

Visual Contrast and Intensity Affect Perch Choice of Brown Tree Snakes (*Boiga irregularis*) and Boa Constrictors (*Boa constrictor*)

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ABSTRACT

Habitat structure can affect animal movement both by affecting the mechanical demands of locomotion and by influencing where animals choose to go. Arboreal habitats facilitate studying path choice by animals because variation in branch structure has known mechanical consequences, and different branches create discrete choices. Recent laboratory studies have found that arboreal snakes can use vision to select shapes and locations of destinations that mechanically facilitate bridging gaps. However, the extent to which the appearance of objects unrelated to biomechanical demands affects the choice of destinations remains poorly understood for most animal taxa including snakes. Hence, we manipulated the intensity (black, gray, or white), contrast, structure, and locations of destinations to test for their combined effects on perch choice during gap bridging of brown tree snakes and boa constrictors. For a white background and a given perch structure and location, both species had significant preferences for darker perches. The preference for darker destinations was strong enough to override or reduce some preferences for biomechanically advantageous destinations such as those having secondary branches or being located closer or along a straighter trajectory. These results provide a striking example of how visual cues unrelated to the physical structure of surfaces, such as contrast and intensity, can bias choice and, in some cases, supersede a preference for mechanically beneficial surfaces. Because these two species are so phylogenetically distant, some of their similar preferences suggest a sensory bias that may be widespread in snakes. The manipulation of surface color may facilitate management of invasive species, such as the brown tree snakes, by enhancing the efficiency of traps or making certain objects less attractive to them.

1. Introduction

Habitat structure can affect animal movement both by affecting the mechanical demands of locomotion and by influencing where animals choose to go. Animals as diverse as snails (Atkinson, 2003), spiders (Tarsitano, 2006), ants (Graham and Collett, 2006), fish (Bisazza et al., 1997), frogs (Munteanu et al., 2016), lizards (Lustig et al., 2013), and cats (Poucet et al., 1983) often plan routes rather than just moving randomly through the environment. Once the capacity for nonrandom movement is established, a deeper understanding of this capacity can be obtained by determining the cues that animals use to choose different routes. The ability of animals to plan and make a detour around an impassible obstacle has been an important and dominant method for gaining insights into path choice (Kabadayi et al., 2018). However, besides the dichotomy of passable versus impassable, a wide variety of physical structures in the environment creates a continuum in variation that can affect the speed and ease of animal locomotion as well as providing the cues that could be used to make choices.

Arboreal habitats are a model system for studying path choice by animals because variation in branch structure has known mechanical consequences, and different branches create discrete choices. The mechanical effects of habitat structure on movement can be affected by variation in behavior and morphology within a body plan as well as among different body plans. For example, the decrease in the running speeds of anole lizards associated with decreased branch diameter is less severe for species with short compared to long limbs (Losos and Sinervo, 1989), whereas decreased branch diameter commonly increases the locomotor performance of arboreal snakes (Jayne et al., 2015). The diameter of branches upon which anoles are found is also positively correlated with the relative limb length of different species (Schoener, 1968; Pounds, 1988; Losos, 1990), but species with different limb lengths have a remarkably uniform preference for the biomechanically beneficial thicker branch when they encounter a branching point as they are running (Mattingly and Jayne, 2005). This emphasizes the importance of using experimental approaches to directly test for the cues that affect path choice rather than relying solely on microhabitat

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preference as well as a likely primacy of mechanical attributes for predicting the paths that animals choose.

The paths that animals choose while they are moving can also be affected by the nature of the task. For example, the preference of snakes for larger rather than smaller diameter cylinders when bridging gaps seems counterintuitive at first glance because the locomotion of snakes on cylinders is impeded by increased diameter (Mansfield and Jayne, 2011; Jayne et al., 2014). However, a larger cylinder diameter increases target size, and this facilitates reaching tasks by requiring less precise motor control (Jayne et al., 2014). Thus, while bridging gaps, the preference of snakes for choosing destinations with a structure that facilitates making first contact may override factors that affect the subsequent locomotion on the surface.

