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ORIGINAL PAPER

Arboreal habitat structure affects route choice by rat snakes

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Abstract In arboreal habitats gaps between branches and branch structure profoundly affect the ability of animals to move; hence, an ability to perceive such attributes could facilitate choosing routes that enhance the speed and ease of locomotion. Although many snakes are arboreal, no previous study has determined whether they can perceive structural variation of branches that is mechanically relevant to their locomotion. We tested whether the gap distance, location, and attributes of two destination perches on the far side of a crossable gap affected the route travelled by North American rat snakes (*Pantherophis*), which are proficient climbers. Snakes usually chose routes with shorter gaps. Within a horizontal plane, the snakes usually went straight rather than crossing an equal distance gap with a 90° turn, which was consistent with our finding that crossing a straight gap was easier. However, decreasing the distance of the gap with a 90° turn eliminated the preference for going straight. Additional factors, such as the width of the landing surface and the complexity of branching of the destination perches, resulted in non-random route choice. Thus, many of the observed biases in route choice suggested abilities to perceive structural variation and select routes that are mechanically beneficial.

Keywords Locomotion · Vision · Arboreal · Habitat structure · Affordance

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Introduction

As stated eloquently by Kording (2007), “The world is complicated, and consequently so is deciding”. Among the many decisions that confront animals are the fundamental issues of where to go and how to get there, and a prerequisite for deciding where to go is the ability to perceive relevant differences in the environment. For the locomotion of animals, vision is often important for perceiving environmental variation as demonstrated by the abilities of diverse species, such as humans, chicks, toads, chameleons, and spiders, to determine what routes are passable or impassable and to plan detours around obstacles (Lock and Collett 1979; Collett and Harkness 1982; Regolin et al. 1994; Tarsitano and Andrew 1999; McVea and Pearson 2009).

The networks of branches in arboreal habitats create discrete choices which can facilitate studying how animals select routes. In addition, the effects of habitat structure on locomotion are especially well documented for some arboreal reptiles. For example, the sprinting speeds of *Anolis* lizards decrease with decreased branch diameter (Losos and Sinervo 1989; Losos and Irschick 1996), whereas the speeds of rat snakes decrease when cylinder diameter increases (Astley and Jayne 2007). Some large diameter cylinders are impassable for rat snakes, but the addition of branch-like projections allows snakes to traverse them easily and quickly (Astley and Jayne 2009). Thus, the effects of environment on locomotor performance may depend on the behavior and body plan of animals, which can provide different affordances (Gibson 1986; Carello and Wagman 2009) for different species in an identical environment.

The combined importance of vision and biomechanical demands in arboreal habitats is further suggested by

