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# The Role of Morphology in the Locomotor Performance of Arboreal Snakes

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UNIVERSITY OF MIAMI

THE ROLE OF MORPHOLOGY IN THE LOCOMOTOR PERFORMANCE OF  
ARBOREAL SNAKES

By

Ronald C. Rozar

A DISSERTATION

Submitted to the Faculty  
of the University of Miami  
in partial fulfillment of the requirements for  
the degree of Doctor of Philosophy

Coral Gables, Florida

August 2010

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The Role of Morphology in the Locomotor  
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Adaptation is difficult to directly demonstrate. However, the role that a morphological character, or suite of characters plays in the fitness of a species can be elucidated by examining the intermediate link between morphology and fitness – performance. Linking morphology to performance, and then performance to fitness can demonstrate the adaptive significance of a morphological character. Arboreal snakes possess a suite of characteristic morphological traits that differentiate these snakes from their terrestrial counterparts, and these characteristic traits have been presumed to be of an adaptive nature. To determine if these characteristic traits are of an adaptive nature I have taken eight closely related snake species pairs – one highly arboreal and one highly terrestrial – and compared the pairs' locomotor performance. Each pair was evaluated in their arboreal locomotor performance capabilities: climbing endurance, vertical sprint speed, gap bridging, and the traversing of narrow diameter objects. Likewise, each pair was evaluated in their terrestrial locomotor performance capabilities: crawling endurance and horizontal sprint speed. With few exceptions, arboreal snakes outperformed their terrestrial counterparts in arboreal tasks, while terrestrial snakes outperformed their arboreal counterparts in terrestrial tasks. These findings indicate that functional locomotor trade-offs have occurred with the evolution of arboreality in snakes. That is, arboreal snakes have forfeited proficiency in the terrestrial plane for increased

performance in the discontinuous arboreal substrate. Furthermore, these same locomotor trade-offs have occurred across each familial line examined. The implications of these findings are great. With the decimation of forested habitats the world over, arboreal snakes would appear ill-suited to the resulting deforested terrestrial habitats. Forced into the terrestrial plane, arboreal snakes would be less able to compete with terrestrial snakes for resources and evade predators. The conservation concerns are self-evident. Now that it has been shown that morphology is linked to performance in snakes, the next stage of inquiry is to determine if performance is linked to fitness, and if so, show that the characteristic morphology of arboreal snakes is in fact an adaptation for life in the trees.

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## CHAPTER 1 INTRODUCTION

Adaptation is a word which is often used too liberally. Adaptation by definition is an evolved trait or set of traits that bestow upon their possessor an increase in fitness. Many traits appear to have an adaptive significance that seems obvious. For example, few would argue that the morphology of a whale, which diverges greatly from the morphology of a terrestrial mammal, represents an adaptation to a marine existence. Yet, as Gould and Lewontin (1979) asserted, the adaptive value of a trait should not be accepted simply because it is plausible. A case in point can be found with giraffes. For over 100 years it was accepted that the elongated neck of the giraffe was an adaptation for feeding at heights not assessable to sympatric browsers (Simmons and Scheepers, 1996). However, this assumption does not accord with their actual feeding behavior: Giraffes largely forage at shoulder height, a height assessable to some of their browsing competitors (Young and Isbell, 1991). Instead of being an adaptation to feeding at novel heights, examination revealed that elongated necks serve to aid in male to male combat and intimidation (Pratt and Anderson, 1985; Simmons and Scheepers, 1996). Furthermore, that a trait exists does not necessarily make it adaptive (Brooks and McLennan, 1991). Tiger salamanders (*Ambystoma tigrinum*) vary widely in color and pattern throughout their range (Behler and King, 1979). Variation in color and pattern may represent adaptations to local environments, but could also be the result of neutral mutations becoming fixed within populations. If color and pattern variation were the result of neutral mutations, these traits would not represent an adaptation at all since the traits did not confer an increase in fitness. In short, before being considered as

adaptations, traits must be rigorously tested to show a correspondence to increased fitness.

Organismal performance provides a bridge between morphological traits and fitness. Arnold (1983) codified a means by which morphology could be linked to fitness through performance. In this context, terms are carefully defined: “morphology” represents behavioral, physiological, and structural attributes, “performance” represents whole organism capability for a specific task, and “fitness” represents the number of surviving offspring produced over a lifetime (Emerson and Arnold, 1989). To assess if a trait was adaptive, Arnold (1983) asserted that analyses must be performed in two steps, first examining how morphology influences performance and then examining how performance influences fitness. In the morphology → performance → fitness paradigm, morphology and performance are linked by virtue of the constraints that morphology imposes on performance. Many examples clearly define a relation between performance and morphological traits. Cane toads (*Bufo marinus*) cannot jump as far, as high, or as quickly as leopard frogs (*Rana pipiens*) due to the cane toads’ larger body mass, shorter hindlimbs, shorter hindlimb extensor muscles, and lesser isometric contractile properties in those hindlimb extensor muscles (Chadwell et al., 2002). Ducks cannot dive as well as penguins because penguins have solid bones, a streamline form, and forelimbs which have been modified into flippers – traits that reduce buoyancy and the energetic demands of diving (Butler, 2000). Primates lacking a prehensile tail and a hallux capable of grasping cannot maneuver through arboreal habitats as well as those primates possessing these traits (Cartmill, 1974). The argument that form is linked to function has been generally well supported.

Performance is linked to fitness by virtue of an organism's ability to accomplish task necessary for survival and reproduction. In performance → fitness studies, performance most often has been viewed in terms of locomotor performance, because locomotion is often quantifiable and because locomotion plays crucial roles in capturing prey, escaping predators, securing mates, dispersing, and so on (Pough, 1989). For example, garter snakes (*Thamnophis sirtalis fitchi*) that exhibit greater burst speed were found to have greater survivorship (Jayne and Bennett, 1990).

While linking performance to fitness is essential to demonstrating adaptation, examinations may not be straightforward in practice, particularly when morphological traits (and by extension performance capabilities) are compared without regard to phylogenetic relationships. Losos and Miles (1994) eloquently illustrated the problem of ignoring historical information in their consideration of the relationships between invariant clutch size and lamella-bearing subdigital pads in lizards. Minimally, 89% of all lizards with invariant clutch sizes also possess lamella-bearing subdigital pads. Superficially the relationship between invariant clutch size and pads would appear tightly linked. However, the relationship exists because of two clades, the geckos (>850 species) and the anoles (>300 species) that possess both traits. In fact, invariant clutch size has evolved at least 20 times among lizards without pads. Thus in a phylogenetic context there is little support to link the two traits. It is thus clear that an awareness of phylogenetic relationships is critical.

Meaningful comparisons in comparative biology come at points of character transitions (Harvey and Pagel, 1991). Examinations along a phylogenetic branch at the point where a character state transitions from the basal to derived condition can be quite

informative because other variables that are shared by congeners are held constant. When examinations are made irrespective of phylogeny the variables that differ among taxa can confound the investigation and prevent the distinguishing of evolutionary cause and effect. Thus, comparing traits of basal taxa to derived taxa represents valid and statistically independent comparisons. This comparative approach has been used in studies on an increasing number of taxa including lizards (Losos, 1990; Glor et al., 2003), snakes (Greene, 1992), and fish (Wainwright and Lauder, 1993; Westneat, 1995). Comparisons at character transition points provide the best means of interpreting evolutionary change.

Snakes provide ideal model systems for using comparative biology to assess morphology, performance and fitness. Worldwide there are over 2,700 species of snakes (Pough et al., 1998), and their phylogenetic relationships are becoming increasingly clear. Snakes are found in almost all habitat types, in nearly all parts of the globe, implying a range of adaptations. Snakes also have divergent morphologies which have been associated with specific habitat types (Guyer and Donnelly, 1990).

Unique among the snakes are the morphologies of arboreal snakes (Lillywhite and Henderson, 1993). Highly arboreal snakes possess a suite of morphological and physiological characters (relative to their terrestrial counterparts) that seem to be associated with an arboreal existence. These characters transcend familial boundaries, thus suggesting evolutionary convergence in response to similar environmental challenges. Arboreal snakes have high length to mass ratios (Guyer and Donnelly, 1990) which is thought to facilitate movement through a discontinuous substrate that often provides little support. Arboreal snakes have a more anterior placement of the heart

(Seymour, 1987), which has been suggested to be a means of maintaining cephalic blood flow during upright postures (Lillywhite, 1987). Arboreal snakes have a lesser heart displacement during upright postures which minimizes the decrease in cardiac output (Young et al., 1997). They have a tighter attachment of the skin to the underlying tissues (Jayne, 1988), and their tissue compartments are relatively non-compliant (Lillywhite, 1993). These modifications aid in the prevention of blood pooling and endema during vertical locomotion. Jayne (1982) noted that arboreal colubroids had longer segmental lengths of semispinalis-spinalis muscle tissue than did terrestrial or aquatic colubroids. Longer muscle tissues should increase the lever arm with which the muscle acts, and in doing so convey a mechanical advantage. Such a mechanical advantage might heighten a snake's ability to support its weight and locomote through a discontinuous substrate. Vertebral architecture has been shown to be distinctive in arboreal snakes (Johnson, 1955). The vertebral column is highly flexible, yet bony reinforcements of the floor of the osteofascial tunnel prevent the downward displacement of epaxial muscles during flexion. This allows the snake to maintain body rigidity while spanning gaps in the substrate (Jayne and Riley, 2007). The trailing ends of each ventral scale of an arboreal snake are bent sharply upwards. These scales are capable of being shifted forward in successive waves (Bogert, 1953) which allows for the exploitation of surface irregularities during climbing. In contrast, the ventral scales of terrestrial snakes are rounded on the ends and incapable of being shifted forward in waves. These differences between arboreal and terrestrial snakes raise questions concerning the adaptive significance of these differences, and thus provide intriguing opportunities for comparative studies.

To evaluate the idea that differences in morphology are related to differences in locomotor performance, my dissertation first compares relative locomotor performance of arboreal tasks of arboreal and terrestrial snakes. The differences in three-dimensional structure of arboreal and terrestrial habitats suggest that contrasting selective forces are acting upon locomotor performance in these two types of habitat (Lillywhite and Henderson, 1993). Arboreal habitats are characterized by a discontinuous, often narrow substrate, which is in stark contrast to the mostly continuous, broad substrate of terrestrial habitats. Key to locomotion through a discontinuous, narrow substrate is the ability to bridge gaps and traverse narrow diameters. How well a snake can bridge gaps and traverse narrow diameters determines how much of the arboreal habitat can be exploited, and directly impacts fitness-related activities such as prey acquisition and predator avoidance. Under the adaptationist argument, the evolutionary transition from a terrestrial to an arboreal existence (Vidal and Hedges, 2004) is predicted to produce adaptive shifts whereby different locomotor tasks such as gap bridging and the ability to traverse narrow diameters result in differential locomotor abilities. In this study, the ability to perform these tasks was quantified for eight species pairs of snakes. Each pair was designed to compare a species which has unambiguously evolved arboreal habits with a close relative (outgroup) that maintains a terrestrial habit. Each species pair represents a phylogenetic character transition point whereby an arboreal habit diverges from a terrestrial habit. Current phylogenies allow for the comparison of eight species pairs which span four families. The goal of this examination was to determine if the morphological differences between arboreal and terrestrial snakes have consequences for locomotor performance. These comparisons allow me to evaluate the idea that the



evolutionary transition from terrestriality to arboreality produces the same performance outcomes.

The next assessment was designed to distinguish between two possible performance outcomes: a trade-off involving optimization of either climbing or crawling ability, or reasonable performance in both tasks. These studies assessed the actual climbing and crawling performances to determine if the degree to which climbing and crawling proficiency differs between the eight paired species. At issue is whether proficiency in one locomotor task results in decreased proficiency in a divergent task. Since performance cannot be simultaneously optimized for two tasks that require mutually incompatible morphologies (Shine et al., 2003), will those species that climb well crawl poorly relative to the other member of their species pair? Does the characteristic morphology of the arboreal snakes constrain their terrestrial performance and produce a locomotor performance trade-off whereby mastery of one locomotor task is achieved at the expense of proficiency in another task? The two possible performance outcomes—a tradeoff versus a varied ability- has important implications for the ecology of these animals. With anthropogenic habitat alteration rapidly converting arboreal habitats into terrestrial ones, existence of a locomotor performance trade-off that sacrifices terrestrial for arboreal performance would be maladaptive for many arboreal species.

My dissertation concludes with a synthesis of the results of the locomotor performance experiments, providing a lucid picture of how arboreal and terrestrial snake morphologies are related to arboreal and terrestrial locomotor performance. If morphology dictates performance, then the divergent morphologies of arboreal and

terrestrial snakes should produce locomotor performance trade-offs. Arboreal snakes should outperform terrestrial snakes in arboreal tasks, and terrestrial snakes should outperform arboreal snakes in terrestrial tasks. However, if morphology does not underlie performance, then little or no difference should be observed between the locomotor abilities of arboreal and terrestrial snakes. While performance optimization may be expected, performing reasonably well over a diverse range of tasks has the advantage of broadening a species ecological niche. Under some selective regimes a broad ecological niche can lead to greater fitness. The ramifications of my findings are deliberated in a current ecological context. Future avenues of research are considered with an emphasis placed upon completing the morphology → performance → fitness paradigm, namely determining if a link exist between locomotor performance and fitness in arboreal species. In all, what does morphology tell us about locomotor performance, and what can locomotor performance tell us about fitness.

The work presented in this dissertation represents the fulfillment of the first half of the morphology → performance → fitness paradigm. Linking morphology to performance is the crucial first step to ultimately linking morphology to fitness. Only with a link to fitness can the divergent morphologies of snakes be considered adaptations.

**CHAPTER 2**  
**BRIDGING GAPS AND TRAVERSING NARROW SURFACES: THE**  
**LOCOMOTOR PERFORMANCE ABILITIES OF ARBOREAL AND**  
**TERRESTRIAL SNAKES**

An animal's morphology can limit the extent to which critical locomotor tasks can be performed (Emerson and Arnold, 1989). The limitations imposed by morphology constrain the range of tasks that can be performed with high proficiency (Arnold, 1983) because locomotor performance cannot be optimized for multiple tasks that require mutually incompatible morphology (Shine et al., 2003). For example, domestic dogs (*Canis lupus familiaris* L.) artificially selected for high-speed running have long, slender limbs optimized for the storage and recovery of elastic strain, whereas dogs artificially selected for combat have short, stout limbs optimized for high force production (Kemp et al., 2005). The disparate morphology required for high speed running and high proficiency fighting necessarily make great combatants poor sprinters, and great sprinters poor combatants. Morphology represents a filter determining what tasks can be performed and how well those tasks can be performed. Understanding how morphology relates to performance is the first step to discerning how morphology relates to fitness and thus the adaptive nature of morphology.

Natural selection acts to produce a continuum of performance abilities ranging from generalist and specialist (Futuyma and Moreno, 1988). Generalists are those species that sacrifice optimization in a narrow range of tasks for reasonable performance throughout a broad range of tasks. Reasonable performance over a broad range of tasks can broaden the ecological niche of a species and allow for the maintenance of fitness over varied environmental conditions. Conversely, specialists optimize performance for

specific tasks which in turn decreases performance in other tasks. Specialists exhibit great fitness within a narrow ecological niche. Locomotor performance generalists or specialists result from selection acting upon the morphology possessed by those animals.

One example in which the generalist/specialist paradigm relates performance to habitat is arboreal snakes. The three-dimension structure of arboreal habitats brings about unique selective pressures that are expected to produce specialized arboreal morphology. Arboreal habitats are characterized by a discontinuous, often narrow substrate, which is in stark contrast to the mostly continuous, broad substrate of terrestrial habitats. The arboreal habitat has relatively narrow surfaces interspaced by sometimes appreciable gaps. Key to locomotion through a discontinuous, narrow substrate is the ability to bridge gaps and traverse narrow diameter surfaces. How well an animal can bridge gaps and traverse narrow diameter surfaces determines how much of the arboreal habitat can be exploited, and directly impacts fitness-related activities such as prey acquisition and predator avoidance. Thus, to cope with the locomotor challenges imposed by the arboreal habitat, specialized morphology would be predicted with highly arboreal species.

Arboreal snakes are a group that exhibit specialized morphology. The morphology of arboreal snakes differs markedly from that of terrestrial snakes. Highly arboreal snakes possess a suite of morphological and physiological modifications (relative to their terrestrial counterparts) that suggest a specialization to an arboreal existence. These modifications are found across family lines, thus suggesting evolutionary convergence to meet similar environmental challenges. Arboreal snakes have high length to mass ratios (Guyer and Donnelly, 1990) which is thought to facilitate

movement through a discontinuous substrate that often provides little support (Jayne and Riley, 2007). Arboreal snakes have a more anterior placement of the heart (Seymour, 1987), which has been suggested to be a means of maintaining cephalic blood flow during upright postures (Lillywhite, 1987; Seymour and Arndt, 2004). Arboreal snakes have a lesser heart displacement during upright postures which minimizes the decrease in cardiac output (Young et al., 1997). A tighter attachment of the skin to the underlying tissues has been observed with arboreal snakes (Jayne, 1988), and tissue compartments are relatively non-compliant (Lillywhite, 1993). These modifications are thought to aid in the prevention of blood pooling and endema during vertical locomotion. Jayne (1982) noted that arboreal colubroids had longer segmental lengths of semispinalis-spinalis muscle tissue than did terrestrial or aquatic colubroids. Longer muscle tissues should increase the lever arm with which the muscle acts, and in doing so convey a mechanical advantage. Such a mechanical advantage might heighten a snake's ability to support its weight and locomote through a discontinuous substrate. Vertebral architecture has also been shown to be distinctive in arboreal snakes (Johnson, 1955). The vertebral column is highly flexible, yet bony reinforcements of the floor of the osteofascial tunnel prevent the downward displacement of epaxial muscles during flexion. This allows the snake to maintain body rigidity while spanning gaps in the substrate. The ends of each ventral scale of an arboreal snake are bent sharply upwards and these scales are capable of being shifted forward in successive waves (Bogert, 1953). This allows for the exploitation of surface irregularities during climbing. In contrast, the ventral scales of terrestrial snakes are rounded on the ends and incapable of being shifted forward in waves. The unique

suite of characters possessed by arboreal snakes appears to represent a specialization to life in the trees.

Do the morphological differences between arboreal and terrestrial snakes result in meaningful differences in the ability to perform arboreal tasks? Does each transition from terrestriality to arboreality result in the same degree of ability? To determine if morphological differences in snakes equates to differences in arboreal abilities a comparative approach was undertaken. Snakes that have unambiguously evolved arboreal habits were compared with close relatives (outgroups) that still maintain a terrestrial habit. These species pair comparisons represent an examination of transition points in character state, and thus are ideally suited for addressing evolutionary questions regarding the linkage of morphology and performance.