In addition to possible mechanical consequences of choosing different destinations, the common preference of large objects by arboreal animals could be the result of larger objects simply being visually more conspicuous. Thus, a lingering problem is that many of the attributes that affect the mechanics of moving on and between branches, such as larger branch diameter, secondary branches or greater width, also seem likely to make a destination visually more conspicuous (Mansfield and Jayne, 2011). Modifying the color or intensity of objects provides a convenient experimental method for altering how visually conspicuous objects are without an attendant effect on the mechanical attributes that would affect the ease of locomotion.

In this study we varied the intensity (white, gray, and black) of objects as well as the distance, location, and structure of artificial branches and used choice tests primarily to determine how visual cues unrelated to the mechanical demands for animal movement affect the choice of destinations. We used snakes bridging gaps for our model system as the mechanical demands of this task and many effects of perch structure on gap bridging performance, locomotion, and perch choice are already well understood, including for our study species (Byrnes and Jayne, 2012; Jayne et al., 2014, 2015; Mauro and Jayne, 2016). We used two phylogenetically distant species (brown tree snakes and boa constrictors) to gain insights into the generality of any possible preferences. First, we tested whether these snakes preferred a particular destination intensity (i.e. shading was black, gray, or white) when all other factors were constant. Second, we tested whether the background intensity (black or white) affected the preference for the intensity of the destination. Finally, we investigated the interactions between different destination intensities, variation in perch structure, and perch location that affected the ease of bridging gaps. For a given perch structure, we expected the snakes to prefer intensities of destinations that made them more visually conspicuous by increasing their contrast relative to the background. We also expected that a preference for biomechanically advantageous destinations would supersede any preferences for intensity or contrast.

2. Materials and methods

2.1. Experimental subjects

Our two study species are phylogenetically very distinct. Brown tree snakes (*Boiga irregularis*) belong to the family Colubridae, which is nested deeply within a large clade of “advanced” snakes (infraorder Caenophidea), whereas boa constrictors (*Boa constrictor*) belong to the family Boidae which is basal to all of the advanced snakes (Figueroa et al., 2016). The clade arising from the most recent common ancestor of *Boa* and *Boiga* contains all but two of the 22 Alethinophidian families, and this clade contains more than 87% of the more than 3,500 of known extant species (Figueroa et al., 2016). The family Colubridae, to which *Boiga* belongs, arose more than 50 million years after its most recent common ancestor with Boidae (Sanders et al., 2010).

Brown tree snakes are highly arboreal (Rodda et al., 1999a), and they have a slender body and anatomical specializations in axial musculature (Hoefer and Jayne, 2013) that have repeatedly evolved within

several clades of arboreal caenophidian snakes (Jayne, 1982). Although boa constrictors lack any obvious morphological specializations for arboreality (Hoefer and Jayne, 2013), they commonly climb trees, especially as juveniles (Greene, 1983). Both of these species have strong nocturnal tendencies, but they are not exclusively nocturnal (Greene, 1983; Rodda et al., 1999a).

The brown tree snakes that we used ($n = 16$) were collected from Guam in 2010 and 2011, whereas the boa constrictors ($n = 14$) were born and raised in captivity. The experiments with the brown tree snakes and boa constrictors were performed during 2017 and 2018–2019, respectively. The brown tree snakes (3 females and 13 males) had average values of snout-vent length (SVL) of 159 cm (range = 119–179 cm) and mass of 808 g (range = 540–1020 g), whereas the boa constrictors (9 females and 5 males) had average values of SVL of 133 cm (range = 126–143 cm) and mass of 1154 g (range = 900–1555 g). We housed the snakes individually in cages with incandescent bulbs that allowed regulation of body temperature to 25–33 °C. We did not test any snakes within 5 days of being fed or when their eyes were cloudy as a result of ecdysis. The care of the animals and experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Cincinnati (protocol number 07-01-08-01), and the brown tree snakes were captured and imported with permits from the U.S. Fish and Wildlife Service (MA214902; MA3500A-0).