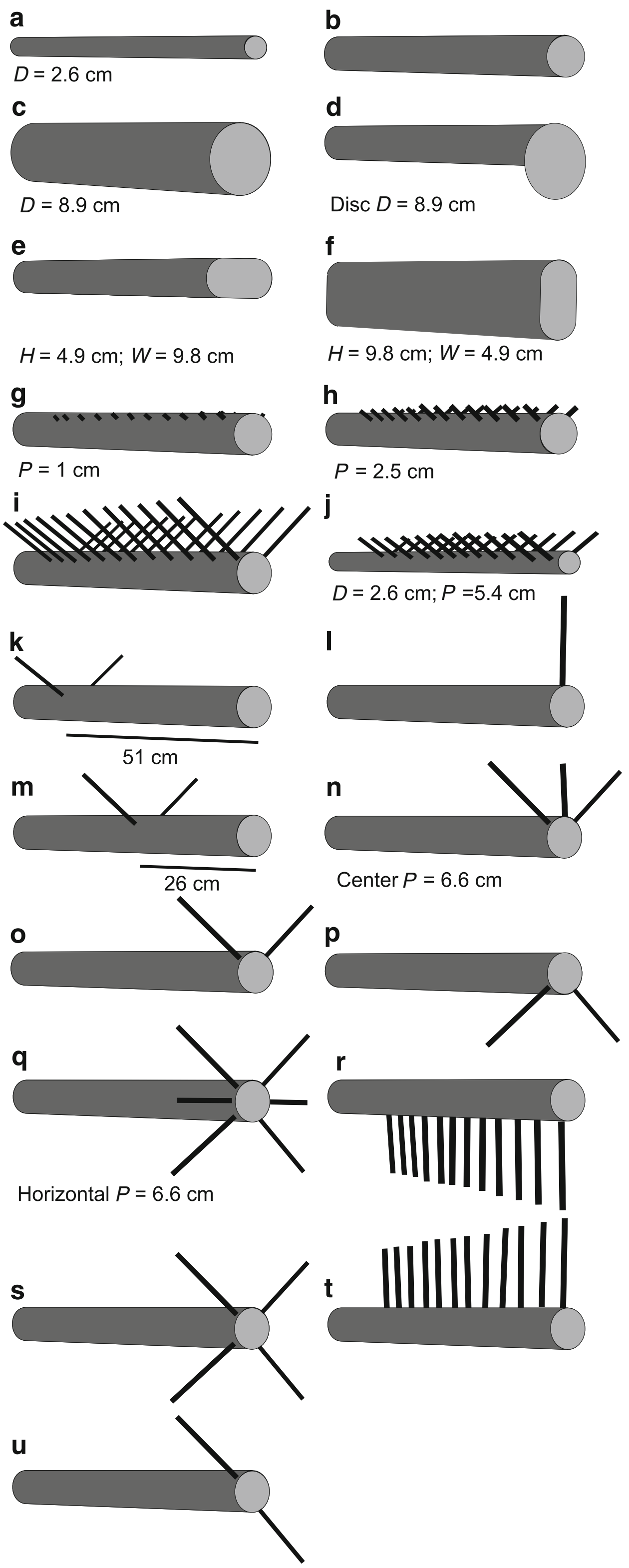


Fig. 1 Types of perches used in experiments. The views of the perches approximate the perspective from sighting along the long axis of the initial perch toward the destination perches that were oriented 45° relative to the initial perch. The right side of each figure indicates the end of the destination first encountered by the snake. Unless indicated otherwise, the diameter (D) of the primary surface was 4.9 cm, the length of the pegs (P) was 10 cm, and the nearest peg was located 1 cm from the end of the perch. H and W are the overall height and width of the perch, respectively ▶

anatomical specializations, such as large eyes and grasping appendages in primates (Strasser et al. 1998) and the convergent evolution of large eyes and slender, light weight bodies in several lineages of arboreal snakes (Henderson and Lillywhite 1993; Pizzatto et al. 2007). Despite these correlations, suggesting that both vision and biomechanical factors are likely to affect route choice of arboreal animals, quantitative data on this topic are sparse despite their considerable ecological relevance and potential for providing general insights into visually guided behaviors. One laboratory study found that three species of *Anolis* lizards preferred routes with the larger perch diameter (Mattingly and Jayne 2005), but whether this bias arose simply from increased object size or benefits for locomotor performance is unclear.

For two species of closely-related snakes that commonly climb trees, we tested for biased choice within pairs of destinations with variable size, shape, and branching structure (Fig. 1) or variable distance and location across a gap. We expected the snakes to prefer destinations that were likely to be biomechanically beneficial. For example, for the range of diameters used in this and previous studies (Astley and Jayne 2007, 2009) the speed of locomotion on the destination should increase and the risk of falling should decrease with decreased cylinder diameter and with the presence of pegs or greater numbers of pegs along the length of the upper half of the surface. In addition, the ease of crossing a gap should increase with decreased gap distance and straighter trajectories (Jayne and Riley 2007), and the ease of landing on the destination should increase with increased destination width. When differences in biomechanical benefits were absent we expected that the snakes might choose perches with larger dimensions or greater numbers of pegs, which could make them more conspicuous.

Methods

Experimental subjects

We studied 15 adults of two closely related species (Pyron and Burbrink 2009) of North American rat snakes (formerly *Elaphe*), *Pantherophis obsoletus* ($N = 8$) and *P. guttatus* ($N = 7$). These species are proficient climbers which are found commonly in trees (Wright and Wright 1957; Conant and Collins 1991). We obtained all snakes from commercial suppliers, and the snout–vent lengths (SVL), of the snakes ranged from 97 to 139 cm. The snakes were housed individually in 100-liter cages with incandescent lights, which allowed the snakes to regulate their body temperature between 25 and 37°C.

General experimental procedures and apparatus

The following general procedures were followed both for experiments determining gap-bridging ability and for tests of perch preference. The snakes were fasted for a minimum of 7 days before experiments, and we did not use any snakes when their eye scales were cloudy from ecdysis. Prior to experiments we placed snakes in a heated chamber to control the body temperature of the snakes, and we used a PE-1 infrared temperature gun (Pro Exotics, Littleton, CO, USA) to verify that the body temperatures of the snakes during experiments were between 29 and 31°C, which is similar to the field active body temperatures of these species (Brattstrom 1965). The room in which tests were conducted had a floor 3.4 × 3.4 m and a ceiling that was 3.2 m high. To provide a uniform visual background, we covered all walls of the room with white drop cloths. The two fluorescent light fixtures in the ceiling created a symmetrical pattern of lighting relative to the starting position of the snake. The far end of the perch upon which the snakes were placed initially was in the center of the room.

With only two exceptions (Fig. 1e, f) the primary surfaces upon which snakes crawled in all experiments were cylindrical. All of these primary surfaces were 78 cm long, and in all experiments the long axes along their top-center positions were in a horizontal plane approximately 1.5 m above the floor. To provide a uniform color and a surface texture that facilitates the locomotion of snakes (Astley and Jayne 2007), we covered all primary surfaces with Nashua 394 duct tape (Berry Plastics, Franklin, MA, USA). To simulate a variety of branching complexity and positions, we often added 6-mm diameter wooden pegs to the primary surface (Fig. 1g–u). We use the term perch to refer collectively to the primary surface and all associated pegs or other objects.