Since key features to arboreal success in moving through a discontinuous arboreal substrate are bridging gaps and traversing small branches, these abilities were compared between each species pair. The minimum surface diameter that can be traversed directly relates to how much of the arboreal habitat is available to be exploited. Bridging gaps and traversing narrow diameter surfaces are both performance tasks that are ecologically relevant and expected to directly relate to the fitness of a species. This evaluation determines if the unique morphology of arboreal snakes allow for greater performance in arboreal tasks relative to terrestrial snakes. This study will show if a link exists in snakes between morphology and performance relating to arboreality. Determining if such a link exists is the initial step in testing the hypothesis that the morphology of arboreal snakes is an adaptation to an arboreal existence.

## Methods

### *Rationale*

The goal of this study was to compare the locomotor performance in arboreal and terrestrial snakes with respect to each environment. To accomplish this goal, closely related arboreal-terrestrial species pairs were compared in their abilities to perform ecologically relevant locomotor tasks associated with arboreal locomotion: gap bridging and the traversing of narrow diameter surfaces. If the morphology of arboreal snakes is specialized for arboreal locomotion then arboreal snakes should be able to bridge larger gaps and traverse smaller diameter surfaces than their terrestrial counterparts. If no difference (or a negative correlation) exists in the arboreal locomotor abilities of arboreal and terrestrial snakes then the evolutionary genesis of arboreal snake morphology must be reconsidered.

### *Study species*

Sets of closely related species pairs, one arboreal and one terrestrial in habit, were examined (Table 2.1). Individuals were wild-caught with the exception of *Sanzinia madagascariensis*, *Acrantophis dumerili*, *Bothrops alternatus*, and *Proatheris superciliaris*. Animals were housed in appropriately sized, commercially produced enclosures with temperature and humidity adjusted to the needs of the individual species. All trials were performed at ambient temperatures within the operational range for each individual species. Animals were not fed the week before or the week of testing to avoid erroneous results owing to sudden changes in relative mass.

### *Gap Bridging*

The procedures used to measure gap bridging ability roughly followed those of

**Table 2.1.** Arboreal – terrestrial species pairs and number of individuals (N).

Arboreal species (N)	Terrestrial species (N)
<i>Candoia bibroni</i> (7)	<i>Candoia aspera</i> (10)
<i>Epicrates striatus</i> (6)	<i>Epicrates cenchria</i> (11)
<i>Morelia viridis</i> (5)	<i>Python curtus</i> (9)
<i>Sanzinia madagascariensis</i> (5)	<i>Acrantophis dumerili</i> (8)
<i>Dipsadoboa flavida</i> (7)	<i>Crotaphopeltis hotamboeia</i> (8)
<i>Bothriechis schlegelii</i> (7)	<i>Bothrops alternatus</i> (8)
<i>Cryptelytrops albolabris</i> (10)	<i>Ovophis monticola</i> (5)
<i>Atheris ceratophora</i> (14)	<i>Proatheris superciliaris</i> (6)



Lillywhite et al. (2000). Animals were placed on a 40 cm long, 7.6 cm diameter wooden dowel (fig. 2.1). Inserted into this main dowel were 7.5 cm long wooden dowels 1.3 cm in diameter that were on 8 cm centers and orientated vertically and at approximately 45° on either side of vertical midway between the vertical dowel rows. All wooden surfaces were roughened with coarse grade sandpaper. The main dowel was secured to a wheeled cart at a height of approximately 1 m. The main dowel was brought near a platform on which was a plastic hide box. As the snake neared the hide box the main dowel was slowly and steadily pulled away until the snake could no longer support its extended body (fig. 2.2). Upon failure the distance at which the snake had extended its body was measured. The distance extended was measured six times for each individual, three times in succession on each of two days.

The results were used to determine a “cantilever ratio” (Lillywhite et al, 2000). The cantilever ratio (CR) was the horizontal distance that the snake was able to extend its body divided by the snake’s total body length. The mean CR was determined for each species.

#### *Minimum Surface Diameter Traversed*

The ability to cross dowels of various diameter surfaces was used to determine what minimum surface diameter could be traversed by each species. Animals were placed on a dowel 1 m above ground level and coerced across a length of 1.2 m to an artificial tree. Dowel diameters in millimeters were 50.80, 44.45, 38.10, 36.51, 31.75, 28.58, 25.40, 22.23, 19.05, 15.88, 12.70, 9.53, 7.94, 6.35, 4.76, 3.18, and 1.59. All dowels were made of wood with the exception of the 3.18 mm and 1.59 mm dowels which for support reasons were steel. All dowels were roughened with coarse



**Figure 2.1.** Main dowel used during gap bridging trials. The pegged surface was 40.0 cm long and 7.6 cm in diameter. Dowels of 7.5 cm in length and 1.3 cm in diameter were placed on 8.0 cm centers along the main dowel orientated at vertical and approximately 45°.



**Figure 2.2.** Snake bridging a gap.

grade sandpaper. As necessary, a mid-length support was added approximately 3 cm below the dowel to limit dowel flexion during trials with heavier animals.

Dowel diameters were randomly assigned during trials to prevent animals from being “trained” to perform the task as could be the case if presenting dowels in order of decreasing diameter. With the successful crossing of a dowel animals were placed on the next selected diameter less than that already crossed. This procedure was repeated until failure, as defined by falling from the dowel. With three failures the next selected diameter greater than that failed was tested. It should be noted that animals were not tested for 24 hours following a failed attempt. Ultimately the minimum diameter that could be traversed was determined. For those animals able to cross a 1.59 mm dowel, a 1 mm steel wire was strung taut and used for a final trial diameter.

The results were used to determine a “diameter ratio”. The diameter ratio (DR) was the minimum surface diameter traversed divided by the maximum circumference of the snake. The goal of the DR was to relate the surface diameter traversed to the diameter of the snake, however, because there is so much variability associated with snake diameter measurements circumference was used instead. Circumference remains an appropriate metric for gauging the width of a snake. Each snake had circumference measured at 30%, 50%, and 70% SVL with the largest measure being used in calculations. Care was taken to avoid measuring snakes with an obviously inflated lung.

#### *Data analyses*

For each species pair maximum and mean CR were compared using *t* tests. The DR for each species pair was compared using Mann-Whitney Rank Sum tests. Analyses were performed using SigmaStat software.



**Figure 2.3.** Snake traversing a dowel.

## Results

### *Gap Bridging*

Each species pair comparison found the arboreal member having a greater ability to bridge gaps than its terrestrial counterpart as indicated by larger mean CR measures (Table 2.2). *Candoia bibroni* had a significantly greater mean CR than did *C. aspera* ( $t = 5.02, P < 0.001$ ) (fig. 2.4). *Epicrates striatus* had a significantly greater mean CR than did *E. cenchria* ( $t = 5.29, P < 0.001$ ). *Morelia viridis* had a significantly greater mean CR than did *Python curtus* ( $t = 7.38, P < 0.001$ ). *Sanzinia madagascariensis* had a significantly greater mean CR than did *Acrantophis dumerili* ( $t = 4.96, P < 0.001$ ). *Dipsadoboa flavida* had a significantly greater mean CR than did *Crotaphopeltis hotamboiea* ( $t = 4.42, P < 0.001$ ) (fig. 2.5). *Bothriechis schlegelii* had a significantly greater mean CR than did *Bothrops alternatus* ( $t = 9.73, P < 0.001$ ) (fig. 2.6). *Cryptelytrops albolabris* had a significantly greater mean CR than did *Ovophis monticola* ( $t = 13.69, P < 0.001$ ). *Atheris ceratophora* had a significantly greater mean CR than did *Proatheris superciliaris* ( $t = 9.69, P < 0.001$ ).

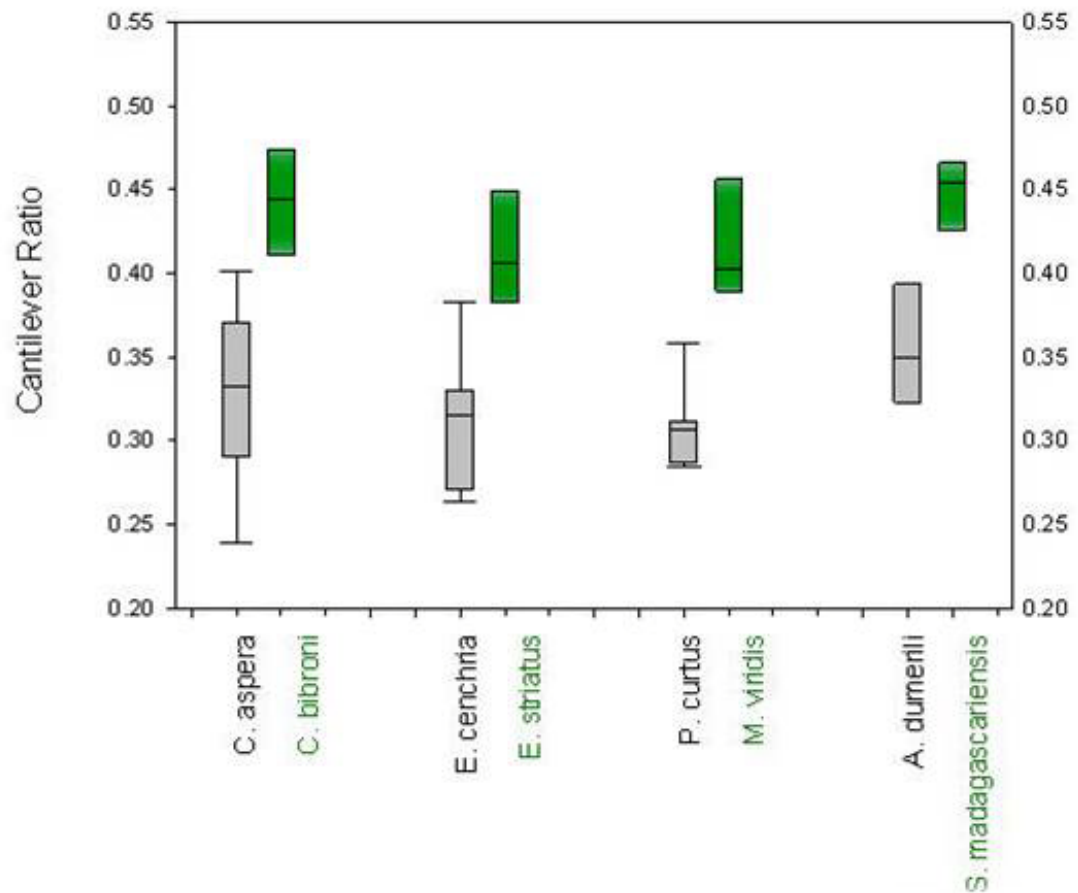
A slight trend was observed where an increase in mean relative mass (mass / total length) resulted in a decrease in CR. The trend was not significant though ( $r = 0.38, P = 0.188$ ) (fig. 2.7).

### *Minimum Diameter Traversed*

Each species pair comparison found the arboreal member able to traverse a smaller diameter than its terrestrial counterpart (Table 2.3). *Candoia bibroni* had a significantly greater DR than did *C. aspera* ( $U = 70, P < 0.001$ ) (fig. 2.8). *Epicrates striatus* had a significantly greater DR than did *E. cenchria* ( $U = 66, P = 0.001$ ). *Morelia*

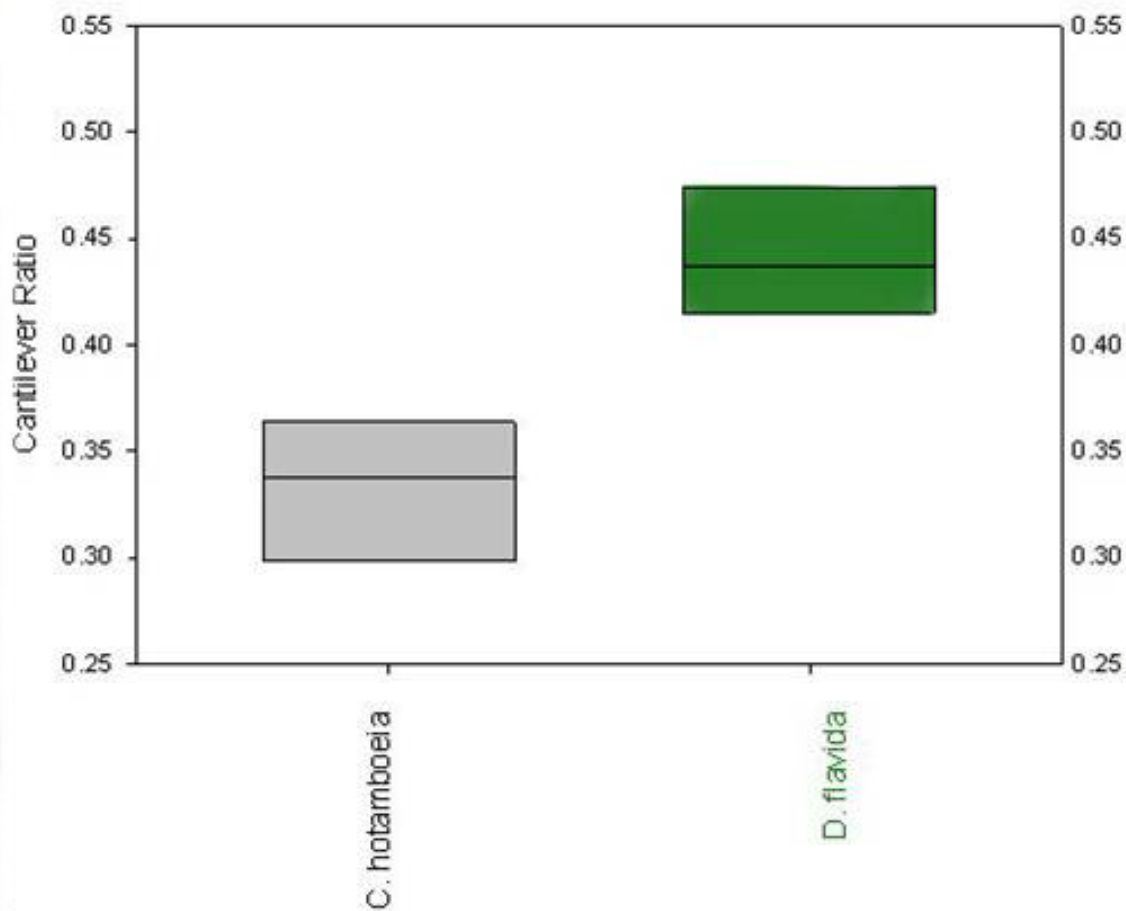
**Table 2.2.** Body mass ratios and cantilever ratios for arboreal and terrestrial species pairs. The cantilever ratio (CR) was the horizontal distance that the snake was able to extend its body divided by the snake's total body length.

Species (N)	Habit	Mass / Total Length g / cm (range)	Mean CR (range)
<b>Boidae</b>			
<i>Candoia bibroni</i> (7)	arboreal	1.00 (0.79-1.62)	0.44 (0.41-0.50)
<i>Candoia aspera</i> (10)	terrestrial	3.47 (0.76-5.34)	0.33 (0.23-0.40)
<i>Epicrates striatus</i> (6)	arboreal	1.64 (0.96-2.80)	0.42 (0.39-0.48)
<i>Epicrates cenchria</i> (11)	terrestrial	2.90 (2.63-3.94)	0.31 (0.26-0.39)
<i>Morelia viridis</i> (5)	arboreal	1.33 (0.87-1.79)	0.42 (0.39-0.47)
<i>Python curtus</i> (9)	terrestrial	3.08 (2.17-4.39)	0.31 (0.28-0.36)
<i>Sanzinia madagascariensis</i> (5)	arboreal	3.55 (0.81-6.60)	0.48 (0.41-0.47)
<i>Acrantophis dumerili</i> (8)	terrestrial	2.03 (1.30-3.64)	0.36 (0.32-0.40)
<b>Colubridae</b>			
<i>Dipsadoboa flavida</i> (7)	arboreal	0.25 (0.24-0.27)	0.45 (0.41-0.52)
<i>Crotaphopeltis hotamboeia</i> (8)	terrestrial	0.74 (0.61-0.98)	0.34 (0.28-0.44)
<b>Crotalidae</b>			
<i>Bothriechis schlegelii</i> (7)	arboreal	1.03 (0.42-2.31)	0.46 (0.43-0.53)
<i>Bothrops alternatus</i> (8)	terrestrial	0.68 (0.51-0.83)	0.30 (0.25-0.34)
<i>Cryptelytrops albolabris</i> (10)	arboreal	0.99 (0.57-1.98)	0.42 (0.40-.044)
<i>Ovophis monticola</i> (5)	terrestrial	1.98 (1.39-2.65)	0.30 (0.28-0.33)
<b>Viperidae</b>			
<i>Atheris ceratophora</i> (14)	arboreal	0.62 (0.40-0.89)	0.46 (0.41-0.51)
<i>Proatheris superciliaris</i> (6)	terrestrial	0.73 (0.64-0.81)	0.35 (0.34-0.37)

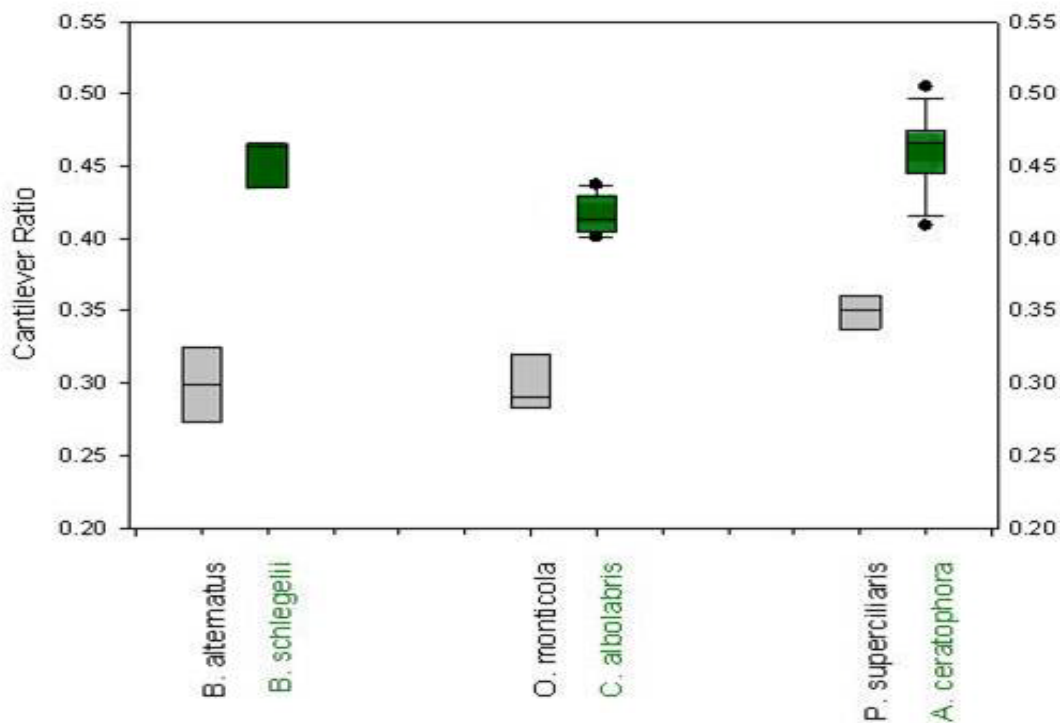


**Figure 2.4.** Cantilever ratios from the species pairs of the Family Boidae. The cantilever ratio was the horizontal distance that the snake was able to extend its body divided by the snake's total body length. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, and non-outlier range values.