2.2. Experimental apparatus

The test apparatus had a cylindrical (length = 80 cm, diameter = 5 cm) starting perch and two destination perches in a horizontal plane 150 cm above the ground (Fig. 1). With the exception of two treatments (Fig. 1C; Table 1 tmt 19, 20), we arranged the perches in a Y-shape so that the trajectories to the alternative destinations from the end of the starting perch had a yaw angle of 45° (Fig. 1A,B; Table 1). In treatments 19 and 20, one of the destinations was along a straight trajectory, whereas the other required a 90° turn (Fig. 1C; Table 1).

With the exception of two treatments (Fig. 1B; Table 1 tmt 17, 18), the standard distances of the gaps between the ends of the starting perch and the destinations were 47 and 45 cm for the brown tree snakes and boa constrictors, respectively. These standard gap distances are approximately 70% of the maximal relative gap distance (%SVL) that our study species can bridge when following a straight horizontal trajectory (Jayne and Riley, 2007; Hoefer and Jayne, 2013). To test the effects of gap distance in treatments 17 and 18, one of the destinations was 10 cm closer than the alternative destination with the standard gap distance.

To create a uniform background, all of the walls of the 3.2 x 2.6 m and 2.4 m high experimental area were covered by canvas cloth, and the inner surface of the chamber wall behind destination perches was also covered either with overlapping 107 cm wide strips of white poster paper (Hewlett Packard durable banner paper with DuPont Tyvek) oriented vertically or a black cloth (only tmt 4, 7). The base and vertical pipe to which the destination perches were attached were placed behind the background material which had 5 cm diameter holes so that each destination perch extended into the arena while the vertical support was hidden. Fluorescent light fixtures (with a total of 18 28 W 3500 K bulbs), suspended 45 cm below the ceiling, provided illumination, and the brightness of the incident light at the edge of the gap was approximately 600 lux.

For ten destinations, we varied the presence of pegs and whether the pegs, the sides, and the end of the large cylinders were black, gray, or white (Fig. 2). The pegs always had a diameter of 4 mm and a length of 10 cm. Whenever pegs were present, they were oriented 45° relative to a horizontal plane (Fig. 2). Each destination cylinder was covered with white, black, or gray Shurtape P-665® gaffer's tape (Shurtape Technologies, LLC; Hickory, NC USA 28602) to provide a uniform color and a texture that reduced the slipping of snakes. We painted the pegs on the destination perches black, white, or gray. To facilitate locomotion