Gap-bridging performance

We first used type i perches (Fig. 1) to determine the gap-bridging ability of all snakes for three trajectories within a horizontal plane (0° = straight, 45° and 90° turns). The turn angles were between the long axes of the initial and destination perches such that the vertex of the angle was at the top-center of the primary surface at the departure end of the initial perch. The experimenter stood in a standardized location directly behind the initial perch to release the snakes with their heads pointed toward the gap. Although the snakes often spontaneously crawled away from the experimenter and crossed the gap, at other times the snakes were coaxed to move by lightly touching their tails. We increased the gap distance by 5 cm after each successful crossing until the snake failed to cross a particular gap in three attempts or refused to attempt to cross five times. After the snake rested 1 day, we again attempted to get the snake to cross that last gap distance attempted the previous day. If the snake did not cross this gap, then we reduced the gap distance by 2.5 cm.

Choice tests

We subsequently used a total of 42 treatments (Fig. 1; Tables 1, 2, 3, 4, 5, 6) to gain insights regarding how diverse stimuli (gap distance, turn angle, and the attributes of perches) might influence the perch choice made by snakes when crossing gaps, which are pervasive in arboreal habitats. In all of these experiments we chose gap distances that could be crossed by all of the snakes, and the surfaces of all destinations were passable to all snakes although the ease and speed of crawling on them could vary substantially. In only 1 of more than 3,000 trials did a snake first touch one destination and then ultimately crawl completely onto the other destination. Thus, for all practical purposes tactile cues were not used to choose between the pair of destinations.

We presented all snakes with only one treatment per day comprised of six trials per snake. In the first round we conducted three trials in rapid succession for each snake, and after at least 1 h of rest and transposing the left and right destination perches, we conducted three more trials per snake. The testing order of the snakes in different treatments was randomized, and the overall order of the 42 treatments was haphazard to reduce the influence of experience and time. In all experiments the perch upon which the snakes were placed initially was type i (Fig. 1). The snakes were handled and released as was done for the tests of gap bridging performance. The initial perch and

Table 1 Overall width (*W*) and height (*H*) of perches

Type	*W* (cm)	*H* (cm)
a	2.7	2.7
b	4.9	4.9
c, d	8.9	8.9
e	9.8	4.9
f	4.9	9.8
g	5.3	5.1
h	7.4	6.2
i, k, m, n, o, p	18.1	11.5
j	8.9	5.8
l, r, t	4.9	14.9
q, s, u	18.1	18.1

Table 2 Effects of turn angle and gap distance on choice of type i perches with oblique rows of pegs

Perch 1	Perch 2	Pref1 (%)	t	P
0° (35 cm)	45° (35 cm)	59 ± 8.9	1.07	0.3025
0° (35 cm)	90° (35 cm)	91 ± 3.9	11.48	<0.0001*
45° (35 cm)	90° (35 cm)	96 ± 2.5	18.51	<0.0001*
90° (20 cm)	0° (40 cm)	53 ± 8.0	0.32	0.7531

Values in parentheses are gap distances

* $P <$ critical value after performing a sequential Bonferroni correction for $N = 42$

Table 3 Effects of gap distance on choice of type i perches with oblique rows of pegs

Perch 1 gap (cm)	Perch 2 gap (cm)	Δgap (cm)	rel. Δgap (%)	Pref1 (%)	t	P
10.0	12.5	−2.5	−22	70 ± 4.9	4.05	0.0012*
10.0	15.0	−5.0	−40	79 ± 5.7	5.03	0.0002*
10.0	20.0	−10.0	−67	85 ± 4.0	8.75	<0.0001*
20.0	22.5	−2.5	−12	72 ± 6.4	2.86	0.0126
20.0	25.0	−5.0	−22	73 ± 5.6	4.06	0.0012*
20.0	30.0	−10.0	−40	77 ± 4.2	6.29	<0.0001*
20.0	40.0	−20.0	−67	99 ± 1.1	44.00	<0.0001*
30.0	32.5	−2.5	−8	63 ± 4.1	3.30	0.0052
30.0	35.0	−5.0	−15	69 ± 4.7	4.01	0.0013*
30.0	40.0	−10.0	−29	85 ± 4.7	7.45	<0.0001*
35.0	40.0	−5.0	−13	66 ± 5.9	2.68	0.0181

* $P <$ critical value after performing a sequential Bonferroni correction for $N = 42$

both destinations were always in a horizontal plane, and with the exception of the four treatments in Table 2, the two destination perches were 45° to the left and right of the initial perch. All treatments other than those in Tables 2 and 3 used 35-cm gaps for both destinations, and all of the destinations for the treatments in Tables 2 and 3 were type i perches (Fig. 1).

In four of our treatments during choice tests we manipulated turn angles ranging from 0° to 90° (Table 2). In 11 treatments we varied the gap distances from 10 to 40 cm and the difference between the distances of the two gaps (Δgap) ranged from 2.5 to 20 cm (Table 3). In seven treatments we manipulated the diameter (2.6–8.9 cm) or the shape of the perches without pegs (Fig. 1a–f; Table 4).