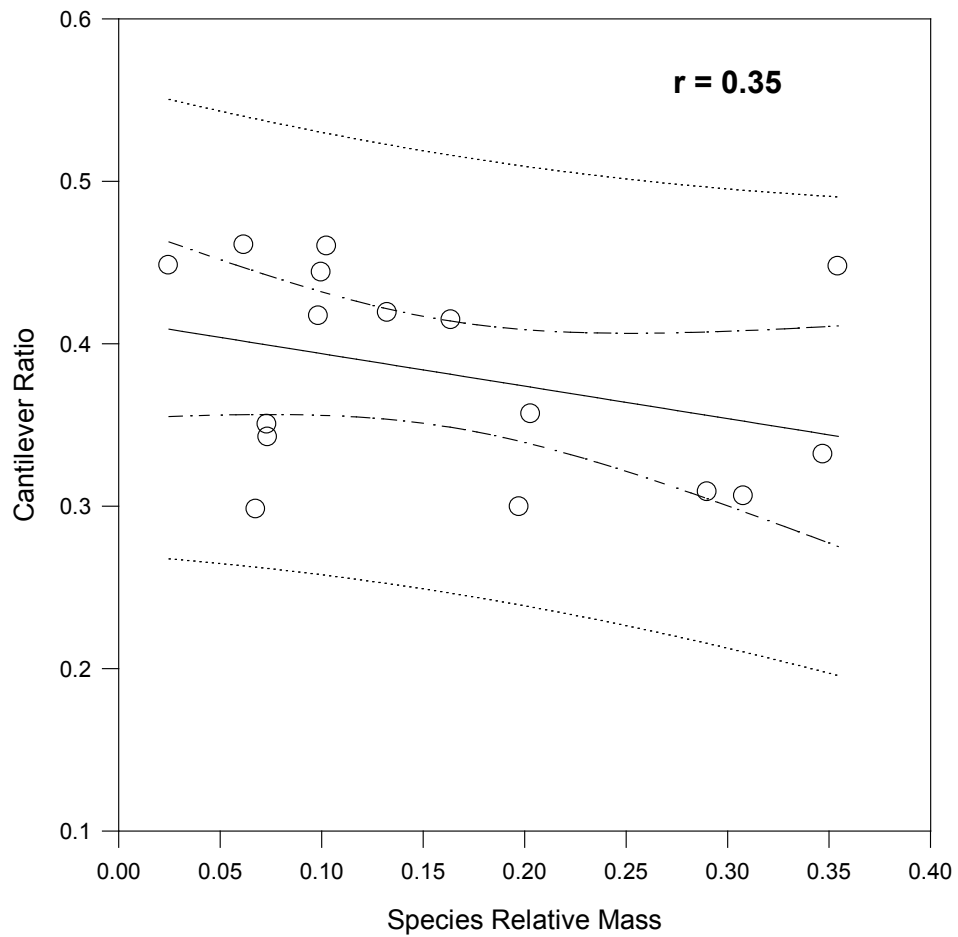




**Figure 2.5.** Cantilever ratios from the species pair of the Family Colubridae. The cantilever ratio was the horizontal distance that the snake was able to extend its body divided by the snake's total body length. The arboreal species is listed in green. Box plots represents median, and upper and lower quartile values.



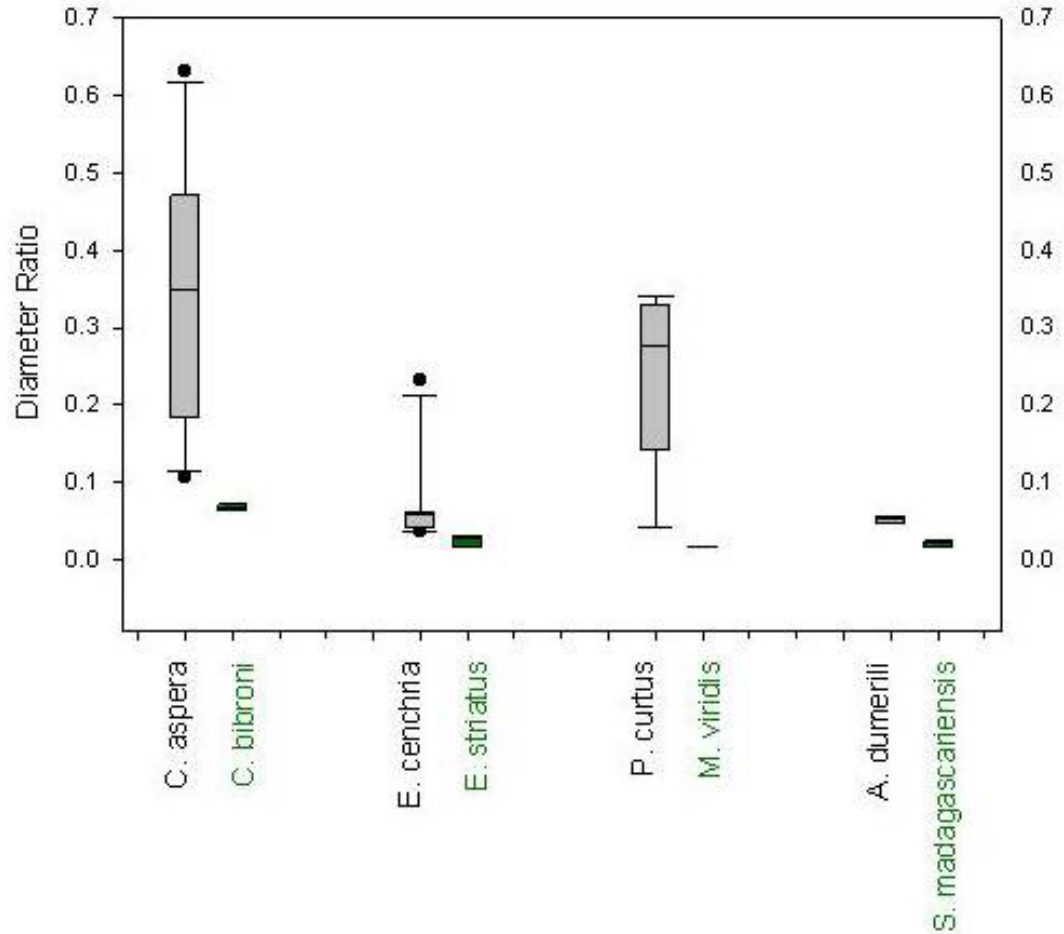
**Figure 2.6.** Cantilever ratios from the species pairs of the Families Crotalidae and Viperidae. The cantilever ratio was the horizontal distance that the snake was able to extend its body divided by the snake's total body length. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



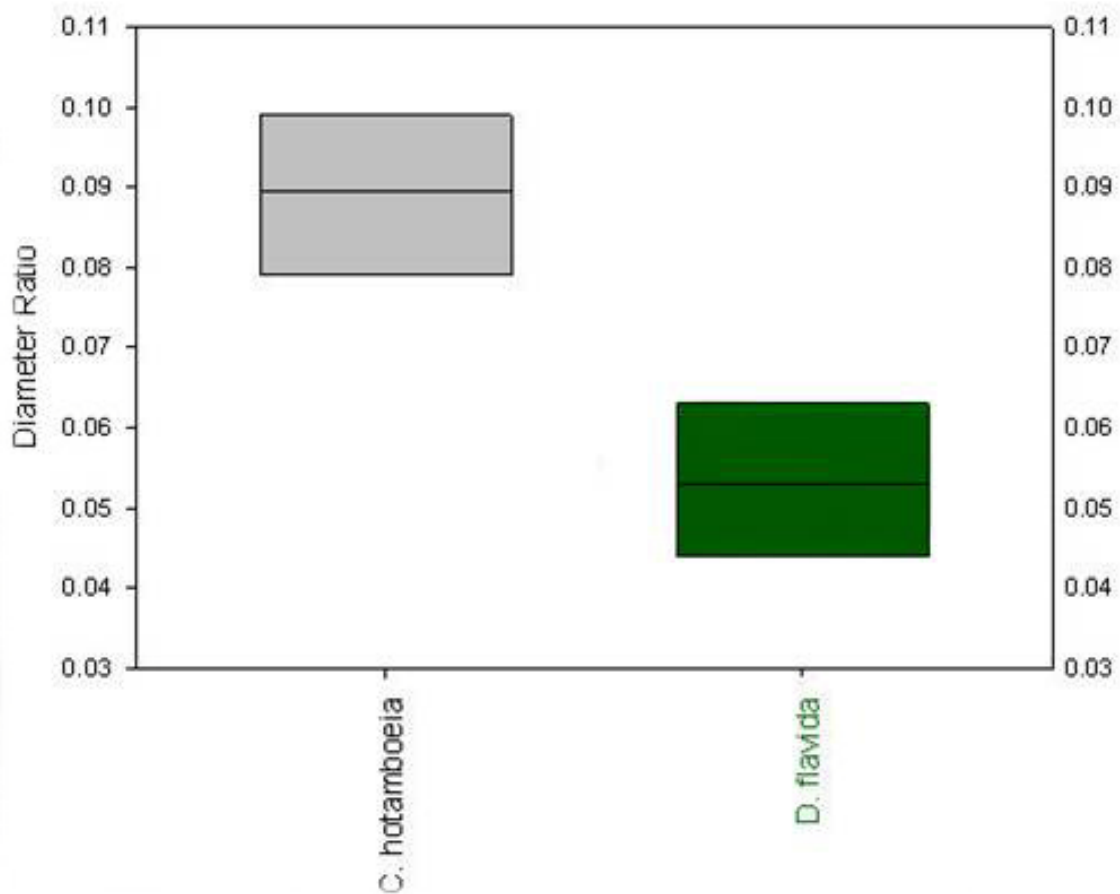
**Figure 2.7.** Relationship between cantilever ratio and relative mass (mass/total length) of snakes. The cantilever ratio was the horizontal distance that the snake was able to extend its body divided by the snake's total body length. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.

**Table 2.3.** Body mass ratios and diameter ratios for arboreal and terrestrial species pairs. The diameter ratio (DR) was the minimum surface diameter traversed divided by the maximum circumference of the snake.

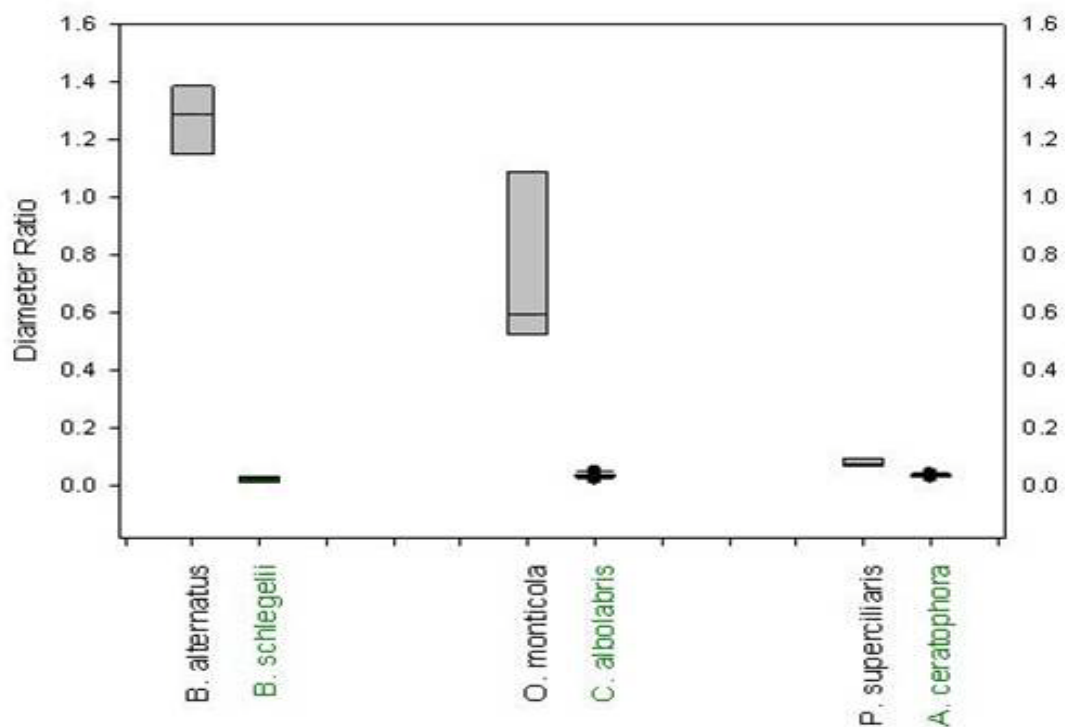
Species (N)	Habit	Mass / Total Length g / cm (range)	Mean DR (range)
<b>Boidae</b>			
<i>Candoia bibroni</i> (7)	arboreal	1.00 (0.79-1.62)	0.067 (0.064-0.079)
<i>Candoia aspera</i> (10)	terrestrial	3.47 (0.76-5.34)	0.339 (0.107-0.630)
<i>Epicrates striatus</i> (6)	arboreal	1.64 (0.96-2.80)	0.025 (0.017-0.033)
<i>Epicrates cenchria</i> (11)	terrestrial	2.90 (2.63-3.94)	0.076 (0.036-0.232)
<i>Morelia viridis</i> (5)	arboreal	1.33 (0.87-1.79)	0.017 (0.016-0.018)
<i>Python curtus</i> (9)	terrestrial	3.08 (2.17-4.39)	0.241 (0.042-0.339)
<i>Sanzinia madagascariensis</i> (5)	arboreal	3.55 (0.81-6.60)	0.022 (0.018-0.025)
<i>Acrantophis dumerili</i> (8)	terrestrial	2.03 (1.30-3.64)	0.052 (0.035-0.059)
<b>Colubridae</b>			
<i>Dipsadoboa flavida</i> (7)	arboreal	0.25 (0.24-0.27)	0.053 (0.040-0.067)
<i>Crotaphopeltis hotamboeia</i> (8)	terrestrial	0.74 (0.61-0.98)	0.089 (0.066-0.106)
<b>Crotalidae</b>			
<i>Bothriechis schlegelii</i> (7)	arboreal	1.03 (0.42-2.31)	0.024 (0.014-0.333)
<i>Bothrops alternatus</i> (8)	terrestrial	0.68 (0.51-0.83)	1.276 (1.058-1.494)
<i>Cryptelytrops albolabris</i> (10)	arboreal	0.99 (0.57-1.98)	0.036 (0.033-0.052)
<i>Ovophis monticola</i> (5)	terrestrial	1.98 (1.39-2.65)	0.765 (0.507-1.270)
<b>Viperidae</b>			
<i>Atheris ceratophora</i> (14)	arboreal	0.62 (0.40-0.89)	0.038 (0.031-0.044)
<i>Proatheris superciliaris</i> (6)	terrestrial	0.73 (0.64-0.81)	0.081 (0.071-0.097)



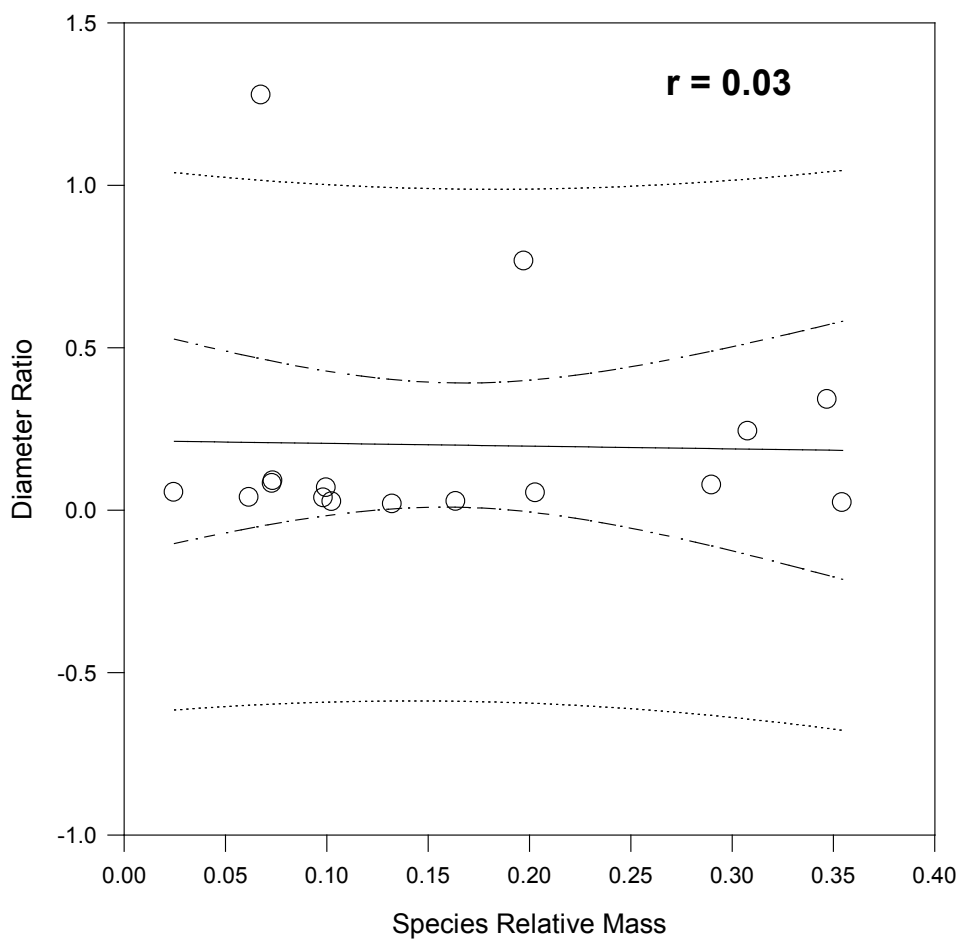
**Figure 2.8.** Diameter ratios from the species pairs of the Family Boidae. The diameter ratio was the minimum surface diameter traversed divided by the maximum circumference of the snake. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 2.9.** Diameter ratios from the species pair of the Family Colubridae. The diameter ratio was the minimum surface diameter traversed divided by the maximum circumference of the snake. The arboreal species is listed in green. Box plots represents median, and upper and lower quartile values.

