)
					Arb	0.013 (0.01)	0.021 (0.01)	NA
					Swim	0.852 (0.11)	1.794 (0.13)	1412 (292)

Note: Pg = *Pantherophis guttatus*, Pa = *Pantherophis alleghaniensis*, Pc = *Pituophis catenifer*, Ts = *Thamnophis sauritus*, Ns = *Nerodia sipedon*. LU = lateral undulation, Conc = concertina, Arb = arboreal, Swim = swimming. NA = not applicable.

between arboreal and concertina speeds for two species (*P. guttatus* and *P. alleghaniensis*; $P > 0.05$; Table 4). Concertina speeds were higher than arboreal speeds for *Pit. catenifer* and *N. sipedon*, while the reverse was true for *T. sauritus* ($P < 0.001$; Table 4). No differences in endurance were found among modes of locomotion in four species ($P > 0.05$; Table 4). However, concertina endurance was significantly lower than both swimming and LU endurance in *N. sipedon* ($P < 0.01$; Table 4).

Substrate use and locomotor performance

The species spent significantly different amounts of time using the three substrates ($\chi^2 = 163.71$, $df = 8$, $P < 0.001$). *Pantherophis guttatus* and *Pit. catenifer* used terrestrial substrates more than the other three species. The semi-arboreal snakes (*P. alleghaniensis* and *T. sauritus*) used perches more than the other species. Additionally, *N. sipedon* (semi-aquatic) spent more time in water than the other four species (Table 4). Interspecific variation in the percentage of time spent utilizing terrestrial, arboreal, and aquatic substrates corroborates numerous observations of the habitat usage in nature of the snake species used in the present study (e.g. Powell *et al.*, 2016) (Table 4).

Maximal speeds and endurance during terrestrial modes (lateral undulation and concertina) were not correlated with terrestrial substrate use for any species (Table 5). Swimming endurance was positively related to time spent in water for three species (Table 5). Maximal swimming speed was positively correlated with time spent in water for *T. sauritus*. Arboreal speed was positively correlated with time spent on arboreal perches for *P. guttatus*, *P. alleghaniensis*, and *N. sipedon* (Table 5). When examining the relationship between average size-relative speeds of each mode of locomotion among species with the corresponding substrate usage, lateral undulation, concertina, and arboreal speeds were not significant ($P > 0.05$). However, swimming speeds were positively related to aquatic usage ($F_{1,4} = 15.15$; $P = 0.03$; Fig. 2).

Table 5. Partial correlations between time spent on terrestrial, arboreal, and aquatic substrates and size-relative speed and endurance during different modes of locomotion used primarily in that substrate in five species of snakes

	Speed				Endurance		
Species	LU	Concertina	Arboreal	Swimming	LU	Concertina	Swimming
Pantherophis guttatus	0.02	0.11	0.84*	−0.19	0.13	−0.07	0.61*
P. alleghaniensis	−0.14	0.09	0.66*	0.16	0.23	0.24	0.45*
Pituophis catenifer	−0.20	0.37	0.45	−0.07	−0.14	0.21	0.30
Thamnophis sauritus	0.19	0.18	0.34	0.79*	0.05	0.10	0.52*
Nerodia sipedon	−0.04	−0.12	0.72*	0.18	0.50	0.29	0.15

Note: Lateral undulation (LU) and concertina were compared with terrestrial substrate usage. Arboreal and swimming were compared with arboreal and aquatic substrate usage, respectively. Arboreal endurance was not measured. *$P < 0.05$.

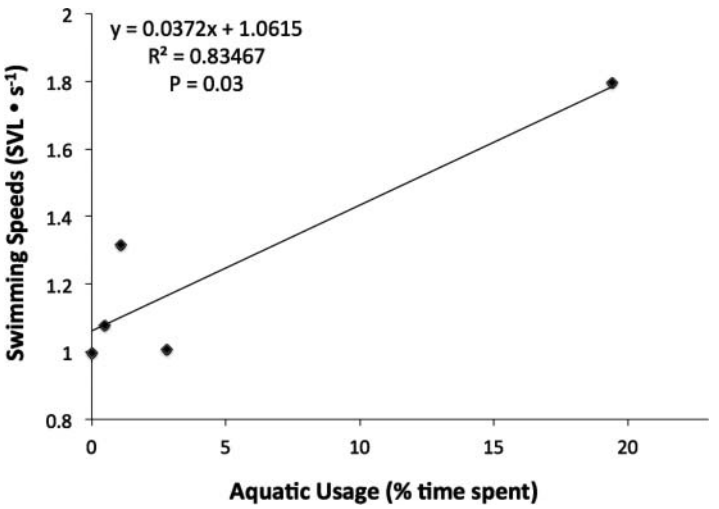

Fig. 2. Relationship between average swimming speeds and the time spent in water for five species of snakes: *Pantherophis guttatus*, *Pantherophis alleghaniensis*, *Pituophis catenifer*, *Thamnophis sauritus*, and *Nerodia sipedon*.