The remaining 20 treatments (Tables 5, 6) used in choice tests varied in the arrangement of pegs on the primary surface. When pegs were in rows along the length of the perch (Fig. 1g–j, r, t), they were spaced at 5-cm intervals. For pegs on the destination perches that were in two rows inclined at 45° relative to the horizontal (Fig. 1e–h), the lengths of pegs, P, ranged from 1 to 10 cm. For a pair of pegs 10 cm long and inclined at 45° relative to the horizontal, we varied their distance from the nearest end of the destination perch from 1 to 51 cm (Fig. 1k, m, o), but in all other cases the peg on the destination perch that was nearest to the snake was 1 cm from the end of the perch. Additional manipulations of the number and orientation of pegs emphasized the location within 1 cm of the end of the destination perch first encountered by the snake crossing the gap (Fig. 1). The different arrangements of pegs created considerable variation in the overall height, H, and width, W, of the perches, which are summarized in Table 1.

To determine whether or not potential olfactory cues left behind by snakes biased perch choice, we conducted preliminary tests with 12 snakes using type i perches (Fig. 1), 35-cm gap distances, 45° turn angles and the general procedures described above. Before the first trial, all the snakes crawled on one of the destination perches, whereas

Table 4 Effects of size and shape of perches without pegs on perch choice

Perch 1 type	Perch 2 type	ΔW (cm)	ΔH (cm)	rel. ΔW (%)	rel. ΔH (%)	Pref1 (%)	t	P
c ●	a •	6.2	6.2	107	107	82 ± 4.9	6.48	<0.0001*
f ▮	b ●	0	4.9	0	67	71 ± 7.3	2.88	0.0119
e ▬	b ●	4.9	0	67	0	69 ± 6.9	2.75	0.0156
e ▬	f ▮	4.9	−4.9	67	−67	60 ± 5.8	1.79	0.0951
a •	b ●	−2.2	−2.2	−58	−58	62 ± 6.9	1.70	0.1116
c ●	b ●	4.0	4.0	58	58	63 ± 9.2	1.46	0.1656
d ●	b ●	4.0	4.0	58	58	58 ± 7.4	1.03	0.3193

* $P <$ critical value after performing a sequential Bonferroni correction for $N = 42$

Table 5 Effects of peg length, location, and orientation versus a bare cylinder on perch choice

Perch 1 type	Perch 2 type	ΔW (cm)	ΔH (cm)	rel. ΔW (%)	rel. ΔH (%)	Pref1 (%)	t	P
Peg length								
i 	b 	13.2	6.6	115	81	89 ± 4.5	8.52	<0.0001*
h 	b 	2.5	1.3	41	20	83 ± 5.7	5.71	<0.0001*
h 	i 	−10.7	−5.3	−41	−23	63 ± 6.6	1.97	0.0687
g 	b 	0.4	0.2	8	4	64 ± 8.4	1.67	0.1176
c 	j 	0	3.1	0	42	53 ± 7.1	0.41	0.6889
Peg distance								
o 	b 	13.2	6.6	115	81	75 ± 3.8	6.60	<0.0001*
m 	b 	13.2	6.6	115	81	66 ± 4.8	3.33	0.0050
k 	b 	13.2	6.6	115	81	71 ± 9.0	2.30	0.0373
Peg orientation								
p 	b 	13.2	6.6	115	81	84 ± 5.8	5.93	<0.0001*
t 	b 	0	10.0	0	101	71 ± 7.0	2.94	0.0108
l 	b 	0	10.0	0	101	68 ± 7.5	2.38	0.0320
r 	b 	0	10.0	0	101	64 ± 9.4	1.50	0.1549

* $P <$ critical value after performing a sequential Bonferroni correction for $N = 42$

for the other destination perch we used materials that had never touched a snake. During the choice tests, after any trial in which the snake crawled upon the clean perch, the tape on the primary surface was replaced with clean tape. Thus, we presumed that the perch that was never cleaned accumulated much more odor than that for which the tape was replaced, but we found no significant difference in preference between these perches ($t_{11} = 1.11$, $P = 0.29$; see below). As an added precaution for unknown olfactory cues in all other choice tests, after each trial we cleaned all surfaces of the perches by wiping them with a clean rag dampened with 70% ethanol, and we replaced the duct tape each day before our first round of testing.

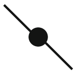
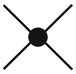
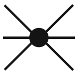
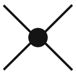
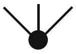
To further clarify the likely importance of vision in this system, we performed one additional treatment in a dark room using a pair of destinations (b and i) for which previous treatments had shown snakes had a biased choice of destination. We used ATN Viper night vision goggles (Black Lion Optics, Union City, IN, USA) to allow us to handle and manipulate the snakes as was done for the treatments in the light. We videotaped these trials using a Sony model HC 42 camcorder with an infrared illuminator that was 120 cm directly above the gap between the initial and destination perches. If the snakes did not cross the gap to a destination after 5 min, the trial was terminated. Only one trial was performed per individual. All procedures were approved by the Institutional Animal Care and Use Committee of the University of Cincinnati (protocol number no. 07-01-08-01: B.C.J.).