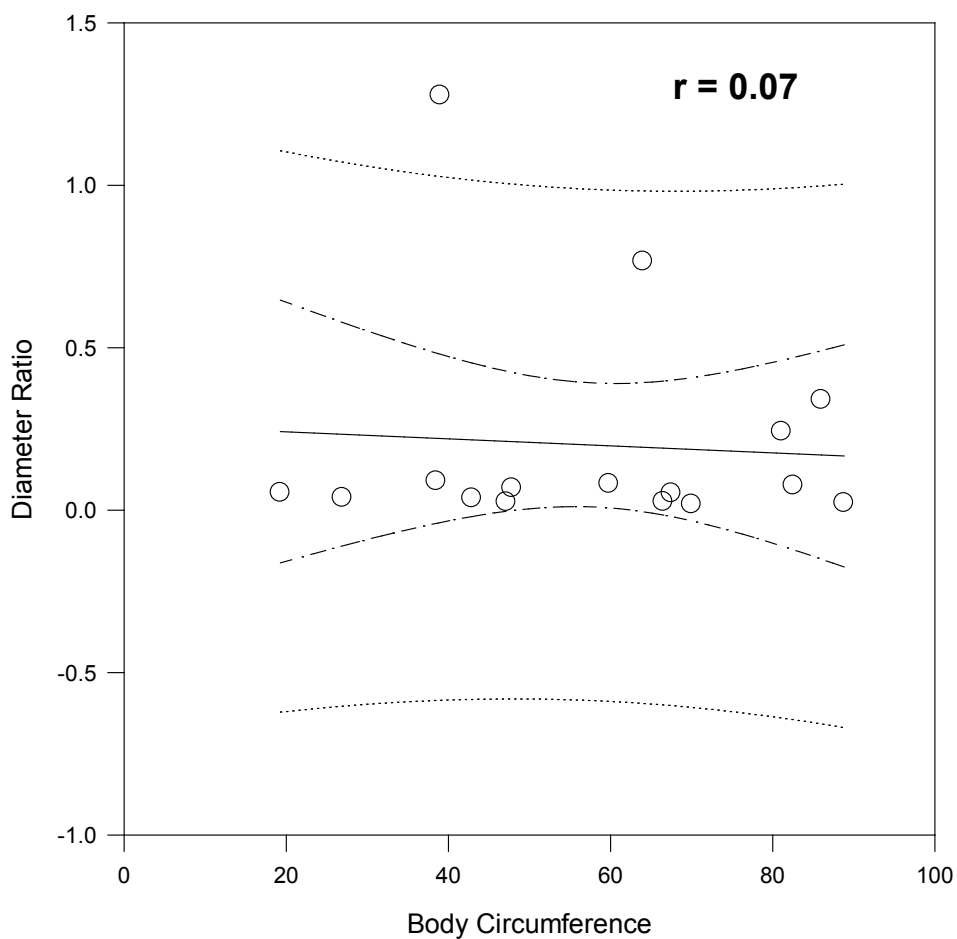


**Figure 2.10.** Diameter ratios from the species pairs of the Families Crotalidae and Viperidae. The diameter ratio was the minimum surface diameter traversed divided by the maximum circumference of the snake. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 2.11.** Relationship between diameter ratio and relative mass (mass/total length) of snakes. The diameter ratio was the minimum surface diameter traversed divided by the maximum circumference of the snake. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.





**Figure 2.12.** Relationship between diameter ratio and body circumference of snakes. The diameter ratio was the minimum surface diameter traversed divided by the maximum circumference of the snake. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.

*viridis* had a significantly greater DR than did *Python curtus* ( $U = 45, P = 0.003$ ). *Sanzinia madagascariensis* had a significantly greater DR than did *Acrantophis dumerili* ( $U = 40, P = 0.002$ ). *Dipsadoboa flavida* had a significantly greater DR than did *Crotaphopeltis hotamboeia* ( $U = 55, P < 0.001$ )(fig. 2.9). *Bothriechis schlegelii* had a significantly greater DR than did *Bothrops alternatus* ( $U = 56, P < 0.001$ ) (fig. 2.10). *Cryptelytrops albolabris* had a significantly greater DR than did *Ovophis monticola* ( $U = 50, P = 0.003$ ). *Atheris ceratophora* had a significantly greater DR than did *Proatheris superciliaris* ( $U = 84, P < 0.001$ ). No trend was observed between DR and mean relative mass ( $r = 0.03, P = 0.922$ )(fig. 2.11), or DR and mean circumference ( $r = 0.07, P = 0.805$ ) (fig. 2.12).

## Discussion

The convergent emergence of arboreal locomotion in snakes can be used as a “natural experiment” to determine if similar environmental challenges lead to similar evolutionary changes in a complex functional system. A snake’s ability to bridge gaps and traverse narrow diameter surfaces during arboreal locomotion is clearly of ecological relevance. But do differences in morphology provide a platform by which arboreal snakes are more adept at bridging gaps and traversing narrow diameter surfaces than terrestrial snakes? The results emphatically show that arboreal snakes excel at tasks associated with locomotion through an arboreal habitat. The characteristic morphology of the arboreal species allow for greater proficiency in gap bridging and traversing narrow diameter surfaces.

### *Gap Bridging*

The arboreal species were significantly greater at spanning gaps than were their terrestrial counterparts. The results presented here follow closely those reported by Lillywhite et al. (2000) with regards to arboreal and terrestrial snake abilities. That arboreal snakes are superior at bridging gaps both in a phylogenetic context and irrespective of phylogeny lends credence to the idea that the characteristic morphology of arboreal snakes is adaptive in nature.

Arboreal snakes have a number of morphological characters that likely contribute to their superior performance in bridging gaps. The vertebral architecture of arboreal snakes is distinctive from that of terrestrial snakes (Johnson, 1955). Arboreal snakes have a highly flexible vertebral column, yet bony reinforcements of the floor of the osteofascial tunnel prevent the downward displacement of epaxial muscles during flexion. The lack of displacement during flexion would provide for greater body rigidity and enable greater cantilever ratios to be achieved. Arboreal snakes also have been shown to have longer segmental lengths of semispinalis-spinalis muscle tissue than do terrestrial snakes (Jayne, 1982). Longer muscle tissues should increase the lever arm with which the muscle acts, and in doing so convey a mechanical advantage. Such a mechanical advantage should heighten a snake's ability to support its weight, particularly useful when bridging gaps (Jayne and Riley, 2007). While this study does not explicitly test the form to function relationship of vertebral and muscular structure to gap bridging ability, that arboreal snakes with their characteristic vertebral and muscular structure are more proficient at bridging gaps than terrestrial snakes who differ in their vertebral and

muscular structure lends support to the idea that the arboreal snake morphology is best suited for arboreal locomotion.

Failure to cope with gaps of sometimes considerable distance would clearly be a detriment to life in the trees. The shortest distance between two points is a straight line. If convoluted routes are required due to an inability to span between arboreal supports, then the negative impact this lack of ability would have on pursuing prey and escaping predators would be self-evident. The supposition that greater gap bridging abilities could lead to greater fitness for arboreal species appears strong and warrants direct testing.

#### *Minimum Surface Diameter Traversed*

As with gap bridging, arboreal snakes outperformed terrestrial snakes in traversing narrow diameter surfaces. A trend among arboreal snakes is to have high length to mass ratios (Guyer and Donnelly, 1990). Low mass and long, laterally compressed bodies would appear advantageous in an arboreal habitat. A key component of the arboreal habitat is that the substrate often provides little support. By distributing a low mass over a greater length the downward force produced at any given contact point with the substrate is reduced. Thus, high length to mass ratios would permit a greater exploitation of the whole of the arboreal environment by allowing movement across low support surfaces.

In being laterally compressed, snakes' bodies are small relative to most tree branch diameters. Again, lateral compression makes available more of the arboreal habitat space. While arboreal snakes are able to traverse relatively small diameter surfaces, performance increased as dowel diameter increased. Like the examined arboreal snakes, arboreal lizards of the genera *Niveoscincus* (Melville and Swain, 2000)

and *Sceloporus* (Sinervo and Losos, 1991) were more adept and able to sprint faster on smaller diameter surfaces than terrestrial members of those same genera, but it was noted that the arboreal subjects were somewhat more adept and faster on larger diameter surfaces than on smaller ones. Lateral body compression of a snake effectively makes a greater proportion of the arboreal habitat “large” relative to the snake’s body.

Arboreal and terrestrial snakes differed in the mode of locomotion used to cross the dowels. The arboreal species exhibited mostly lateral undulation with occasional episodes of concertina locomotion while traversing the dowels (see Edwards, 1985, for a review of modes of snake locomotion). In contrast, the terrestrial species almost exclusively used concertina locomotion.

An exception to the use of concertina locomotion by terrestrial snakes was displayed by *Candoia aspera* and *Python curtus*. *Candoia aspera* and *Python curtus* exhibited rectilinear locomotion. Successful crossings of the dowel were usually associated with coiling around the dowel in a constricting fashion and spiraling across the length of the dowel. Attempts made without coiling around the dowel most often resulted in failure.

This coiled rectilinear locomotion used by *C. aspera* and *P. curtus* likely represents a behavioral modification to a novel task. Both *C. aspera* and *P. curtus* are stout, sit and wait predators that would be unlikely to traverse tree branches in nature. Aspects of the known behavioral repertoire of these two species were incorporated into the challenge of traversing the dowel. However, tree architecture is often complex, with travel along branches rarely being unimpeded. A coiling rectilinear strategy may be less effective under natural conditions than under laboratory conditions. Thus, the DR for *C.*

*aspera* and *P. curtus* presented in this study are likely inflated values relative to those that would be achieved under natural conditions. That a significant difference was noted in the minimum surface diameter traversed between these two species and their respective arboreal counterparts despite inflated terrestrial DR values suggest that the arboreal species possess an even greater disparity in this locomotor task. The greater than observed disparity in the ability to traverse narrow diameter surfaces further strengthens the argument that the morphology of arboreal snakes allow for increased proficiency in arboreal locomotion.

### *Conclusions*

The evolution of arboreality in snakes has brought about a divergent morphology well suited to life above the ground. The differential morphology exhibited by arboreal and terrestrial snakes have led to differential levels of proficiency in locomotor performance. Arboreal snakes are able to bridge gaps and traverse narrow diameter surfaces with greater proficiency than closely related terrestrial snakes. These heightened abilities were documented across several family lines. Since arboreality has evolved multiple times with snakes (Greene, 1997) the findings of this study suggest that similar selective pressures lead to similar morphological ends. The convergent arboreal morphology that has been shaped by natural selection in turn produces similar levels of locomotor performance relative to terrestrial snakes. Linking morphology to performance is the first step to ultimately linking morphology to fitness. A rigorous testing of the linkage between morphology and fitness is necessary to elucidate the true adaptive nature of the unique morphology of the arboreal snakes.

### CHAPTER 3

## PERFORMANCE TRADE-OFFS IN ARBOREAL AND TERRESTRIAL LOCOMOTION

Locomotor performance, of particular importance to a species because it is directly related to prey acquisition, predator avoidance, and dispersal abilities, is under strong selection pressure but may be subject to trade-offs. In any one type of habitat, locomotor proficiency may have distinctive morphological adaptations, and these adaptations may limit proficiency in a different habitat. Further, the invasion of a new habitat type often brings with it a new set of selective pressures that would be expected to shape the morphology of the species to best adapt it to the new type of habitat (Irschick and Losos, 1999). Morphology adapts a species to a particular habitat type by way of performance (Arnold, 1983) and conversely locomotor performance can be particularly sensitive to changes in morphology (Emerson and Arnold, 1989). Such adaptations to a particular habitat, however, may negatively impact performance in different habit types that have different selective pressures (Gillis, 1998; Biewener and Corning, 2001; Ashley-Ross and Bechtel, 2004).

When adapting to a new habitat type, depending upon the nature of the selective forces imposed by each habitat, minimally two morphological outcomes are possible. First, a phenotype may be selected that allows a degree of locomotor proficiency in both habitat types. Under this “jack of all trades” scenario, adequate locomotor performance in both habitat types would be achieved but performance would not be optimized for either habitat type. As examples, Van Damme et al. (1997) reported no difference in the clinging and sprinting abilities of arboreal and terrestrial populations of the lizard *Podarcis hispanica*, Nauwelaerts et al. (2005) found a semi-aquatic frog to be equally

proficient in both swimming and jumping, and Gvozdik and Van Damme (2006) found no conflict between swimming and running in *Triturus* newts. Thus, some species forego optimal performance in one habitat type in order to maintain adequate performance in multiple habitat types.

Second, in the “trade-off” scenario, optimal performance in one habitat may be traded for optimal performance in a divergent habitat. Underlying the notion of locomotor performance trade-offs is the idea that performance cannot be simultaneously optimized for two tasks that require mutually incompatible morphologies (Shine et al., 2003). The trade-off scenario predicts that performance in one habitat type would be optimized at the expense of performance in the ancestral habitat type (Bonnet et al., 2005). Locomotor performance trade-offs have been shown between sprinting and clinging abilities in chameleons (Losos et al., 1993) and between swimming and crawling abilities in sea snakes (Shine et al., 2003). The degree to which trade-offs exist would be dependent upon the differential intensity of the selective pressures between the two habitat types.

While habitat use is conserved across most phylogenetic lineages, some groups do exhibit dramatic shifts in their use of habitat types (Shine and Shetty, 2001). Snakes are a group which has undergone shifts in their use of habitat types, between terrestrial and arboreal. Although there is debate as to whether the ancestor to all living snakes was aquatic (Lee, 2001; Caprette et al., 2004) or terrestrial (Vidal and David, 2004; Vidal and Hedges, 2004), even those who posit an aquatic origin for snakes suggest an early evolutionary transition to terrestriality (Lee, 2005). Since the time that snakes first became fixtures on the terrestrial landscape, arboreality has evolved multiple times



independently (Greene, 1997). Radiation from a terrestrial to arboreal existence would be expected to produce adaptive shifts whereby different locomotor task, climbing and crawling, would result in differential locomotor abilities. Arboreal and terrestrial habitats suggest different challenges for locomotion, according to their different three-dimensional structures (Lillywhite and Henderson, 1993). Arboreal habitats are largely vertical in orientation, in stark contrast to the mostly horizontal orientation of terrestrial habitats. Key to locomotion through arboreal and terrestrial habitats is thus the ability to climb or to crawl.

In accord with arboreality as an adaptation derived from terrestrial ancestors, arboreal snakes possess a suite of morphological characters that separate them from their terrestrial counterparts. The characters possessed by arboreal snakes have been presumed to function in reducing the pooling of blood while vertical and in supporting the snake's body in space. Gravity exerts a downward force on the body fluids of vertically oriented snakes. To reduce the pooling of blood while vertical arboreal snakes have high length to mass ratios (Guyer and Donnelly, 1990), a more anterior placement of the heart (Lillywhite, 1987; Seymour, 1987), a lesser heart displacement during upright postures (Young et al., 1997), tighter skin attachment to the underlying tissues (Jayne, 1988), and relatively non-compliant tissue compartments (Lillywhite, 1993). These morphological characters counteract the effects of gravity on the body fluids of snakes and reduce the pooling of fluids posteriorly while vertical.

The arboreal snake morphology would also appear to provide a mechanical advantage towards self-support of the snake's body in space. Arboreal snakes must cope with a discontinuous arboreal substrate with often sizable gaps. To assist in bridging

gaps, arboreal snakes have longer segmental lengths of semispinalis-spinalis muscle tissue (Jayne, 1982) and a distinctive vertebral architecture (Johnson, 1955) that prevents the downward displacement of epaxial muscles during flexion. These morphological characters allow arboreal snakes to maintain body rigidity while spanning gaps in the arboreal substrate.

It is unclear if the morphological differences between arboreal and terrestrial snakes result in arboreal and terrestrial locomotor performance that are meaningfully different. Equally unclear is whether each transition from terrestriality to arboreality results in locomotor performance that has the same degree of proficiency. To determine if morphological differences in snakes equates to differences in climbing and crawling ability a comparative approach is required. Climbing and crawling performance among snakes that have unambiguously evolved arboreal habits were compared with close relatives (outgroups) that still maintain a terrestrial habit. This direct comparison, of arboreal and terrestrial snakes matched phylogenetically, was used to determine if the evolution of arboreality in snakes has produced locomotor performance trade-offs.

## **Methods**

### *Rationale*

The goal of this study was to determine the relationship between arboreal and terrestrial snake morphology, and arboreal and terrestrial locomotor performance. To accomplish this goal, closely related arboreal-terrestrial species pairs were compared in their abilities to climb and crawl. If the morphology of arboreal snakes is specialized for arboreal locomotion, then arboreal snakes should climb more proficiently than their terrestrial counterparts. If arboreal snakes are specialized for arboreal locomotion, then

performance in the terrestrial task of crawling will be lessened as a result of the morphological specializations. If no difference (or a negative correlation) exists in the arboreal and terrestrial locomotor abilities of arboreal and terrestrial snakes, then the evolutionary genesis of arboreal snake morphology must be reconsidered.

### *Study species*

Sets of closely related species pairs, one arboreal and one terrestrial in habit, were examined (Table 3.1). All individuals were wild-caught with the exception of *Sanzinia madagascariensis*, *Acrantophis dumerili*, *Bothrops alternatus*, and *Proatheris superciliaris*. Animals were housed in appropriately sized, commercially produced enclosures with temperature and humidity adjusted to the needs of the individual species. All trials were performed at ambient temperatures experienced within the normal activity range for each individual species. Animals were not fed the week before or the week of testing to avoid erroneous results owing to sudden changes in relative mass.

### *Climbing*

The metrics appropriate for gauging climbing proficiency are climbing endurance and vertical sprint speed. Climbing endurance and vertical sprint speed are directly related to a snake's survivorship via the ability to acquire prey and evade predators. A snake's climbing endurance was measured by the distance climbed until exhaustion. The distance an animal can climb will affect that animal's ability to stalk prey, escape dedicated predators, and disperse. Vertical sprint speed was measured as the rate at which 1 m was climbed. Sprint speed is a common measure in locomotor performance

trials because of its ecological relevance. Obtaining maximum speed over short distances is necessary when subduing prey and avoiding predation. Together, distance climbed and vertical sprint speed allows climbing proficiency to be appropriately gauged.