Table 6. Partial correlations between size-relative speeds of four modes of locomotion and between speed and endurance of each mode for five species of snakes

		Speed				
Species	Mode	LU	Concertina	Arboreal	Swimming	Speed vs. endurance
Pantherophis guttatus	LU	1.0				0.56*
	Concertina	0.35	1.0			0.21
	Arboreal	0.15	−0.34	1.0		−0.08
	Swimming	0.39*	−0.10	0.06	1.0	0.87*
P. alleghaniensis	LU	1.0				0.73*
	Concertina	0.22	1.0			−0.25
	Arboreal	0.19	0.21	1.0		0.08
	Swimming	0.29	−0.12	−0.70*	1.0	0.06
Pituophis catenifer	LU	1.0				0.79*
	Concertina	−0.53*	1.0			0.11
	Arboreal	0.30	−0.28	1.0		0.08
	Swimming	0.24	−0.07	−0.05	1.0	−0.14
Thamnophis sauritus	LU	1.0				0.30
	Concertina	0.12	1.0			0.19
	Arboreal	0.24	−0.10	1.0		0.15
	Swimming	0.77*	0.49*	0.46*	1.0	0.64*
Nerodia sipedon	LU	1.0				0.20
	Concertina	0.05	1.0			0.18
	Arboreal	0.14	−0.11	1.0		−0.09
	Swimming	0.52*	−0.02	−0.62*	1.0	0.69*

Note: LU = lateral undulation. *$P < 0.05$.

Table 7. Partial correlations between endurance of three modes of limbless locomotion in five species of snakes

Species	Mode of locomotion	LU	Concertina
Pantherophis guttatus	LU	1.0	
	Concertina	0.78*	1.0
	Swimming	0.56	0.38
Pantherophis alleghaniensis	LU	1.0	
	Concertina	0.33	1.0
	Swimming	0.11	0.08
Pituophis catenifer	LU	1.0	
	Concertina	0.83*	1.0
	Swimming	−0.06	0.18
Thamnophis sauritus	LU	1.0	
	Concertina	0.61*	1.0
	Swimming	0.20	0.11
Nerodia sipedon	LU	1.0	
	Concertina	−0.04	1.0
	Swimming	0.44	0.08

Note: LU = lateral undulation. *$P < 0.05$.

Locomotor performance trade-offs

Partial correlations of intraspecific relationships among modes of locomotion for speed and endurance revealed few trade-offs (Tables 6, 7). Significant negative relationships were found only between arboreal and swimming speeds for *P. alleghaniensis* and *N. sipedon*; and between lateral undulation (LU) and concertina speeds for *Pit. catenifer* (Table 6). Although most comparisons showed no significant relationships among modes, there were five positive relationships among modes of locomotion for speed, and three positive relationships among modes of locomotion for endurance (Tables 6, 7). Most notably, there were significant positive relationships between LU and swimming speeds in three species (Table 6) and between LU and concertina endurance in three species (Table 7). Additionally, there were no trade-offs between speed and endurance for any condition (Table 6). Instead, speed and endurance were either not related or else positively related.

DISCUSSION

My primary goal in this study was to start with Arnold's (1983) paradigm and examine the role of body morphology and habitat use on variation in locomotor performance of different modes of limbless locomotion. Relationships between morphology and performance differed among species. Interspecific variation in performance among modes of locomotion was, in turn, influenced by habitat (i.e. substrate) usage and species' natural history. Moreover, this interspecific variation led to some negative (i.e. trade-off) and positive relationships in performance between modes of locomotion.

Morphology and locomotor performance

My results are in line with those of previous studies (i.e. that certain morphological traits have a marked influence on locomotor performance). Results from many studies indicate that larger (both mass and SVL) snakes perform better than smaller ones during terrestrial lateral undulation (Arnold and Bennett, 1988; Plummer, 1997) and during swimming (Aubret *et al.*, 2005; Hopkins and Winne, 2006). But, to my knowledge, the present study is the first to look at the relationships between body size and shape and performance of additional modes of limbless locomotion.