Data analysis

In order to pool the results of the gap-bridging performance tests, we converted the values of maximum gap distance crossed by each snake to a percentage of its SVL. For all of the possible pairs of three turn angles used in the performance tests, we used paired t tests to determine if gap-bridging performance of all 15 snakes differed significantly between turn angles ($P < 0.05$).

To characterize the perches used in the choice tests, we calculated the absolute difference in gap distance (Δgap)

Table 6 Effects of peg number and orientation on perch choice

Perch 1 type	Perch 2 type	ΔW (cm)	ΔH (cm)	rel. ΔW (%)	rel. ΔH (%)	Pref1 (%)	t	P
Constant peg orientation, variable number								
i 	o 	0	0	0	0	52 ± 7.7	0.32	0.7555
Variable peg orientation, constant number								
t 	r 	0	0	0	0	67 ± 7.3	2.32	0.0362
u 	o 	0	6.6	0	45	55 ± 6.3	0.80	0.4377
p 	o 	0	0	0	0	55 ± 6.9	0.69	0.4999
Variable peg orientation and number								
o 	l 	13.2	−3.4	115	−26	79 ± 6.0	4.82	0.0003*
s 	o 	0	6.6	0	45	76 ± 5.3	4.87	0.0003*
q 	s 	0	0	0	0	66 ± 5.1	3.13	0.0074
o 	n 	0	0	0	0	54 ± 4.4	0.89	0.3878

Note perches i, r, and t have rows of pegs along their length

* $P <$ critical value after performing a sequential Bonferroni correction for $N = 42$

between a pair of destination perches within a treatment and the relative differences in gap distance (rel. Δgap), overall width (rel. ΔW), and overall height (rel. ΔH) by converting the absolute difference to a percentage of the mean value of an attribute for both destination perches (Tables 3, 4, 5, 6). For example, in the treatment for which perches 1 and 2 had gap distances of 10 and 20 cm, respectively, $\Delta\text{gap} = -10$ cm and rel. $\Delta\text{gap} = -67\%$. We estimated the angular size of different dimensions (H angle, W angle) as twice the arctangent of one-half of the dimension of interest divided by the distance from the edge of the initial perch to that object of interest as seen from an end-on view of the destination perch.

For each individual within each treatment in the choice tests, we calculated preference as the percentage of the total number of crossings that were made by a snake to a particular destination. For each treatment we then calculated the mean value of the individual preferences for perch 1 (Pref1). With only one exception (perch c vs. b), preliminary analyses using two-sample t tests revealed no significant differences in Pref1 between the two species within any treatment. Thus, to simplify presentation of the results, we relied primarily on pooled data from all 15 individuals of both species to calculate Pref1 for each treatment before performing a t test to determine if the value of Pref1 differed significantly ($P < 0.05$) from the value expected (50%), if the snakes chose randomly. In all of the tabular summaries of results perch 1 by definition is the perch within a pair with the higher value of Pref1.

To facilitate evaluating the effects of making multiple comparisons as suggested by Moran (2003), we provide exact P values (Tables 2, 3, 4, 5, 6). In addition, our tabular data compare our original uncorrected P values to the critical values resulting from performing a sequential Bonferroni correction (Rice 1989) that divided 0.05 by the rank order of the P values for all 42 treatments. Unless stated otherwise, all mean values are reported ± SE.

Results

Gap-bridging performance

The gap-bridging performance for a 90° turn (mean = 42.7% SVL) was significantly shorter than that of both the 45° turn ($t_{14} = 2.70$, $P = 0.02$) and the straight trajectory ($t_{14} = 3.21$, $P = 0.006$). The gap-bridging performance for snakes crossing gaps with a 45° turn (mean = 45.4% SVL) did not differ significantly from that of snakes moving straight (mean = 45.4% SVL).

Choice tests

Gap distance and turn angle

For identical types (i) of destination perches with oblique rows of pegs, the snakes crossing gaps of equal distances preferred a route with a 0° or 45° turn rather than a 90° turn (Table 2). However, when the route with the 90° turn had a gap distance one half that of the straight route, we found no significant preference (Table 2). For trials with equal (45°) turn angles, snakes preferred crossing shorter gaps. The preference for a particular perch (Pref1) for the 11 trials in Table 3 was significantly correlated with Δgap ($r = -0.91$, $P < 0.001$) and rel. Δgap ($r = -0.88$, $P < 0.001$) but not with mean gap distance within each pair of destinations ($r = -0.07$, $P = 0.82$).

Size and shape of perches without pegs

For destinations without pegs (Table 4), the snakes strongly preferred the very large diameter cylinder compared to the smallest diameter cylinder (c vs. a), but some other smaller differences in diameter were chosen randomly (c vs. b). The snakes had marginally significant preferences for the short and wide perch relative to a cylinder with the same overall height (e vs. b) and for the tall and narrow perch relative to a cylinder with the same overall width (f vs. b). In pairings where H and W of the primary surface differed by less than 60%, no significant preference was detected (Table 4).