To measure climbing ability, a vertical peg array was used (fig. 3.1). The peg array simulates protruding tree branches (though regularly spaced) that provide contact points for vertical locomotion. The peg array stood 2.30 m high. The pegs were 1.59 cm diameter wooden dowels that extended outward 7.50 cm. The dowels were placed in alternating rows of one and two dowels. The vertical distance between single dowel rows was 10.16 cm, and the center to center horizontal distance between dowels in the same row was 6.35 cm.

Climbing endurance was measured by placing the snakes directly on the lower-most pegs of the peg array and allowing them to climb. Gentle tail tapping ( $\leq 1$  tap per 5 seconds) was used to encourage climbing since tail tapping is perhaps the best, and most appropriate stimuli for eliciting movement in snakes (Mullin and Cooper, 2002). When the animal reached the top of the array it was quickly but calmly removed from the top of the array and put back to the original starting position. Transfer from top to bottom was done quickly enough to prevent muscular recovery from taking place. These procedures were repeated until the snake reached exhaustion. Exhaustion was gauged by the snake refusing to climb any further. Three climbing trials were performed for each individual, with minimally 24 hours between trials. Mean distance climbed was determined.

Vertical sprint speed was determined concurrently with climbing endurance. Each of the first 3 m climbed were independently timed. A total of nine vertical sprint speeds were recorded for the three climbing trials. Of the nine recorded vertical sprint

**Table 3.1.** Arboreal – terrestrial species pairs and number of individuals (N).

Arboreal species (N)	Terrestrial species (N)
<i>Candoia bibroni</i> (7)	<i>Candoia aspera</i> (10)
<i>Epicrates striatus</i> (6)	<i>Epicrates cenchria</i> (11)
<i>Morelia viridis</i> (5)	<i>Python curtus</i> (9)
<i>Sanzinia madagascariensis</i> (5)	<i>Acrantophis dumerili</i> (8)
<i>Dipsadoboa flavida</i> (7)	<i>Crotaphopeltis hotamboeia</i> (8)
<i>Bothriechis schlegelii</i> (7)	<i>Bothrops alternatus</i> (8)
<i>Cryptelytrops albolabris</i> (10)	<i>Ovophis monticola</i> (5)
<i>Atheris ceratophora</i> (14)	<i>Proatheris superciliaris</i> (6)

speeds only the overall maximum speed was used in analyses.

### *Crawling*

To determine terrestrial locomotor proficiency, crawling endurance and sprint speed were measured. Crawling endurance and sprint speed are the horizontal analogues of climbing endurance and vertical sprint speed. The ability to crawl over relatively great lengths and move rapidly over short distances is key to dispersal, finding mates, and escaping predators. Thus, crawling endurance and sprint speed provide a means of assessing terrestrial locomotor performance.

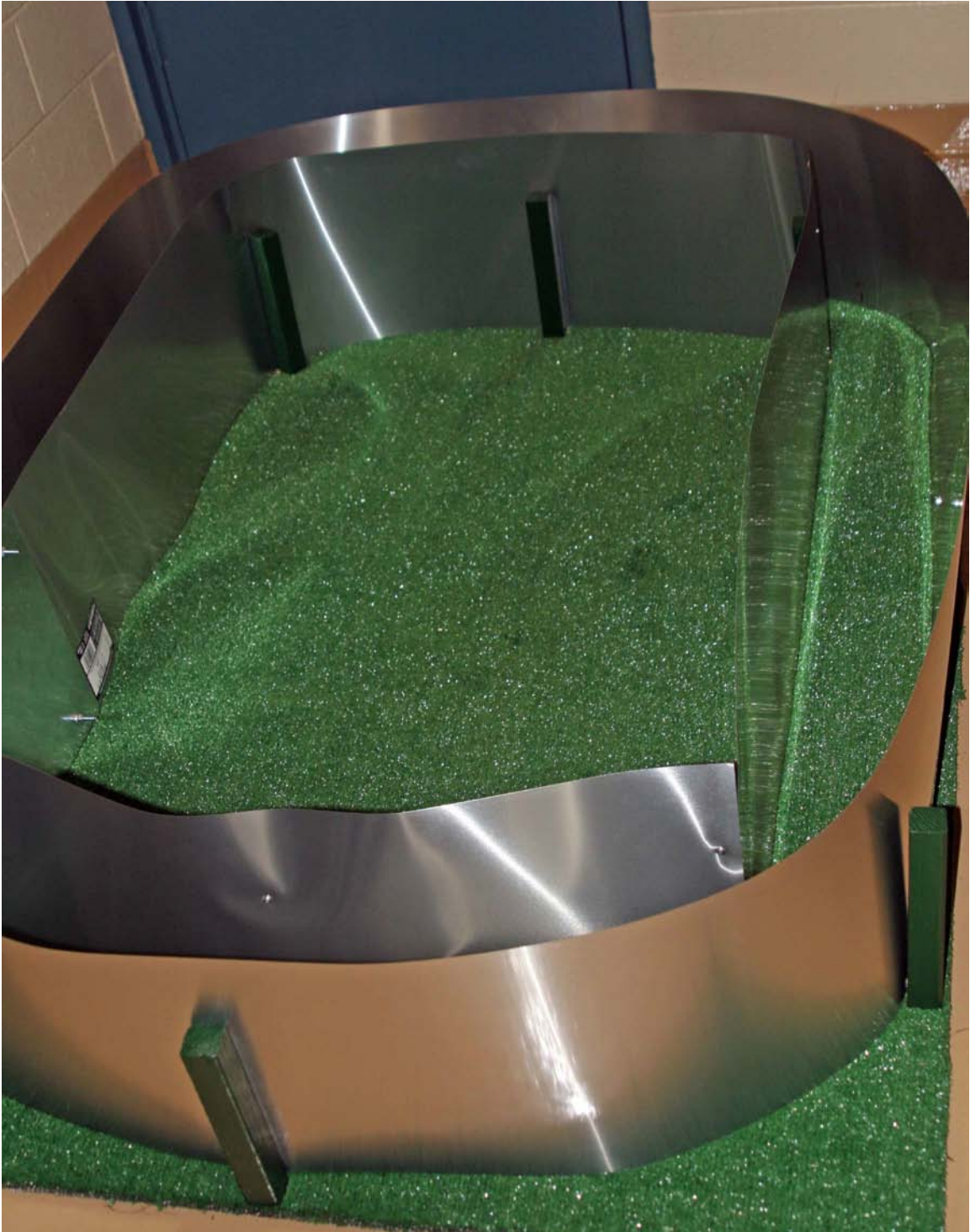
To measure crawling endurance and sprint speed an oval raceway was used (fig. 3.2). The outside dimensions of the raceway were 1.5 m x 1.2 m. The walls of the raceway were aluminum, 36 cm high. The raceway channel (where animals were placed) was 25 cm wide. The substrate of the raceway was commercially available outdoor carpeting. The linear distance for one loop around the raceway was 5.2 m.

Snakes were placed in the raceway channel at the beginning of a straight-away and allowed to crawl. Gentle tail tapping was used to ensure maximum crawling effort. Animals were encouraged to crawl until exhaustion, as determined by the snake's refusal to crawl any further. Three crawling trials were performed for each individual, with minimally 24 hours between trials. Mean distance crawled was determined.

Sprint speed was determined concurrently with crawling endurance. Sprint speed was timed over 1 m stretches of straight-away in the race arena. Each of the first three 1 m straight-aways traversed was independently timed. A total of nine sprint speeds were



**Figure 3.1.** Vertical peg array. The peg array stood 2.30 m high. The pegs were 1.59 cm diameter wooden dowels that extended outward 7.50 cm. The vertical distance between single dowel rows was 10.16 cm, and the center to center horizontal distance between dowels in the same row was 6.35 cm.



**Figure 3.2.** Raceway. The outside dimensions of the raceway were 1.5 m x 1.2 m. The walls of the raceway were aluminum, 36 cm high. The raceway channel (where animals were placed) was 25 cm wide. The substrate of the raceway was outdoor carpeting. The linear distance for one loop around the raceway was 5.2 m.



recorded for the three crawling trials. Of the nine recorded sprint speeds only the overall maximum speed was used in analyses.

### *Analyses*

Analysis of Covariance (ANCOVA) was used to compare mean climbing distance, maximum vertical sprint speed, mean crawling endurance, and maximum sprint speed among species pairs. The dependent variable was distance climbed, distance crawled, vertical sprint speed, or sprint speed, species habit (arboreal or terrestrial) was a factor, and body size (mass/total length) was used as a covariate. ANCOVAs were performed using XLStat software.

## **Results**

### *Climbing*

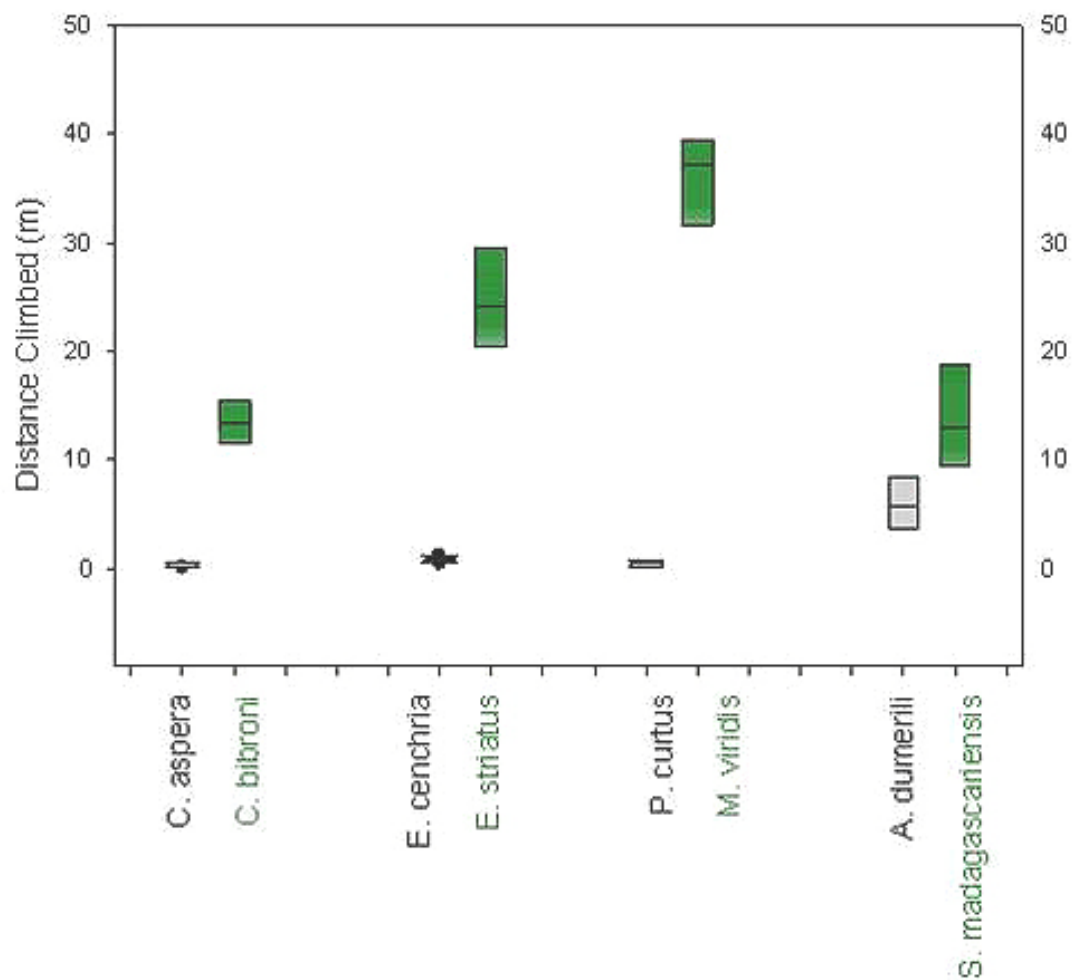
In all instances the arboreal species was able to climb further than their terrestrial counterpart. *Candoia bibroni* climbed significantly further than did *C. aspera* ( $F_{2,13} = 90.36, P < 0.001$ ) (fig. 3.3). *Epicrates striatus* climbed significantly further than did *E. cenchria* ( $F_{2,13} = 67.76, P < 0.001$ ). *Morelia viridis* climbed significantly further than did *Python curtus* ( $F_{2,10} = 314.30, P < 0.001$ ). *Sanzinia madagascariensis* climbed significantly further than did *Acrantophis dumerili* ( $F_{2,9} = 7.11, P = 0.014$ ). *Dipsadoboa flavida* climbed significantly further than did *Crotaphopeltis hotamboeia* ( $F_{2,13} = 90.36, P < 0.001$ ) (fig. 3.4). *Bothriechis schlegelii* climbed significantly further than did *Bothrops alternatus* ( $F_{2,11} = 17.35, P < 0.001$ ) (fig. 3.5). *Cryptelytrops albolabris* climbed significantly further than did *Ovophis monticola* ( $F_{2,11} = 29.85, P < 0.001$ ).

*Atheris ceratophora* climbed significantly further than did *Proatheris superciliaris* ( $F_{2,16} = 76.26, P < 0.001$ ).

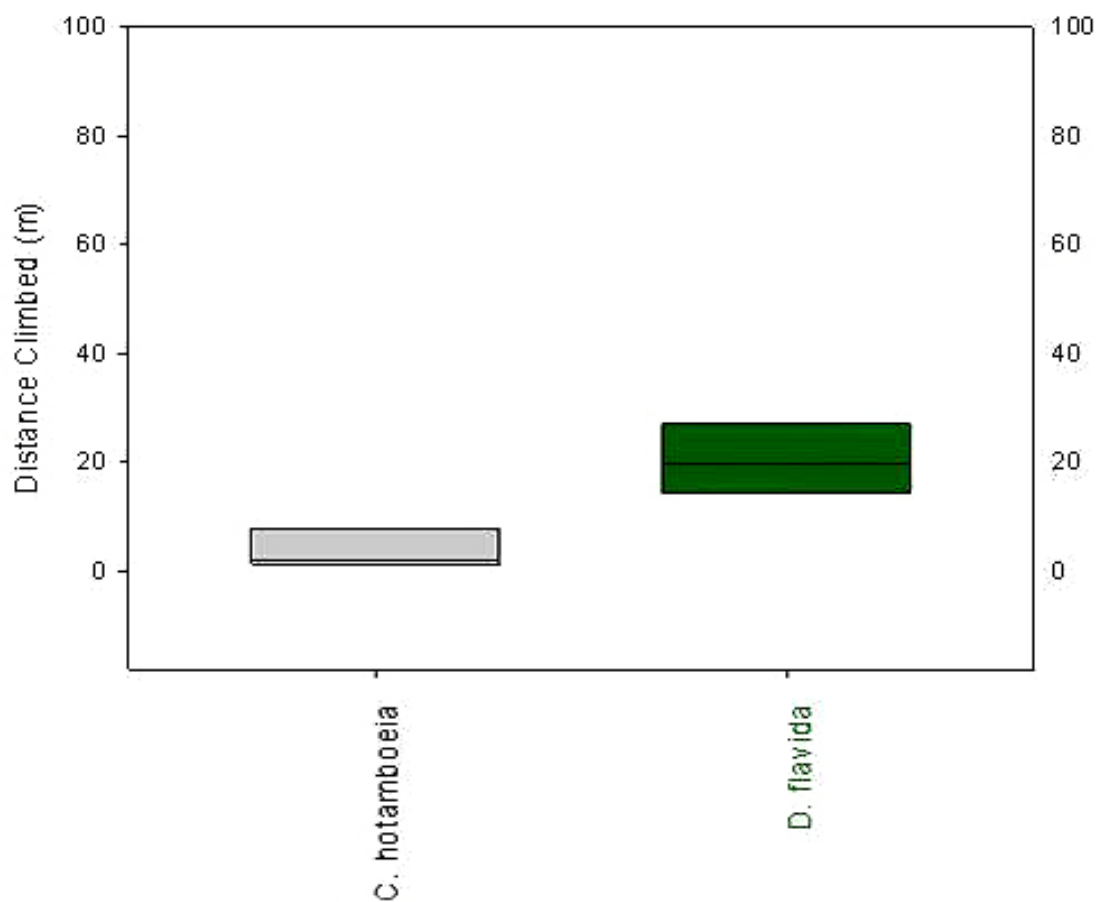
A slight trend was observed between the distance climbed and body size (mass/total length) with smaller snakes climbing farther, but the trend was not significant ( $r = 0.28, P = 0.299$ ) (fig. 3.6). However, the observed power of the regression analysis was low ( $<0.800$ ). To ensure that body size did not affect analyses, ANCOVAs were performed to remove any possible effect of body size.

Vertical sprint speed was found to be greater for arboreal species in six of the eight species pairs. *Candoia aspera*, *Epicrates cenchria*, and *Python curtus* were excluded from statistical analyses because most to all individuals of these species failed to climb 1 m. However, it remains that *C. aspera*, *E. cenchria*, and *P. curtus* were outperformed by their respective arboreal counterparts. Statistical analyses then were limited to five species pairs. Of the five species pairs, three found the arboreal species having greater vertical sprint speeds (fig. 3.7). *Sanzinia madagascariensis* sprinted significantly faster than *Acrantophis dumerili* ( $F_{2,9} = 7.17, P = 0.014$ ), *Dipsadoboa flavida* sprinted significantly faster than *Crotaphopeltis hotamboeia* ( $F_{2,11} = 9.17, P = 0.005$ ), and *Cryptelytrops albolabris* sprinted significantly faster than *Ovophis monticola* ( $F_{2,9} = 14.11, P = 0.001$ ). There was no statistical difference in vertical sprint speed noted for *Bothriechis schlegelii* and *Bothrops alternatus* ( $F_{2,11} = 0.96, P = 0.414$ ), or for *Atheris ceratophora* and *Proatheris superciliaris* ( $F_{2,16} = 0.51, P = 0.610$ ).