Covariation among measured morphological traits revealed two body types that influenced performance differently among modes and species. First, snakes that were longer and thicker (i.e. cross-sectional area at mid-body) relative to mass with fewer vertebrae had the largest effect on the speeds of all modes of locomotion studied. However, the modes of locomotion in which this morphological type was positively correlated differed among species, making generalizations difficult. This body type was positively related to speed during frequently used modes of locomotion in most of the species examined and for all species combined (Table 3). The finding that both relative length and mid-body circumference contribute mostly to this body type in the PCA is puzzling because species that have relatively narrow habitat usages often possess either relatively long and thin or short and thick bodies for living in arboreal or terrestrial habitats, respectively (Greene, 1997). Thus an interspecific trade-off may exist between length and thickness depending on the habitat being traversed. The utilization of less specialized species for this study may have complicated the relationship between length and thickness. Intraspecifically, possessing both increased relative length and thickness could enhance speeds in species with more generalist body types. Longer individuals have more opportunities for pushing off, gripping, and balance while increased thickness is indicative of more muscle mass capable of more force.

The longer and thicker body type was positively related to arboreal speeds in both species known to be excellent climbers (*P. alleghaniensis* and *P. guttatus*). A longer body can form more alternating loops around a branch. This should improve arboreal performance by enhancing stability and increasing balance when moving across perches, all the while providing more opportunities to produce force (Astley and Jayne, 2007; Pizzatto *et al.*, 2007; Gerald *et al.*, 2008). However, despite there being a relationship for all species combined, the finding that this body type improved arboreal performance in only two species indicates that other factors also play a significant role in determining arboreal speeds (Table 3).

The aforementioned body type was also positively related to swimming speeds in the semi-aquatic *N. sipedon* (as well as two other species), to terrestrial lateral undulation in two species, and to concertina speeds in the bullsnake (*Pit. catenifer*). Snakes with longer bodies and fewer vertebrae relative to length should attain faster speeds resulting from the presence of larger (in terms of cross-sectional area) and longer epaxial muscles that produce the strong unilateral muscle activity needed for lateral bending (Jayne, 1988b; Moon and Gans, 1998; Moon, 2000).

The results highlight a second body type worth special mention. This one possesses thicker ventral scales and more vertebrae relative to mass. This type is related to size-relative speeds of only three modes in two species (Table 3). Most notably, this type was positively related to arboreal speeds in the watersnake (*N. sipedon*), a species known to climb vegetation so as to bask on branches overhanging water (Ernst and Ernst, 2003). This suggests a potential performance trade-off between swimming and arboreal performance in *N. sipedon*

because the longer morphological type was related to increases in swimming speeds. For both body types, the interspecific variation observed in the relationship between morphology and speeds indicates that potential morphological adaptations interact with other factors to determine the locomotor performance capabilities of different species.

Differences in locomotor performance among modes of locomotion

All species studied exhibited the fastest speeds during swimming, followed by terrestrial lateral undulation. Meanwhile snakes moved most slowly during concertina and arboreal locomotion (Table 3). Previous studies have also found that most snakes swim much faster than when they move on land (Finkler and Claussen, 1999; Shine *et al.*, 2003; Gerald and Claussen, 2007; Isaac and Gregory, 2007). Snakes probably use the same muscles to move in water and on land (lateral undulation). However, the functional roles of each epaxial muscle may be different in water and land (Gillis and Blob, 2001). So snakes are likely able to achieve faster speeds while swimming than while moving on land because of the drastic reduction in friction involved in moving a buoyant, streamlined body through water, and because, when swimming, they have more lateral surface area to push against the surrounding medium.

Studies comparing performance of modes other than terrestrial lateral undulation and swimming are scarce. Gerald and Claussen (2007) found that concertina velocities of neonate brown snakes (*Storeria dekayi*) were much lower than those of lateral undulation and swimming. This is not surprising because of the stop-and-go nature of concertina motion (Jayne and Davis, 1991) and its high energetic cost (Walton *et al.*, 1990). I also expected slow arboreal speeds because, despite this mode involving a combination of undulatory and concertina movements (Astley and Jayne, 2007), snakes must move while simultaneously maintaining their balance.

Two species (*Pit. catenifer* and *N. sipedon*) exhibited concertina speeds that were significantly higher than their arboreal speeds. Because concertina speeds tend to decrease as tunnel width relative to maximum body width decreases (Jayne and Davis, 1991; Gerald and Claussen, 2007) and because arboreal speeds can be affected by perch diameter (Astley and Jayne, 2007; Gerald *et al.*, 2008), one should be careful when comparing performance of these two modes of locomotion among studies.