Peg length, longitudinal location and circumferential orientation

Depending on their size and where they are located around the circumferences or along the length of the primary surface, pegs could provide benefits for the crawling and landing of snakes after crossing a gap. Thus, we tested how these three factors might bias choice for a variety of destinations with pegs compared mostly to cylinders lacking pegs (Table 5). All but one of the treatments in Table 5 involved perches with the same diameter of the primary surface. Perches with two oblique rows of pegs along their length were preferred strongly compared to a cylinder lacking pegs, unless the pegs were so short that they barely increased the overall height or width of the perch (g vs. b). No significant preferences were observed either for a small diameter cylinder with pegs of moderate length compared to a large cylinder with equal overall width (c vs. j) or for the longest pegs compared to intermediate length pegs on similar cylinders (h vs. i). One pair of pegs oriented either obliquely up (o) or down (p) was also sufficient to elicit a strong preference compared to a simple cylinder, but the strength of this preference decreased as the pegs were located farther from the snake and the far edge of the gap (Table 5). Compared to a simple cylinder, perches either with a longitudinal row of pegs (t) or single peg (l) pointing up elicited a marginally significant preference, whereas a vertical row of pegs pointed down (r) was not preferred significantly.

Destinations with pegs varying in number and orientation

All remaining treatments with constant turning angle and gap distance (Table 6) compared destinations that both had pegs. We manipulated the numbers of pegs while holding peg orientation constant and vice versa as well as simultaneously varying these two factors. Collectively, these treatments sought to isolate the effects of peg numbers from some of the confounding effects of different peg orientation and overall dimensions. The snakes did not prefer the perch with two oblique longitudinal rows of pegs (i) compared to a perch (o) with a single V-shaped pair of pegs near its end. The snakes had a marginally significant preference for the perch with a vertical row of pegs pointing up (t) rather than down (r), but they had no preference for whether or not the oblique pair of pegs was oriented up (o) or down (p). The snakes strongly preferred the perch with a V-shaped pair of pegs (o) compared to a single peg pointing up (l), and the X-shaped pattern of four pegs (s) was strongly preferred to the V-shaped peg pattern (o). For the two pairs of destinations with no differences in either overall height or width, in one case (q vs. s) the snakes preferred the destination with the greater number of pegs, but in the other case (o vs. n) no significant preference occurred. We detected preferences in only two of the five trials for which both ΔW and ΔH were zero (Table 6).

Multiple regression analysis

To gain additional insights into which differences between attributes of destinations may be necessary but not sufficient to predict the decisions made by the snakes, we performed forced-fit multiple regressions with ΔW, ΔH, Δarea, Δgap, Δangle as independent variables and Pref1 as the dependent variable. Our final choice of model was the regression with the highest value of r^2 and one in which each of the independent variables had a significant coefficient. Although ΔW by itself did not significantly affect path choice across all trials, ΔW was significant ($P = 0.00147$) in the final model, which also included Δgap ($P = 0.00002$) and Δangle ($P = 0.00001$) and accounted for nearly half of the variance observed in preference ($r^2 = 47\%$). When multiple regression models included ΔW, Δgap and Δangle, neither ΔH nor Δarea contributed significantly to predicting preferences.

Darkness versus light

For the first trial of each individual in the treatment with perches b and i in the light, the mean time taken to cross the gap to a destination was 16 ± 5 s, and the longest time taken to cross to a destination was 80 s. By contrast, 11 of the 15 individuals tested in darkness neither touched nor crawled onto a destination before the trials were terminated after 300 s. Of the four snakes that did cross to a destination, two individuals chose perch b (after 33 and 255 s) and two chose perch i (after 225 and 239 s). All four of the snakes that crawled completely onto a destination in darkness only touched the one destination that they ultimately crawled onto.

Discussion

All of the options encountered by the snakes in the choice tests involved passable routes with variation in the destinations that was likely to affect three major biomechanical demands (extending across a gap; landing and crawling performance on the destination) and visual appearance. Many of the preferences that we observed for the snakes in our study suggest that they have a capacity to make decisions regarding route choice and can evaluate options based on action-relevant properties (Fajen 2009).

Biomechanical factors

Several biomechanical factors related to arboreal locomotion facilitate interpreting the variation in behavior that we observed. The forces required to resist pitching downward when a snake cantilevers are proportional to a quadratic function of gap distance because both the mass of the snake and the lever arm through which this mass acts increase as the snake extends across a gap (Jayne and Riley 2007). Thus, for the greatest values of Δgap in a pair of destinations used in choice tests in this study (Table 3, 10 vs. 20 cm; 20 vs. 40 cm), we would expect a fourfold increase in the forces required to support the cantilevering snake to reach the more distant destinations. Increasing the distance between the near edge of the gap and center of mass of the body of the snake on the initial perch facilitates cantilevering (Jayne and Riley 2007) by opposing the tendency to pitch downward, but a right angle turn effectively precludes this option. The strong preference we observed for snakes crossing shorter gaps was consistent with avoiding the rapid increase in forces associated with supporting weight while bridging larger gaps. The strong preference for bridging a shorter gap also appeared to override the aversion to bridging a gap requiring a right angle turn.