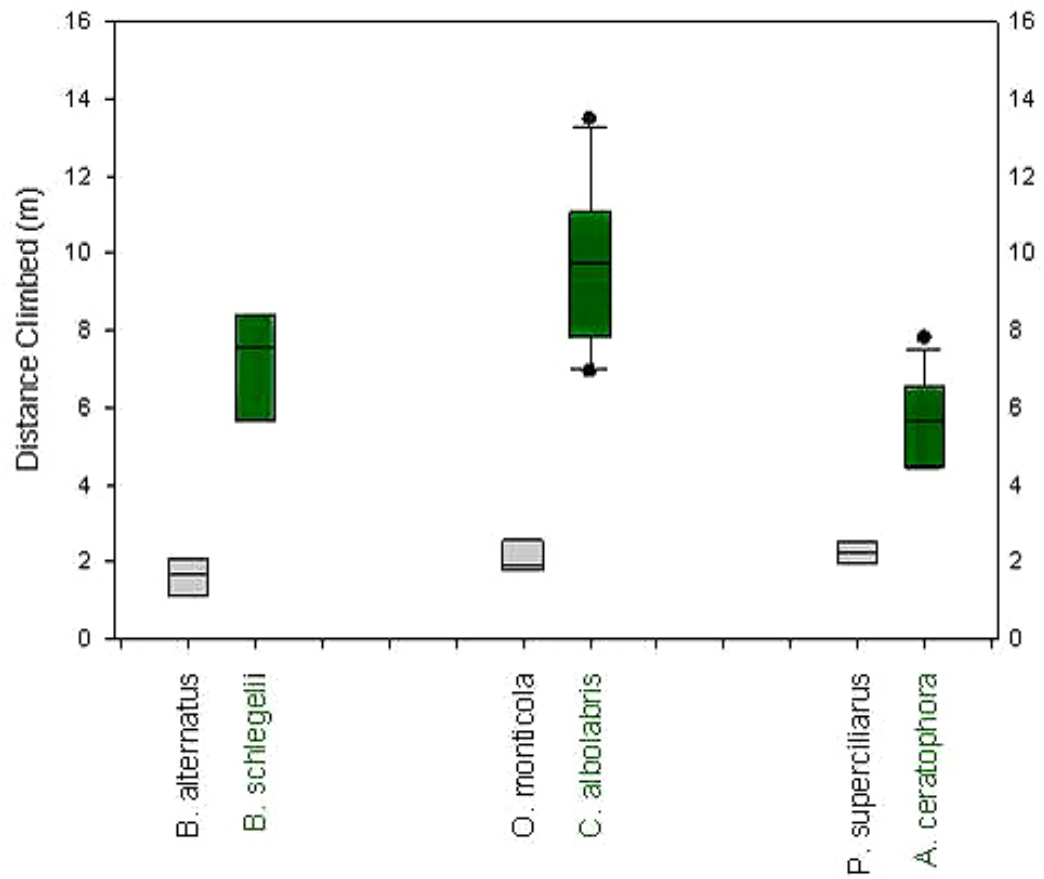
A slight trend was observed between vertical sprint speed and relative mass (mass/total length) with smaller snakes sprinting faster, but the trend was not significant ( $r = 0.09, P = 0.778$ ) (fig. 3.8). However, the observed power of the regression analysis was low



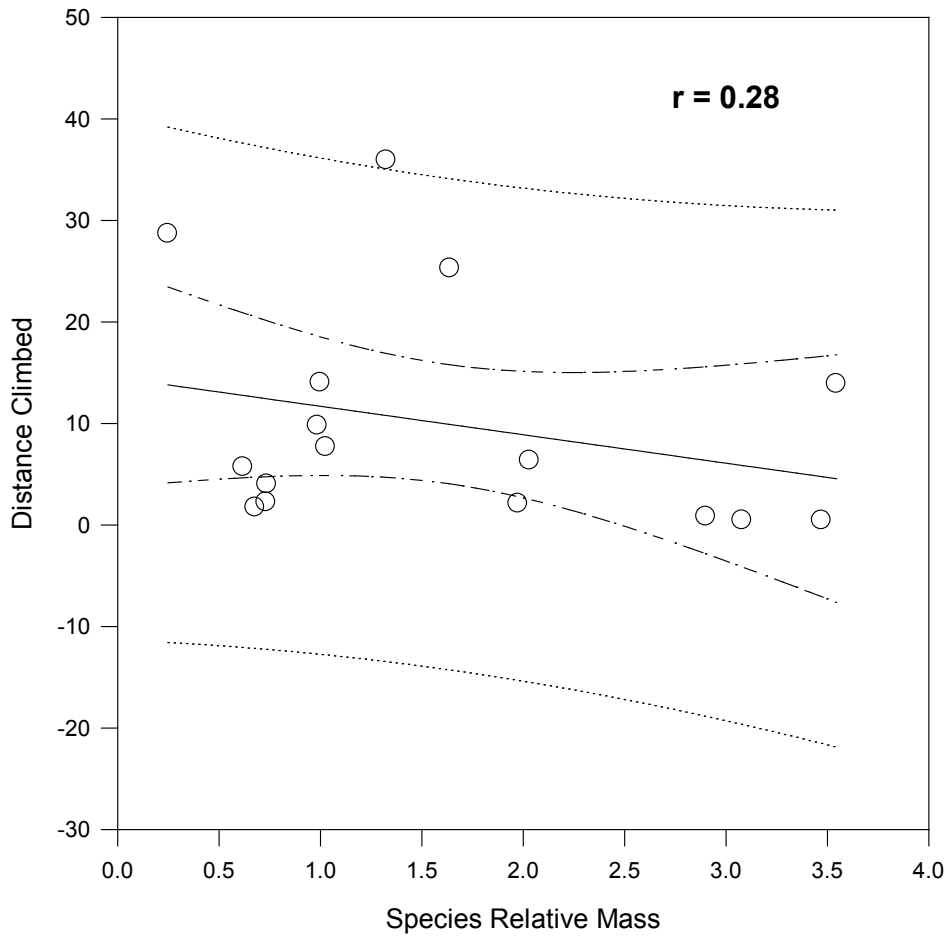
**Figure 3.3.** Distance climbed by the species pairs of the Family Boidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



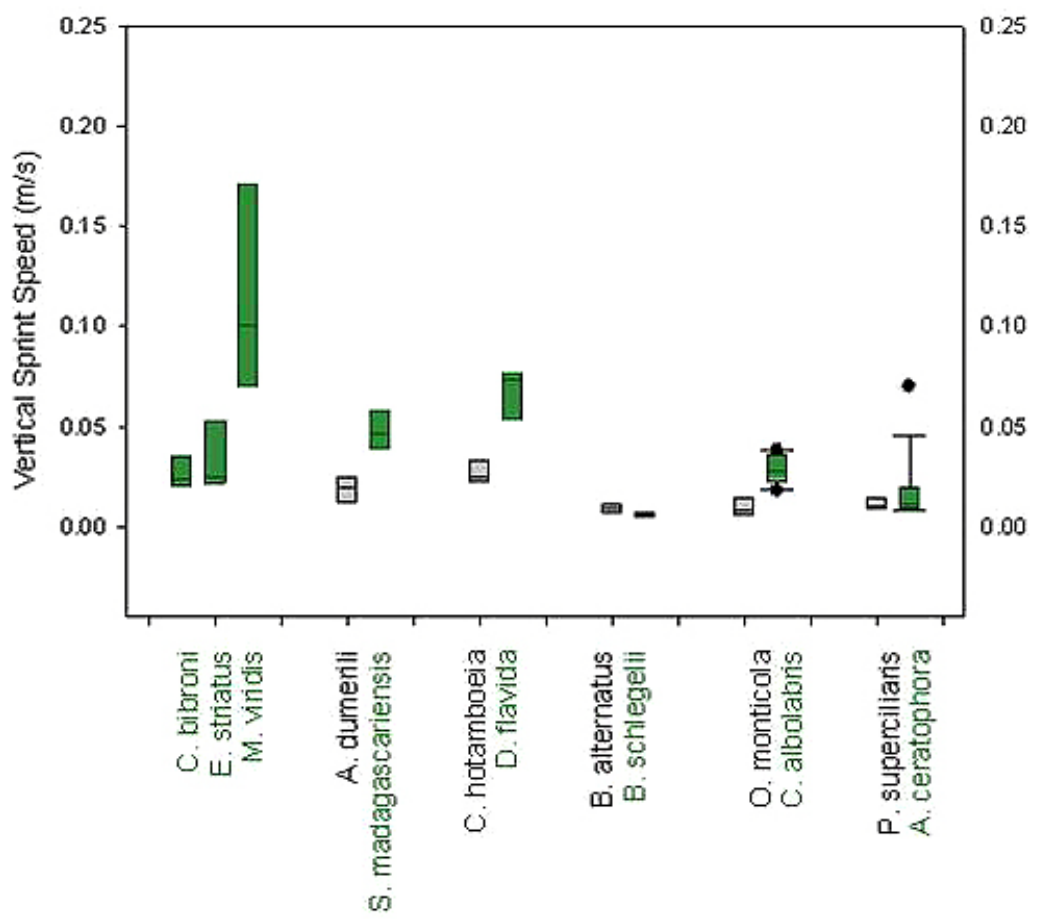
**Figure 3.4.** Distance climbed by the species pair of the Family Colubridae. Arboreal species is listed in green. Box plots represent median, and upper and lower quartile.



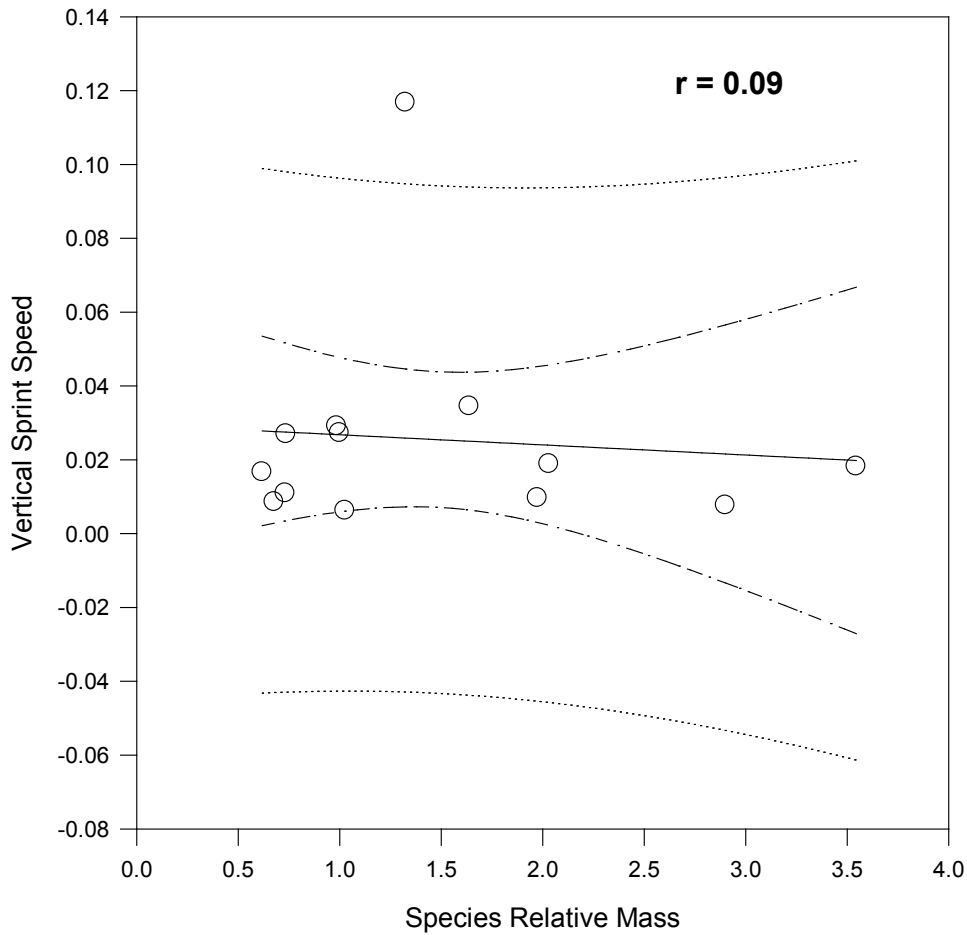
**Figure 3.5.** Distance climbed by the species pairs of the Families Crotalidae and Viperidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 3.6.** Relationship between distance climbed and relative mass (mass/total length) of snakes. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.



**Figure 3.7.** Vertical sprint speeds of each species pair. Excluded from consideration were *Candoia aspera*, *Epicrates cenchria*, and *Python curtus* due to failure to climb a minimum of 1 m. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 3.8.** Relationship between vertical sprint speed and relative mass (mass/total length) of snakes. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals. Excluded from consideration were *Candoia aspera*, *Epicrates cenchria*, and *Python curtus* due to failure to climb a minimum of 1 m.



(<0.800). To ensure that body size did not affect analyses ANCOVAs were performed to remove any possible effect of body size.

### *Crawling*

In six of the eight species pairs the terrestrial species exhibited greater crawling endurance than the arboreal species. *Epicrates cenchria* crawled significantly farther than *Epicrates striatus* ( $F_{2,13} = 10.26$ ,  $P = 0.002$ ) (fig. 3.9). *Acrantophis dumerili* crawled significantly farther than *Sanzinia madagascariensis* ( $F_{2,9} = 11.34$ ,  $P = 0.003$ ). *Crotaphopeltis hotamboeia* crawled significantly farther than *Dipsadoboa flavida* ( $F_{2,11} = 11.41$ ,  $P = 0.002$ ) (fig. 3.10). *Bothrops alternatus* crawled significantly farther than *Bothriechis schlegelii* ( $F_{2,11} = 21.10$ ,  $P < 0.001$ ) (fig. 3.11). *Ovophis monticola* crawled significantly farther than *Cryptelytrops albolabris* ( $F_{2,11} = 16.48$ ,  $P < 0.001$ ). *Proatheris superciliaris* crawled significantly farther than *Atheris ceratophora* ( $F_{2,16} = 32.23$ ,  $P < 0.001$ ).

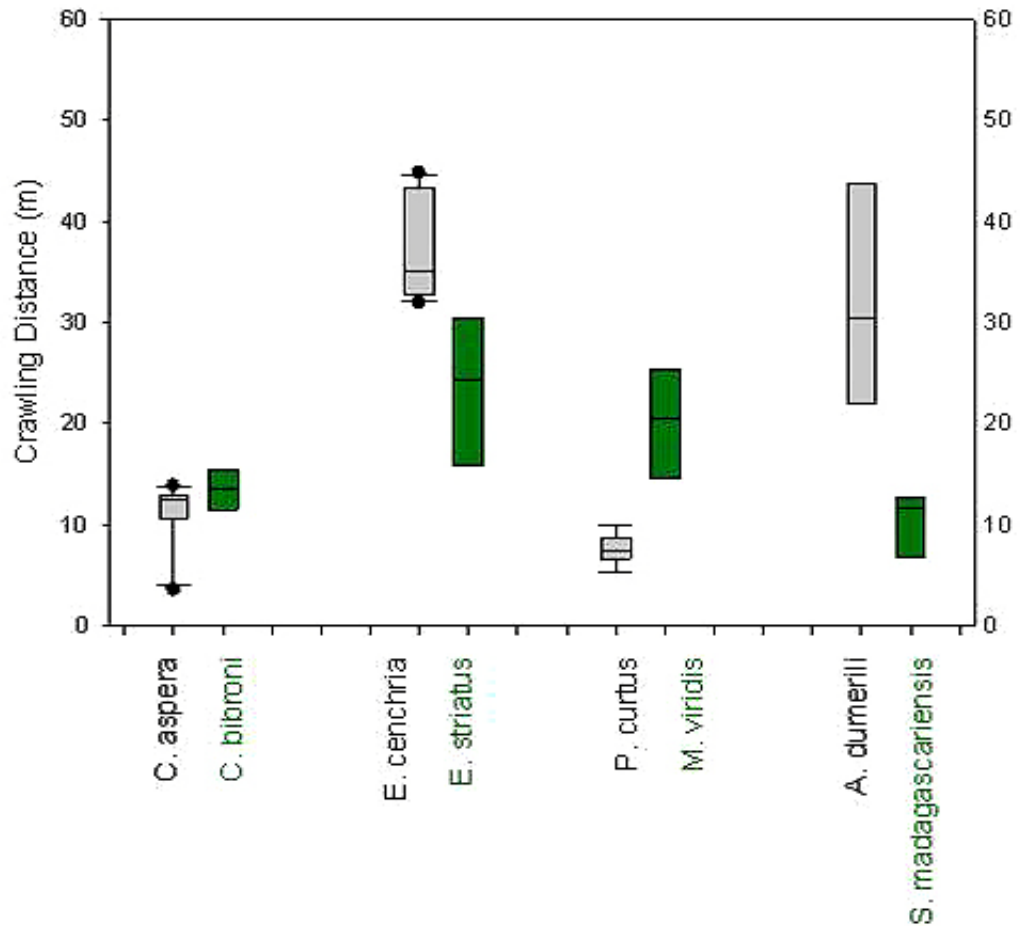
The two arboreal species that outperformed their terrestrial counterparts in crawling endurance were *Candoia bibroni* and *Morelia viridis* (fig. 3.9). *Candoia bibroni* crawled significantly farther than *Candoia aspera* ( $F_{2,13} = 4.19$ ,  $P = 0.039$ ). *Morelia viridis* crawled significantly farther than *Python curtus* ( $F_{2,10} = 19.09$ ,  $P < 0.001$ ).

No trend was observed between mean crawling endurance and relative mass (mass/total length) ( $r = 0.00$ ,  $P = 0.994$ ) (fig. 3.12). However, the observed power of the regression analysis was low (<0.800). To ensure that body size did not affect analyses ANCOVAs were performed to remove any possible effect of body size.