Variation in endurance among modes of locomotion and species was substantial, making mean differences difficult to detect. Because of the variation in behavioural reactions to being chased, individuals may not have been exhausted at the conclusion of each trial. And sometimes individuals would become stationary and coil their bodies to strike at the stimulus instead of utilizing the flight behaviours needed to measure endurance (Brodie, 1993). Snakes may not have been exhausted during these trials, since shifts in anti-predator strategies can depend on a number of different factors associated with the likelihood of the snake surviving the predation attempt (Hertz *et al.*, 1982).

Substrate use and locomotor performance

During this study, species varied in their use of terrestrial, arboreal, and aquatic substrates in ways that mostly reflected published habitat associations. For example, the terrestrial *Pit. catenifer* spent the most time (98%) on the ground, while the semi-aquatic *N. sipedon* spent the most time (19%) in water. Use of the perch was dominated by the two semi-arboreal species (*P. alleghaniensis* and *T. sauritus*). Interestingly, neither performance of terrestrial lateral undulation nor concertina locomotion was significantly related to the

use of terrestrial substrates in any species. Time spent in water was positively related to swimming endurance in *P. guttatus*, *Pit. catenifer*, and *T. sauritus*, and related to swimming speeds in *T. sauritus*. Arboreal speeds were related to perch use in *P. guttatus*, *P. alleghaniensis*, and *N. sipedon*, all of them known to climb often in nature (Ernst and Ernst, 2003). Therefore, in some species, individuals that more often swim perform better at swimming while those that use arboreal substrates are often better at arboreal locomotion.

Variation among species in size-relative maximal speeds mostly mirrored substrate use of each species (Table 4). However, when examining average speeds for all species combined, the relationship between speed and substrate use was significant in only one case (aquatic; Fig. 2). Most likely the small sample size (five species) accounts for the lack of significance in other cases.

Aubret and Shine (2008) showed that tiger snakes (*Notechis scutatus*) exhibit locomotor plasticity after being reared in one of three conditions (terrestrial, arboreal, and aquatic), with snakes increasing performance in modes of locomotion most often experienced during rearing. In the present study, all individuals of all species, except for the semi-aquatic *N. sipedon*, were captive-raised with unknown rearing conditions. Perhaps because they were wild-caught, *N. sipedon* were superior swimmers because they inhabited aquatic habitats prior to the experiment, whereas the other species' aquatic usage was artificially limited. This argument cannot be made for the relationship between arboreal use and arboreal locomotion, since the superior climbers were likely maintained in environments with limited climbing opportunities similar to the other species. Consequently, superior arboreal performance likely results from morphological or physiological traits that increase efficiency of movement in arboreal habitats. It is unclear why there was no relationship between terrestrial use and locomotion. A study examining this relationship using a larger number and variety of species might better evaluate this potential relationship.

In lizards, locomotor performance correlates with habitat use (Irschick and Jayne, 1998, 1999; Irschick and Garland, 2001; McElroy *et al.*, 2007), which likely represents selection for traits that improve locomotion in that habitat. In snakes, few studies have shown that variation in locomotor performance is related to qualitative differences in ecology. Scribner and Weatherhead (1995) and Isaac and Gregory (2007) provide some exceptions using *N. sipedon* and the genera *Natrix* and *Thamnophis*.

The present findings indicate that habitat experiences and usage can impact locomotor performance across multiple modes of locomotion, usually enhancing more frequently used modes. Moreover, my results support the hypothesis that continued use of a restricted set of habitats leads to increased performance in these habitats, which, in turn, leads to increased preferences for the habitats that permit effective movement, resulting in a positive feedback loop (Aubret and Shine, 2008). The influence of habitat experiences and preferences on snake locomotor performance across modes of locomotion could have evolutionary consequences. These might have been a contributing factor during the evolution of limb reduction in early squamates. More detailed studies investigating the roles of both experience and habitat use on the mechanisms resulting in plasticity in performance might be helpful in shedding more light on questions related to the evolution of limblessness.