In addition to the probable ease of going straight rather than bridging a gap with a 90° turn, going straight would maximize the rate at which the animal moves away from a presumed averse stimulus. However, this latter factor does not appear to be sufficient to explain the behavior of the snakes because they had no preference for going straight across a longer gap compared to making a right angle turn to cross a shorter gap.

In addition to gap distance and orientation, the structure of the destinations often had biomechanical consequences and affected the choices of the snakes. For example, opposite its effect on limbed animals such as lizards (Losos and Sinervo 1989; Losos and Irschick 1996), increased cylinder diameter (including from 2.6 to 8.9 cm for horizontal surfaces) decreases the maximum speeds of rat snakes (by 50%) and in extreme cases (diameter >20 cm) creates a nearly impassable surface (Astley and Jayne 2007). However, projections such as pegs can make large diameter and inclined at cylindrical surfaces passable to snakes as well as increasing their speed more than tenfold compared to horizontal cylinders lacking pegs that are passable without pegs (Astley and Jayne 2009). While crawling horizontally rat snakes create alternating left and right loops of the body that usually contact only the upper one-half of the cylindrical surfaces or droop down vertically from the sides of the cylinder (Astley and Jayne 2007, 2009). Consequently, projections are most useful for enhancing crawling performance either when they arise from the top half of a cylinder or extend beyond the sides of a cylinder when they arise from its lower half.

The snakes in our study preferred several types of destinations with greater overall width. Since the final approach of snakes was from above the perch, greater width seems the aspect of size most relevant for facilitating landing on the perch after bridging a gap. A well-established finding for human reaching is that performance is improved by larger target size, which makes the target more conspicuous and decreases the precision of motor control required to reach and touch it (Fitts 1954; Murata 1999). The strong preference for V-shaped patterns of pegs compared to simple cylinders seems to be easier to understand because this structure benefits both landing and crawling, is likely to be visually more conspicuous and has no apparent costs. Unlike the greater width created by longer pegs, the greater width of simple cylinders creates a biomechanical trade-off between benefiting landing and impeding the crawling of snakes. Thus, the preference of snakes for largest diameter cylinder rather than the narrowest one may indicate that perch attributes that facilitate landing are favored compared to those that facilitate crawling.

The snakes in our study and those studied previously (Jayne and Riley 2007) usually bridge gaps by placing their chin on the top-center of the destination before crawling on it. Peg-like projections on the top-center of the near edge of the destination perch hinder this behavior of landing on the most horizontal portion of the cylinder, as evidenced by the frequent sideways slipping of snakes in our study when they landed on such perches (Fig. 11l, t). However, the marginally significant preferences for destinations with top-center projections compared to destination of equal overall width lacking these (t vs. b, l vs. b and t vs. r) may indicate either that this cost for landing is trivial or it is small compared to the benefits for crawling.

Collectively, when only biomechanical factors are considered, most choices of the snakes were consistent with the following hierarchy for making decisions. First and foremost, choose the destination that is easiest to reach. For destinations with equal proximity (in a horizontal plane), chose the one with the straightest trajectory. For combinations of different proximity and trajectories, closer proximity trumps straighter trajectory. If the ease of getting to destinations is similar, then select one that increases the ease of landing. If the ease of landing is similar, then choose the destination that increases the ability to crawl. Thus, the overall hierarchy of decision making may reflect the order of the tasks rather than an equal weighting of all factors influencing the sequence of tasks (cantilevering, landing, and crawling) involved in this composite behavior.

Possible visual cues

The visual properties of different destinations may help explain some of the outcomes that did not appear conform to the scheme above based only on biomechanical factors. Contrary to the biomechanical expectation that for a given Δgap preference should increase with increased mean gap distance, the reverse was often observed (Table 3). Perhaps this seeming paradox occurs because the angular dimensions of the destination increase with decreases in the distance to the animal (Collett and Harkness 1982), and thus detecting disparities in gap distance may be easier when a pair of perches is closer to the animal. Snakes, especially highly arboreal species, have a significant binocular overlap, and they have the ability to accommodate (Walls 1942; Sivak 1977; Caprette 2005; Ott 2006). These traits may allow snakes to use many of the mechanisms used by other animals to estimate distance and object size (Collett and Harkness 1982), but definitive experimental data on this topic are lacking.

Perhaps diverse animals could share a bias for selecting visually more conspicuous destinations regardless of their biomechanical consequences. For limbed animals such as mice (Barnum et al. 1992) and anole lizards (Mattingly and Jayne 2005), it is difficult to determine whether they prefer moving on larger cylinders because they benefit running speed or because they are more conspicuous. The preference for larger cylinders by snakes in our study may provide stronger support for a bias favoring a more conspicuous destination in light of the costs for crawling (Astley and Jayne 2007), but the potential benefits for landing on the surfaces after crossing a gap could confound this issue. Thus, additional trials were designed to help resolve the roles of appearance versus biomechanical benefits in deciding between destinations.