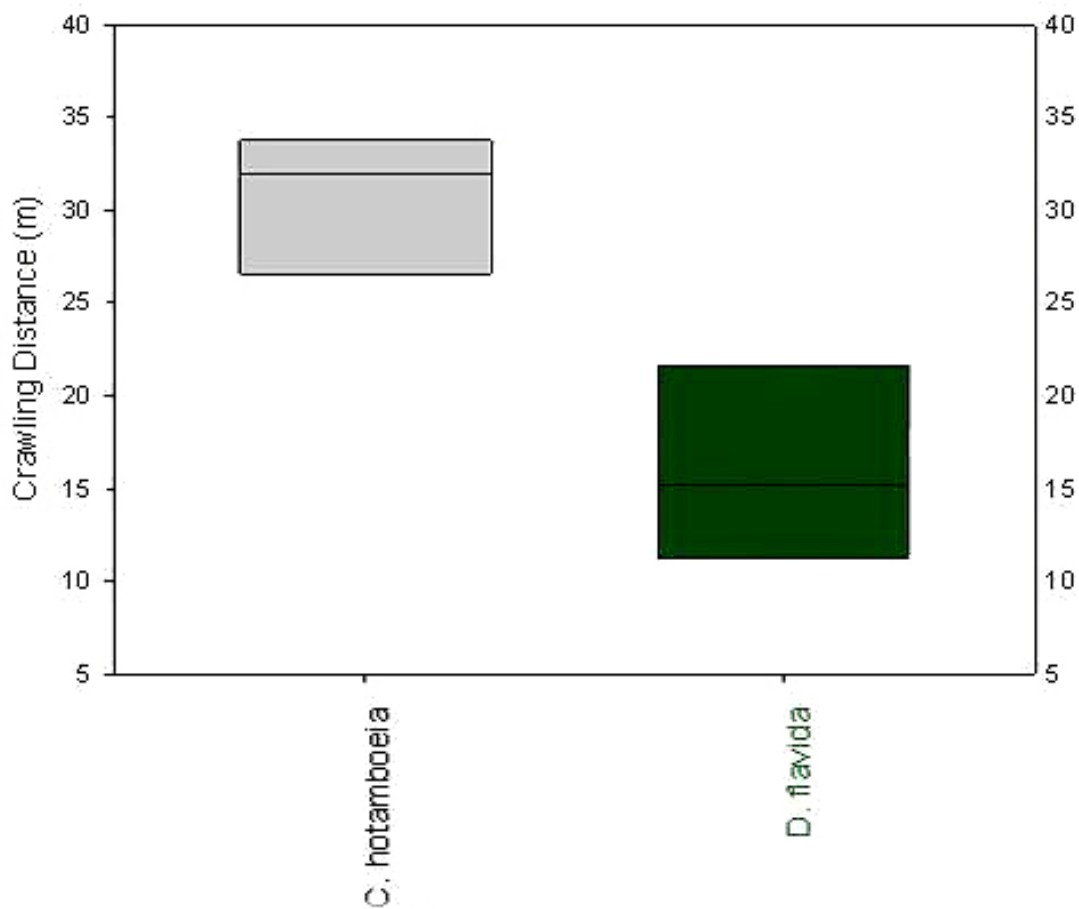
In five of the eight species pairs the terrestrial species exhibited greater sprint speed than the arboreal species. *Candoia aspera* sprinted significantly faster than *Candoia bibroni* ( $F_{2,13} = 6.67, P = 0.010$ ) (fig. 3.13). *Epicrates cenchria* sprinted significantly faster than *Epicrates striatus* ( $F_{2,13} = 11.23, P = 0.001$ ). *Acrantophis dumerili* sprinted significantly faster than *Sanzinia madagascariensis* ( $F_{2,9} = 7.32, P = 0.013$ ). *Bothrops alternatus* sprinted significantly faster than *Bothriechis schlegelii* ( $F_{2,11} = 10.93, P = 0.002$ ) (fig. 3.14). *Proatheris superciliaris* sprinted significantly faster than *Atheris ceratophora* ( $F_{2,16} = 216.24, P < 0.001$ ).

One arboreal species, *Morelia viridis*, outperformed its terrestrial counterpart in sprinting, and in two comparisons there was no difference in the sprinting ability of the species pair. *Morelia viridis* sprinted significantly faster than *Python curtus* ( $F_{2,10} = 4.33, P = 0.044$ ) (fig. 3.13). There was no difference in the sprint speeds of *Crotaphopeltis hotamboeia* and *Dipsadoboa flavida* ( $F_{2,11} = 3.73, P = 0.058$ ) (fig. 3.15), or of *Ovophis monticola* and *Cryptelytrops albolabris* ( $F_{2,11} = 2.20, P = 0.157$ ) (fig. 3.14). In each instance where no statistical difference was observed there was a slight trend towards the arboreal species having a somewhat greater sprint speeds.

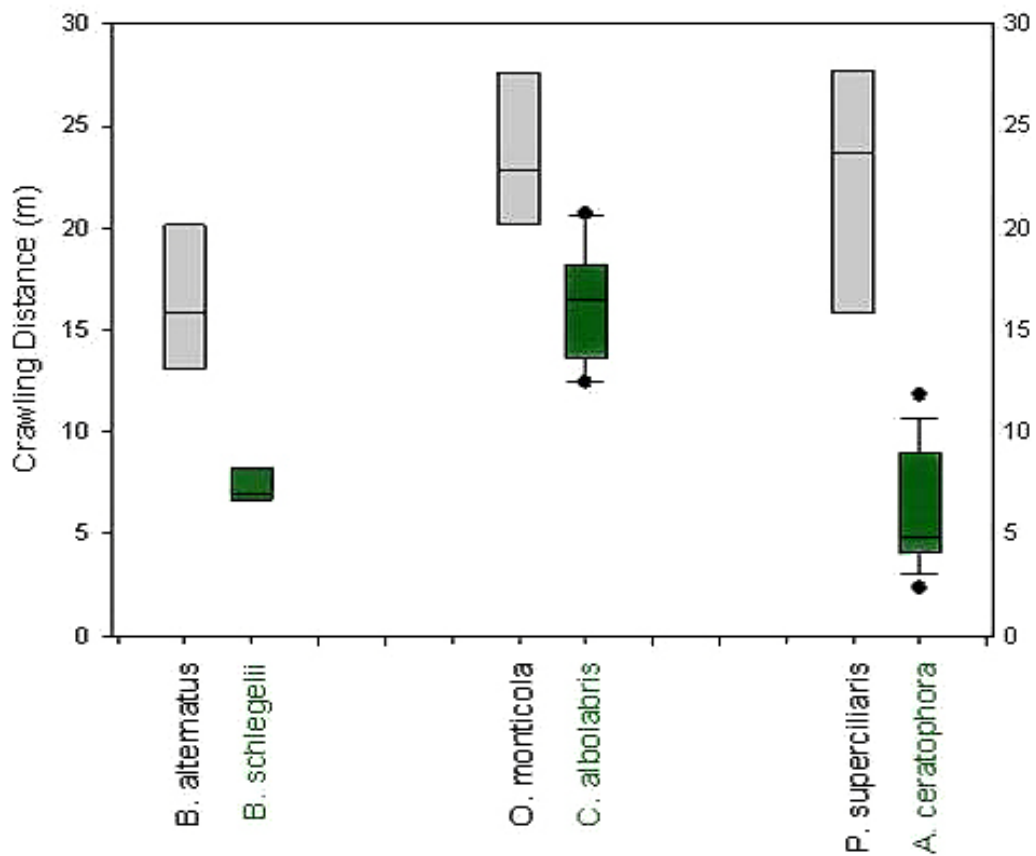
A slight trend was observed between sprint speed and relative mass (mass/total length) with larger snakes sprinting faster, but the trend was not significant ( $r = 0.06, P = 0.832$ ) (fig. 3.16). However, the observed power of the regression analysis was low ( $<0.800$ ). To ensure that body size did not affect analyses ANCOVAs were performed to remove any possible effect of body size.



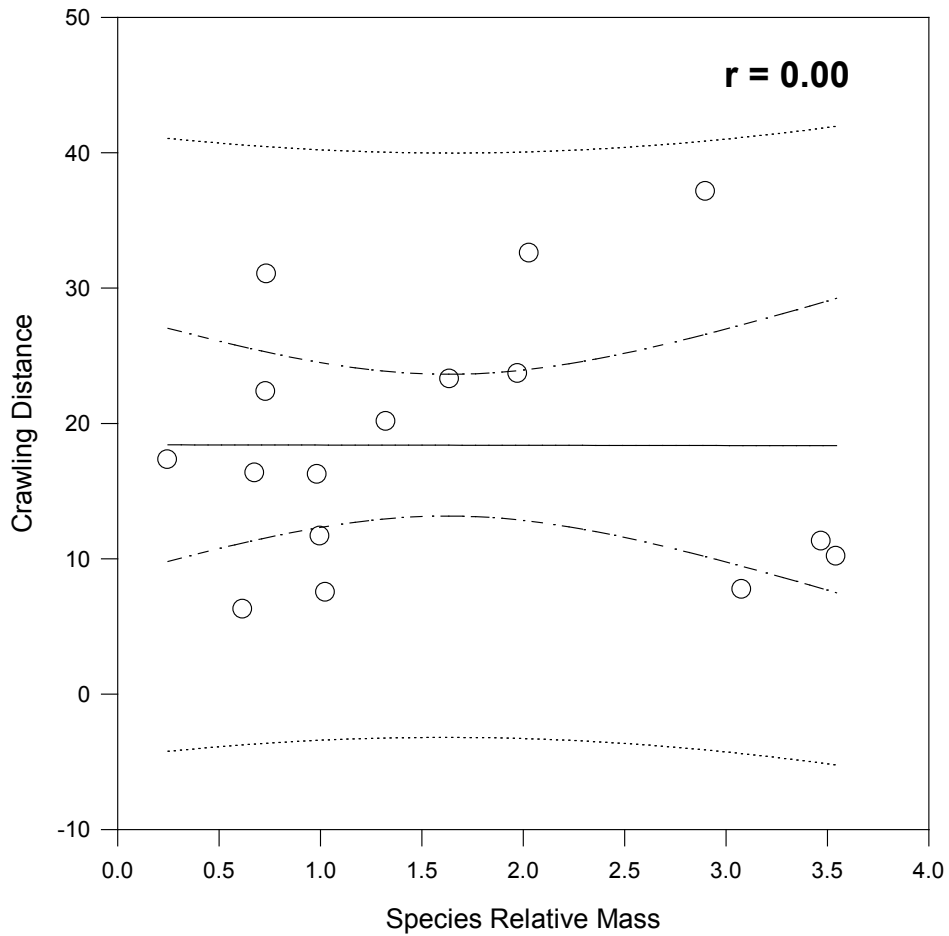
**Figure 3.9.** Distance crawled by the species pairs of the Family Boidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



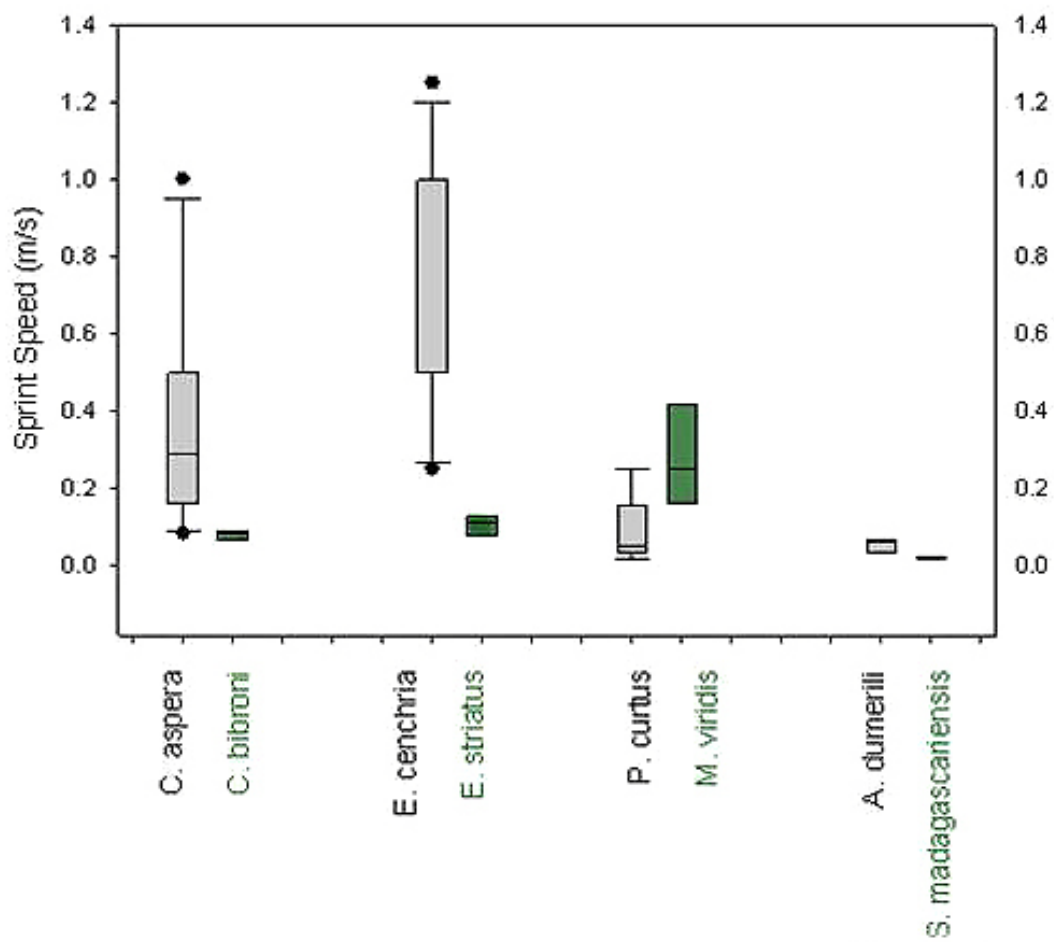
**Figure 3.10.** Distance crawled by the species pair of the Family Colubridae. Arboreal species is listed in green. Box plots represents median, and upper and lower quartile values.



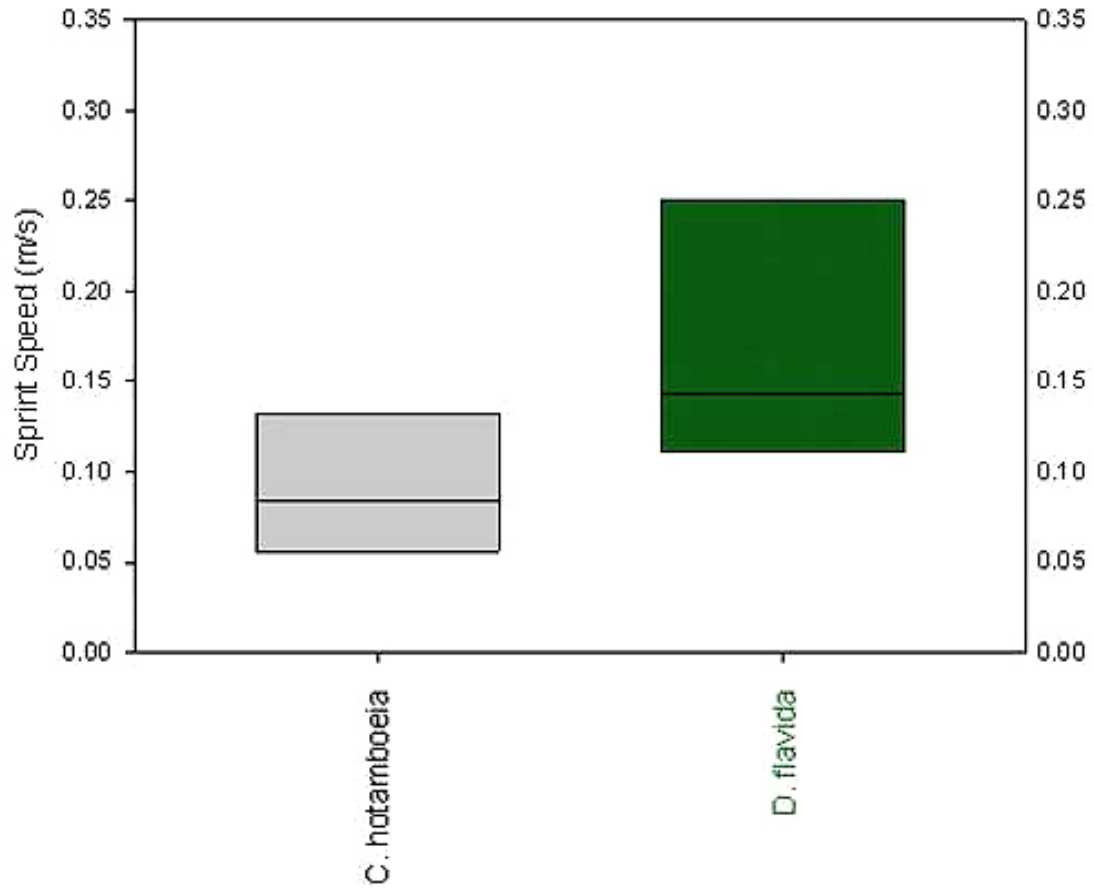
**Figure 3.11.** Distance crawled by the species pairs of the Families Crotalidae and Viperidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 3.12.** Relationship between distance crawled and relative mass (mass/total length) of snakes. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.

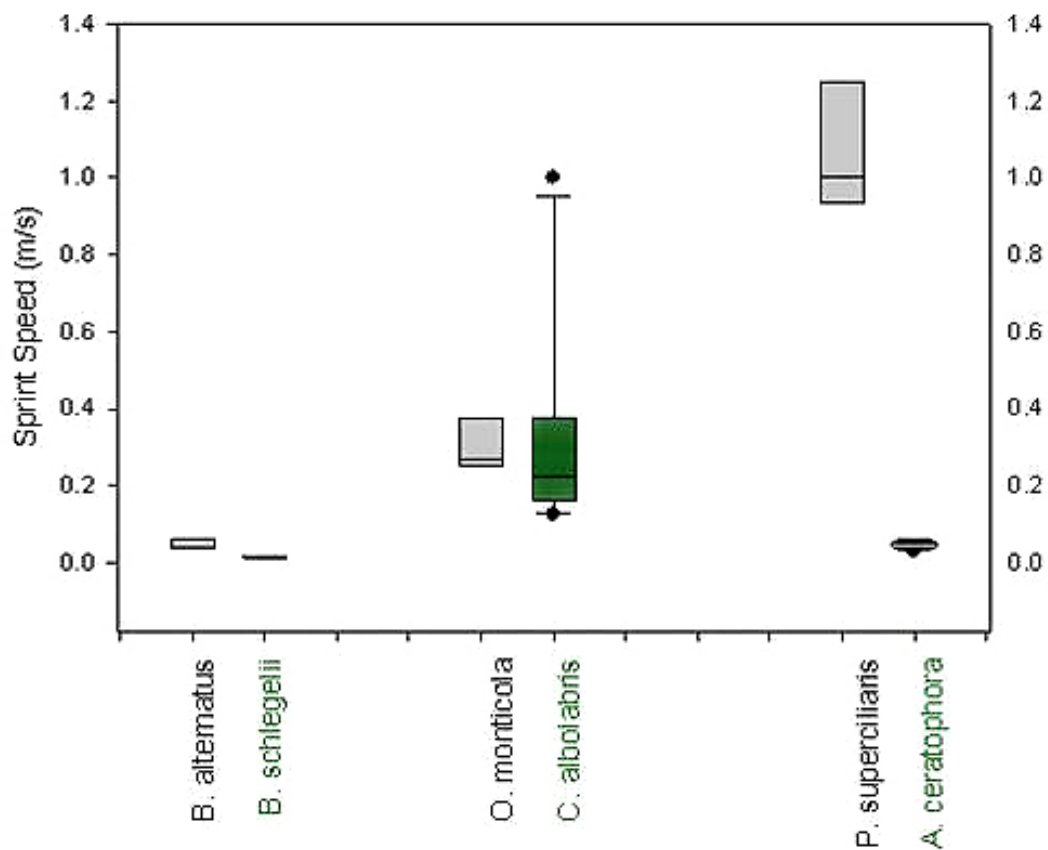


**Figure 3.13.** Sprint speed by the species pairs of the Family Boidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.