Locomotor performance trade-offs

Cundall (1987) reviewed the suggestion that snakes cannot simultaneously maximize performance across multiple modes of locomotion because biomechanical adaptations that

enhance each mode can conflict. For example, several investigators hypothesized that snakes will exhibit a trade-off in locomotor performance between terrestrial lateral undulation and swimming because of differences in the kinematic and muscle activity requirements needed to move a limbless body on land versus water (Jayne, 1986; Cundall, 1987; Shine *et al.*, 2003). However, when comparing performance among modes of locomotion within each of the five species studied, only three comparisons showed a trade-off (out of 45 total comparisons; Tables 6, 7). It should be noted that the findings could also result from the elevated risk of Type I errors due to the large number of comparisons. However, I detected trade-offs between arboreal and swimming speeds in *P. alleghaniensis* and *N. sipedon*, species that are semi-arboreal and semi-aquatic, respectively. This suggests that trade-offs may be more detectable in species that are more specialized for one particular mode of locomotion (i.e. habitat specialists).

Most comparisons between modes of locomotion resulted in either positive (8 of 45 comparisons) or non-significant (34 of 45 comparisons) relationships (Tables 6, 7). Terrestrial lateral undulation and swimming were positively correlated in three species. Other studies have found that lateral undulation on land and lateral undulation in water either are not related or are positively related in several snake species (Finkler and Claussen, 1999; Shine and Shetty, 2001; Gerald and Claussen, 2007; Isaac and Gregory, 2007). Contrary to predictions, results indicate that snakes actually can simultaneously maximize performance of lateral undulation on land and in water despite biomechanical differences.

There is limited information about potential trade-offs between concertina and other modes of limbless locomotion. Because of the kinematic differences of concertina compared with the other modes, and because concertina uses up so much energy (Walton *et al.*, 1990), adaptations that favour increasing concertina performance might conflict with those that enhance other modes of locomotion. Gerald and Claussen (2007) observed no correlations between concertina locomotion and either terrestrial lateral undulation or swimming in neonate *Storeria dekayi*. In the present study, I detected a trade-off between the speeds of concertina and lateral undulation only in bullsnakes (*Pit. catenifer*), indicating that trade-offs are usually not present between these two modes of locomotion.

Having found trade-offs in only three comparisons (7% of all comparisons), I suggest that the underlying mechanisms that optimize locomotion across multiple modes do not usually conflict. Alternatively, because I made intraspecific comparisons, differences in individual quality resulting from characteristics such as physical fitness, health, motivation, or nutrition may have made it more difficult to achieve statistical significance (Huey and Hertz, 1984; Wilson *et al.*, 2014). Because some individuals might have exhibited superior performance during all modes of locomotion for the aforementioned reasons, one must be cautious when inferring evolutionary patterns from these results (Huey and Hertz, 1984). That said, the data do suggest that species that are not habitat specialists are locomotor generalists (i.e. capable of moving well during most modes of locomotion). Though the species studied here varied in their habitat usage, none could be considered habitat specialists. Studies are required that examine specialist species and utilize interspecific comparisons to tease apart how mechanisms that maximize multiple modes can potentially conflict.

Lastly, previous studies found trade-offs between speed and endurance for muscles *in vitro* due mostly to physiological differences in muscle fibre types (Rivero *et al.*, 1993; Wilson *et al.*, 2002). Thus I expected a speed–endurance trade-off at the whole-animal performance level. Instead, speed and endurance were either not related or else positively related for all modes and species (Table 6). This is in line with other studies that failed to detect trade-offs

between speed and endurance at the whole-animal level (Ford and Shuttlesworth, 1986; Jayne and Bennett, 1990; Secor *et al.*, 1992; Wilson *et al.*, 2002). Although the reasons for the lack of a trade-off are unclear, inter-individual variation in the physiological support systems involved in power production and endurance, outside of muscle fibres, could amplify variation in whole-animal performance.

CONCLUSIONS

Performance of each mode of locomotion in snakes is a result of many factors, including morphology, underlying physiology (e.g. muscle fibre type and recruitment), underlying biochemistry (e.g. plasticity of enzyme activities), and behaviour. These factors are, in turn, influenced by snakes' earlier experiences of various modes of locomotion and habitats, these being determined by a species' natural and evolutionary histories. The present study found that both morphology and habitat use interact to define maximal locomotor speeds across multiple modes. Yet, it is difficult to tease apart the influence of morphological variables from that of habitat usage. Also, increased performance during one mode of locomotion usually did not hinder performance of other modes (i.e. no trade-offs). The results also support the notion that the limbless body plan appears to be well suited for movement and radiation into a variety of different habitats. Future studies should further investigate such factors as feeding frequencies and strategies, and other morphological variables across a wider range of species to further clarify the relationships between morphology, habitat use, and locomotor performance.

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