The importance of visual conspicuousness for decision making by the snakes in our study may be supported best by the preferences within those pairs lacking any conspicuous differences in biomechanical benefits for either landing or crawling (Tables 4 f vs. b, 6 s vs. o, q vs. s). Although we do not know the visual perspective of the snakes at the time they choose a route, the end-on and 45° perspectives seem reasonable to emphasize. Objects can be visually more conspicuous as a result of increased size in one dimension, increased area or increased amount of edges. Thus, the slight preference for perch f compared to b could result from its more than twofold increase in the area from the end-on view, greater height or greater area as seen from an oblique perspective (Fig. 1).

The preferences for s vs. o and q vs. s were correlated with an increased number of pegs at the end of the destination without any obvious benefits for either landing or crawling. These and other results (Tables 5 r vs. b, 6 i vs. o) may indicate that increased amount of edges at the end and to the sides of a destination may receive greater weighting for decision making rather than just the total amount of pegs and edges. Another interesting issue regarding the number of pegs (or branches) is whether or not at some density they create crevices that are perceived as shelter from a threat or as an obstacle like the barriers resembling picket fences used by Lock and Collett (1979) to study the detouring behavior in toads.

We only studied route choice by snakes that were probably motivated to evade the experimenter, during which greater importance may be placed either on the benefits surfaces provided for locomotion or for shelter from a threat. However, especially in a natural setting, visual attributes of perches and perch choice are also likely to be correlated with behaviors and functions other than locomotion such as providing camouflage from prey, facilitating thermoregulation or choosing a microhabitat likely to have prey (Shine et al. 2002).

For the oblong perches with equal cross-sectional areas (Fig. 1e, f) the short-wide perch was preferred slightly to the tall-narrow perch. Although the context is very different, the classic studies of the feeding response of toads (Ewert 1982) provide ample precedent for how animals can perceive and respond differently to objects with identical areas but unequal height and width. In addition, different lengths and depths of chasms affect whether toads take a detour, step into the chasm or hop over it (Lock and Collett 1979). Adding pegs to our smallest diameter cylinder (j) so that overall width equaled that of the largest cylinder (c) eliminated the preference for the larger diameter, and this further suggests the importance of width and other visual cues rather than only the overall projected area of an object. The primacy of overall width over other cues may be further supported by the biomechanically unexpected results that the V-shaped pair of pegs was not preferred to the inverted V shape or the oblique pair (Table 6 p vs. o, u vs. o).

When pegs were recessed far back beyond the edge of the destination perch (Fig. 1m, k), the landing benefits were eliminated, but benefits for crawling could still occur belatedly. Accordingly, snakes preferred them to a bare cylinder, but the strength of preference decreased as the pegs were farther from the gap (Table 5). Perhaps this diminished preference indicates that the decreased angular width of the pegs with increased distance from the snakes, or that the farthest pegs might have been approaching limits of their perceptual range.

The perch with rows of 1-cm long pegs (Fig. 1g) was not preferred to the same size cylinder without pegs (Table 5, g vs. b) despite markedly enhancing the ability of the snakes to crawl and despite other choices favoring perches beneficial for crawling but not landing (Table 5 t vs. b, l vs. b). The 1-cm pegs did not appreciably alter either the overall height or width of the perch compared to a cylinder, which may have contributed this apparent inability of the snakes to perceive some surfaces as beneficial for crawling. Friction also has profound consequences for the locomotion of animals, especially snakes, but this property is often not evident from visual cues. In addition to some low-friction artificial cylindrical surfaces being impassable (Astley and Jayne 2007, 2009), some combinations of bark texture and trunk diameter prevent rat snakes from climbing trees to gain access to the nests of birds upon which they prey (Mullin and Cooper 2002). Perhaps these snakes might not be able to discern this possibility visually, and instead they may have to attempt to climb some surfaces to determine if they are passable.

How animals use space has profound consequences for diverse behaviors, such as dispersal, exploiting resources, and evading predators, and locomotor performance is a key determinant of how space can be used. A related issue is the extent to which habitat structure has predictive value for locomotor performance, and this has been clarified by integrative studies of locomotor performance, behavior and habitat partitioning in model systems such the arboreal anole lizards (Schoener 1968; Losos 1990; Losos and Irschick 1996). However, the rather uniform proximate choices between discrete routes that are correlated with performance benefits may not correspond to the overall preferences for different habitat structure among different ecomorphs (Mattingly and Jayne 2004). Our results not only emphasize the role of biomechanical benefits for predicting route choice, they also illustrate the importance of sensory cues. For example, some biomechanically beneficial surfaces apparently could not be perceived, and other choices may have resulted primarily from a sensory bias toward more salient perches rather than from an obvious biomechanical benefit. Consequently, these latter types of information appear to hold great promise for generating a more integrated understanding of locomotor behaviors of animals than can be attained from either performance or habitat preference in isolation.

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