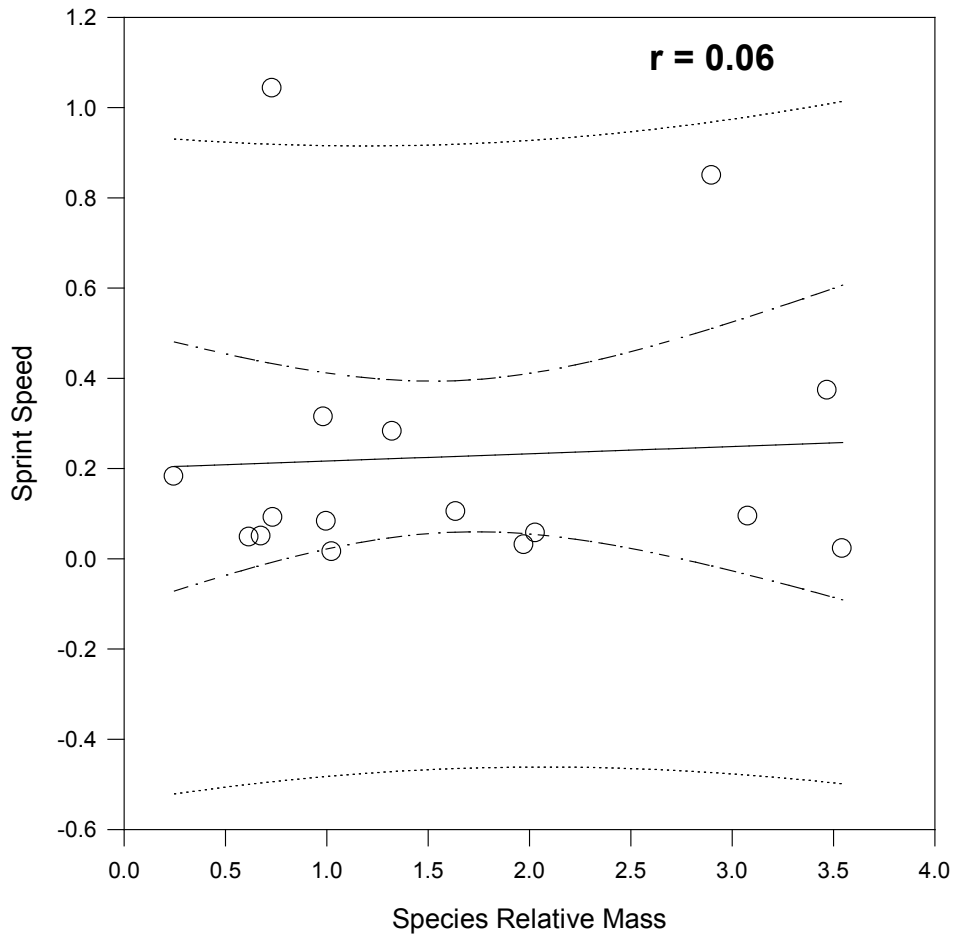


**Figure 3.14.** Sprint speed by the species pair of the Family Colubridae. Arboreal species is listed in green. Box plots represents median, and upper and lower quartile values.





**Figure 3.15.** Sprint speed by the species pairs of the Families Crotalidae and Viperidae. Arboreal species are listed in green. Box plots represent median, upper and lower quartile, non-outlier range, and outlier values.



**Figure 3.16.** Relationship between sprint speed and relative mass (mass/total length) of snakes. Data points represent mean values for species. The solid line represents the regression line, and the dashed lines represent the prediction and confidence intervals.

## **Discussion**

The evolution of arboreality in snakes has brought about a characteristic suite of morphological traits in accord with specialization for life in the trees. Being highly specialized for a given environment is expected to make those animals less capable in divergent environments. The idea that arboreal snakes are proficient in arboreal locomotor tasks at the expense of proficiency in terrestrial tasks is supported by the findings of this study. Locomotor performance trade-offs have arisen due to the characteristic morphology of arboreal snakes. Arboreal snake morphology provides advantages to arboreal locomotion, but, relative to terrestrial snakes, disadvantages to terrestrial locomotion

### *Climbing*

Understanding why an arboreal snake should have greater climbing endurance than a terrestrial snake begins by considering the effects of fluid dynamics and gravity. Snakes are tube-like in form. In a horizontal tube, fluid distributes itself evenly throughout the tube. However, orient that tube vertically and gravity forces the fluid towards the bottom of the tube. Gravity affects the body fluids of snakes in the same way. When climbing, the snake's body is orientated vertically and gravity acts upon the blood by forcing the blood downward. Pooling of blood in the posterior portion of the body is problematic for a snake because its brain is located in the anterior portion of the body. Maintaining cephalic blood flow is of critical importance to the immediate survival of the individual. In order to be an effective climber, snakes must overcome the effects of gravity on their body fluids.

The characteristic morphology of arboreal snakes appear well-suited to coping with the demands of gravity while climbing. One adaptation serves to control the effects of gravity on blood pressure differences in vertical and horizontal orientations. The heart of an arboreal snake is positioned more anteriorly than in a terrestrial snake (Seymour, 1987). A more anterior placement of the heart helps to sustain adequate blood flow to the brain during upright postures (Lillywhite, 1987). Seymour and Arndt (2004) determined that lessening the distance between the heart and head was the most important factor in maintaining blood pressure in the head while vertically oriented. Arboreal snakes have a smaller heart displacement when vertical than do terrestrial snakes (Young et al., 1997). As the heart is displaced further anteriorly, cardiac output is decreased (Young et al., 1994). Decreased cardiac output leads to decreased cephalic blood flow. A second adaptation affects blood circulation. Arboreal snakes have an integument that is more tightly bound to underlying tissue (Jayne, 1988). A tighter integument, along with relatively non-compliant tissue compartments (Lillywhite, 1993), works to lessen edema and blood pooling during climbing episodes (Lillywhite, 1996). For instance, blood pooling and reduced carotid blood flow during upright posturing has been shown in large-bodied terrestrial snakes that lack these morphological traits of arboreal species (Lillywhite and Smits, 1992). The arboreal morphology thus provides solutions to the problems imposed by gravity.

Vertical sprint performance was generally championed by the arboreal species. In six of the eight species, pairs the arboreal species outperformed the terrestrial species. Although three terrestrial species were excluded from analyses as they failed to achieve a minimum height of 1 m during the vertical sprint trials, these three species were clearly

outperformed by their arboreal counterparts. More compelling, the other three arboreal species, in comparison with the terrestrial members of their species pair, displayed vertical sprint speeds that were distinctly larger. Based upon the previous discussion of climbing endurance performance, it is not surprising that arboreal species would perform vertical sprints well. However, in two species pairs there was no difference in vertical sprint performance. *Atheris ceratophora* and *Bothriechis schlegelii* were found to be slow relative to the other arboreal species examined. These exceptions may be due to differential adaptation: e.g., stealth might be more important behaviorally to *A. ceratophora* and *B. schlegelii* in locomotor activities such as foraging, so that vertical burst of speed has been undeveloped. However, since no terrestrial snake was able to climb as far as its arboreal counterpart, it is clear that arboreal snakes are superior in climbing performance.

### *Crawling*

The characteristic morphology that makes arboreal snakes proficient climbers does generally accord with lowered proficiency in crawling. In six of eight species pairs comparisons, the terrestrial species outperformed the arboreal species in crawling endurance. The terrestrial anatomy has advantages for horizontally oriented activity: In terrestrial snakes the heart is more centrally located than with arboreal snakes. During horizontal posturing, this more central heart placement allows for an energetically favorable distribution of blood throughout the entire body. Greater blood distribution would be advantageous during crawling, but may not be adequately achieved with the more anterior placement of the heart in arboreal species.

That the terrestrial species did not outperform all the arboreal species in crawling may be due to species differences in foraging mode. While most of the species examined are active foragers, the two terrestrial species that rated lower than their arboreal counterparts in crawling endurance, *Candoia aspera* and *Python curtus*, are sit-and-wait predators. In nature, these two species are idle much of the time, and their behavioral repertoire lacks episodes of extended crawling. Accordingly, their low crawling endurance could be due to morphological modifications for their preferred foraging mode, or to lack of physical training. One other locomotor characteristic of these two species that could explain their different endurance is a difference in their gait. Although all snakes examined crawled using lateral undulation, *C. aspera* and *P. curtus* soon switched to a sidewinding gait. Sidewinding has been shown to have a lesser net energetic cost than lateral undulation (Secor et al., 1992). Given these complexities, further examination is required to elucidate the role morphology plays in the crawling endurance of these two species, although overall, terrestrial species were more proficient at crawling than were arboreal species.

As with performance in crawling endurance, the trend in sprint speed performance was towards terrestrial snake superiority, but superiority was not achieved in all instances. In five of the eight species pairs, the terrestrial member had the greatest sprint speeds. Two species pairs, *Dipsadoboa flavida*-*Crotaphopeltis hotamboeia* and *Cryptelytrops albolabris*-*Ovophis monticola*, failed to show a statistical difference in performance, and in one comparison the arboreal *Morelia viridis* sprinted faster than *Python curtus*, though the difference verged on non-significance ( $P = 0.044$ ). *D. flavida*, *C. albolabris*, and *M. viridis*, while all arboreal, will on occasion descend to the ground to

forage. This correlation suggests that a pressure to forage over a broad prey spectrum may force the maintenance of short burst ability in some arboreal snakes. The overall trend though supports the idea that arboreal snake morphology limit terrestrial locomotor proficiency.

### *Conclusions*

The results indicate that arboreal snakes outperform terrestrial snakes in arboreal tasks, and terrestrial snakes outperform arboreal snakes in terrestrial tasks. Such a scenario suggests the existence of locomotor performance trade-offs. The specialized morphology of arboreal snakes that make them more adept in the arboreal environment make them less adept in the terrestrial environment. Being less adept in the terrestrial environment can be a critical issue for an arboreal snake since so much of the planet's arboreal habitat is being converted anthropogenically to terrestrial habitat. In such a terrestrial habitat, an inability to perform as well as terrestrial snakes would reduce fitness among arboreal species. Thus, to manage conservation effective in arboreal snakes consideration of locomotor performance trade-offs is crucial.

## CHAPTER 4 SUMMARY AND CONCLUSIONS

Documenting a link between morphology and fitness in a manner that clearly establishes adaptation is challenging. Morphological traits can rarely be shown as adaptive, and attempts to do so are difficult and only rarely accomplished. Such testing, however, may be more achievable if morphology is linked to fitness through an intermediate link with performance. The morphology → performance → fitness paradigm proposed by Arnold (1983) states that morphological characters set limitations on performance, and in turn, performance sets limitations on fitness. Determining if a link exists between morphology and performance can be accomplished in a controlled laboratory setting. If a relationship is found, then such tests can be followed by testing for a link between performance and fitness in the field. This two-step paradigm represents a theoretical framework by which the adaptive nature of a morphological trait can be supported.

Problems may arise when comparing morphologies, unless the comparisons consider phylogenetic context. Shared evolutionary histories may be the source of interspecific morphological character values, and by extension of performance values. Species sharing a trait due to a phylogenetic relationship thus cannot be viewed as independent entities in comparative biology. However, at the point where two species diverge in a trait, then those species become independent with regard to that trait. Thus, species at points of evolutionary divergence are resources for fruitful comparative inquiries. Focusing on such species can circumvent problems that can arise from ignoring phylogenetic history.



Arboreal snakes are a group that allow for insightful comparative inquiries due to their characteristic morphologies and divergent evolutionary histories. Arboreal snakes have a suite of morphological characters that differentiate them from terrestrial snakes. Furthermore, snake phylogenies have become increasingly clearer, and points of divergence have been identified between several arboreal and terrestrial species. The divergent morphologies and divergent evolutionary histories of arboreal snakes create the ideal elements for testing hypotheses concerning the adaptive nature of arboreal morphological characters.

Determining the link between morphology and performance in arboreal snakes, the initial step in testing for adaptation, is the goal of this dissertation. To achieve this goal, closely related arboreal and terrestrial snake pairs were compared in their relative proficiency in arboreal and terrestrial locomotor tasks. Eight species pairs, spanning four families, were compared in their abilities in tasks related to arboreal versus terrestrial functions, their abilities to bridge gaps, traverse narrow diameter surfaces, climb, and crawl. Results established a strong link between arboreal morphology and arboreal locomotor performance.

The differential locomotor abilities of arboreal and terrestrial snakes show that the characteristic arboreal morphology represents a phenotype that is more adept, and more specialized for the arboreal environment. Arboreal snakes were superior in their abilities to bridge gaps and traverse narrow diameter surfaces. Without exception, arboreal snakes were able to cantilever their bodies a greater relative distance than their terrestrial counterparts. Likewise, arboreal snakes were able to cross surfaces of much narrower relative diameters than the terrestrial members of their species pairs.

Arboreal snakes were overall superior in their climbing abilities, but inferior in their crawling abilities relative to terrestrial snakes. In every instance arboreal snakes were found to have greater climbing endurance than their terrestrial partners. A trend for arboreal snake superiority in vertical sprint speeds was also observed, though in two of the eight species pairs there was no difference in this performance parameter. A lack of difference in vertical sprint speed performance suggests that in some terrestrial species natural selection may be acting to maintain the ability in terrestrial snakes to perform short, vertical bursts of locomotion. Such activities could be advantageous in avoiding a predator or overtaking a prey species by climbing into a low bush. It may be too that the morphological traits that afford arboreal snakes a high climbing endurance capacity may not always provide a differential performance over an initial, short-term interval. However, over longer term intervals arboreal snakes were found to always be the better climbers. The overall trend in climbing performance strongly suggests that the arboreal morphology provides for greater climbing proficiency.

Arboreal snakes however were not as proficient of crawlers. In the horizontal plane, arboreal snakes were generally outperformed by their terrestrial counterparts. Six of the eight species pairs found the terrestrial species having greater crawling endurance than the arboreal species. In the two exceptions, the terrestrial species were sit-and-wait predators. Adoption of a sit-and-wait foraging mode may bring with it conflicting selective pressures that constrain the ability to crawl relatively great distances. Extended periods of inactivity incurred while waiting for prey may also limit the physical training required for long distance movements. Again though, the overall trend was for arboreal inferiority in crawling proficiency.

As with crawling endurance, arboreal snakes were found to be less adept horizontal sprinters. In five of the eight species pairs, the arboreal species were outperformed by the terrestrial species. In two instances there was no difference in sprint speed between the arboreal and terrestrial species, and in one instance the arboreal species did outperform the terrestrial species, though the difference approached non-significance ( $P = 0.044$ ). Natural selection may be maintaining sprint speed in some arboreal species, but the overall trend supports the idea that arboreal snakes perform relatively poorly in the horizontal plane.

High proficiency locomotor performance in arboreal tasks with low proficiency performance in terrestrial tasks indicates that the arboreal morphology incurs a locomotor performance trade-off. Two tasks cannot simultaneously be performed optimally when the tasks require mutually exclusive morphologies (Shine et al, 2003). Arboreal snake morphology allows for locomotor adeptness in the arboreal environment, but at an apparent cost to locomotor adeptness in the terrestrial environment. Those morphological characters that counteract the effects of gravity on a vertically oriented snake make the animals less proficient when horizontal. The observed locomotor performance trade-off indicates a link between arboreal snake morphology and proficiency in arboreal locomotor performance.

Showing the link between morphology and performance is the first step towards establishing a link between morphology and fitness. Determining if a link exists between performance and fitness is the next step required to complete the test of the hypothesis that the characteristic morphology of arboreal snakes is in fact an adaptation for locomotion through the trees. The locomotor performance trade-offs observed with

arboreal snakes lends credence to the presumption that arboreal snakes have an adaptive advantage in vertical situations over other snakes.

Locomotor performance trade-offs have direct implications as to how and where an animal can exist (Zug, 1976). Animals cannot persist in environments where their performance levels are sub-minimal. The locomotor performance trade-offs observed with arboreal snakes suggest that arboreal snakes may lack the ability to persist in a terrestrial environment.

Unfortunately for arboreal snakes, anthropogenic alteration of forested habitats worldwide has converted much arboreal habitat into terrestrial habitat. The forests of Brazil have been reduced by 88% (Brown and Brown, 1992), and the forests of the eastern United States have been reduced to fragments that at present collectively represent 1-2% of their pre-colonial extent (Simberloff, 1992). For each year between 1990 and 1997 approximately 5,800,000 ha of tropical forests were lost, with another 2,300,000 ha being visibly degraded (Achard et al., 2002). The grand scale on which alteration of forested habitats is taking place is nearly beyond comprehension.

The conservation of forest-dependent species becomes a challenge with so much arboreal habitat being transformed into terrestrial habitat. Several vertebrate groups have suffered population declines associated with the anthropogenic alteration of forested habitats (Newmark, 1991). Those vertebrate groups include primates (Struhsaker, 1998; Von Hippel et al., 2000), bears (McLelland and Schackleton, 1988), birds (Willis, 1974; Newmark, 1991; Kattan et al., 1994), and amphibians (Gibbons et al., 2000; Burrowes et al., 2004). Arboreal snakes, with their specialized morphology and relatively low

proficiency in terrestrial locomotor performance would certainly be a group negatively impacted by the loss of forested habitats.

Quantifiable measures are needed to assess a species' vulnerability to habitat alteration (Laurance, 1991; Harcourt, 1996). Because not all species respond negatively to habitat alteration (Wilson and Johns, 1982; Laurance and Laurance, 1996; Neufeld, 1998; Anderson, 2001; Germano et al., 2003), a means is necessary to discern which species are at most risk. With snakes, vulnerability to habitat alteration may be able to be ascertained through measures of locomotor performance. By sampling snakes as a group (terrestrial, arboreal, intermediate) it may be learned if threshold locomotor performance values exist whereby animals above the threshold are able to persist in altered habitats while those below the threshold perish. Existence of a performance threshold may explain the current distribution of snake species with regards to altered habitats.

Examining potential performance thresholds has utility in interspecific comparisons, but also is of interest in intraspecific comparisons. Do some species exhibit enough plasticity in locomotor performance to allow some individuals to exploit altered habitats while other individuals cannot? Inter and intraspecific comparisons of locomotor performance thresholds in snakes provide much fodder for such future research inquiries. It may be found that locomotor performance measures allow conservationists the ability to predict which species would be most vulnerable to the alteration of forested habitats.

In all, the findings presented in this dissertation show that a link exists between the morphology and performance of arboreal snakes. The differences in arboreal-terrestrial snake morphology afford arboreal snakes greater proficiency in arboreal locomotor performance. Superiority in arboreal locomotor performance however comes

at the expense of proficiency in terrestrial locomotor performance. The morphology that allows arboreal snakes to excel in the trees constrains their relative performance when on the ground. Such a trade-off in locomotor performance will certainly have ecological repercussions, particularly with regards to the anthropogenic alteration of forested habitats. The morphology → performance → fitness paradigm is now half complete with regards to arboreal snakes. Future research is needed to complete the paradigm, and in doing so, complete a rigorous testing of the hypothesis that arboreal snake morphology is in fact, an adaptation for life in the

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