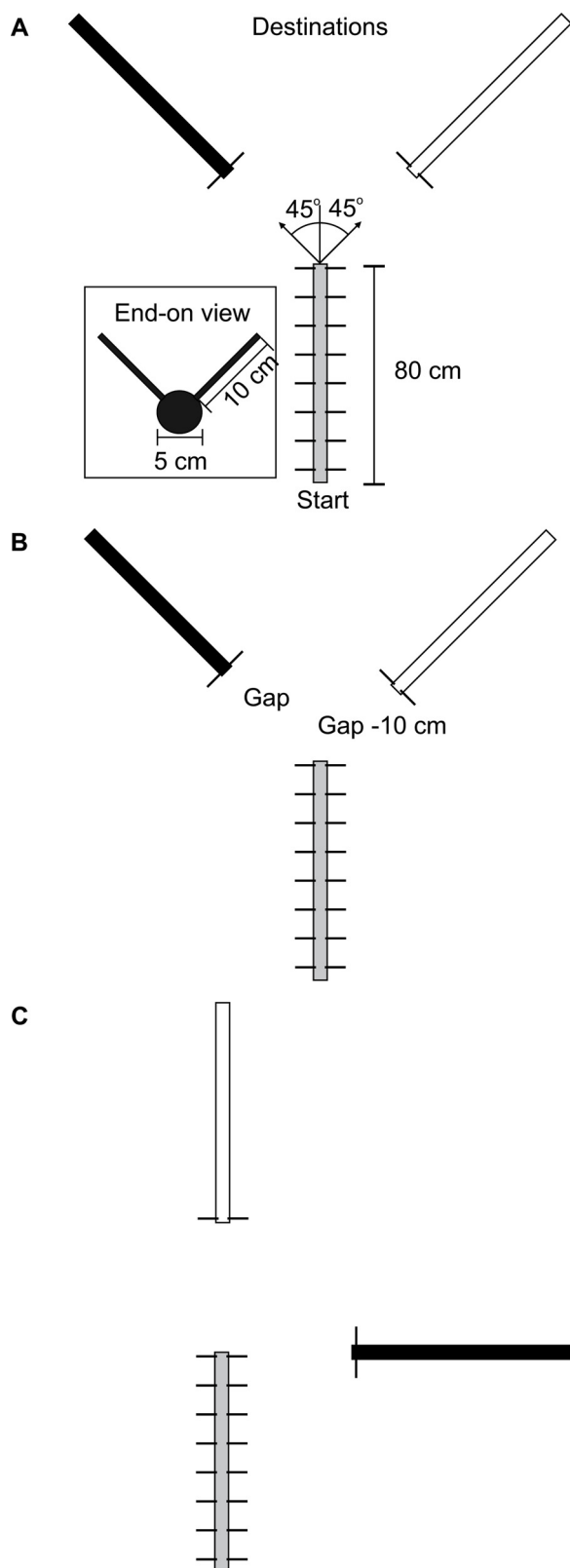


Fig. 1. Overhead view of the experimental apparatus. All perches were 1.5 m above the ground, and the standard gap distances were 47 cm for *B. irregularis* or 45 cm for *B. constrictor*. **A.** For treatments 1–16 (Table 1) both destinations had a standard gap distance and a yaw angle of 45° from the end of the starting perch. **B.** For treatments 17–18, one of the gap distances was 10 cm less than the standard distance. **C.** For treatments 19–20, both destinations had a standard gap distance, but the yaw angles were 0° and 90°.

Table 1

Mean $\pm$ s.e.m. preference for perch 1 (Pref1) of the two destinations (Fig. 1) placed 47 cm (*B. irregularis*) or 45 cm (*B. constrictor*) and oriented 45° from the starting perch, unless noted otherwise. As in Fig. 2, text indicates surface intensities of white (w), gray (g) or black (b), for the destinations (sides, end, pegs) and background (Bkg). *P*-values are uncorrected for multiple comparisons, but * indicates significant after a table-wide sequential Bonferroni correction.

Tmt	Destination			<i>B. irregularis</i> (n = 16)		<i>B. constrictor</i> (n = 14)	
	Perch 1	Perch 2	Bkg	Pref1 (%)	<i>p</i>	Pref1 (%)	<i>p</i>
1	A (b,b,b)	B (w,w,w)	w	84 $\pm$ 4	< 0.001*	85 $\pm$ 5	< 0.001*
2	A (b,b,b)	C (g,g,g)	w	63 $\pm$ 6	0.024	67 $\pm$ 4	0.001*
3	C (g,g,g)	B (w,w,w)	w	79 $\pm$ 4	< 0.001*	86 $\pm$ 5	< 0.001*
4	A (b,b,b)	B (w,w,w)	b	67 $\pm$ 6	0.004	37 $\pm$ 5	0.013
5	D (b,b,-)	B (w,w,w)	w	48 $\pm$ 7	0.389	51 $\pm$ 6	0.452
6	A (b,b,b)	D (b,b,-)	w	78 $\pm$ 6	< 0.001*	86 $\pm$ 5	< 0.001*
7	A (b,b,b)	I (w,w,-)	b	68 $\pm$ 7	0.015	86 $\pm$ 3	< 0.001*
8	G (b,b,w)	D (b,b,-)	w	68 $\pm$ 6	0.003	82 $\pm$ 5	< 0.001*
9	A (b,b,b)	E (w,w,b)	w	75 $\pm$ 5	< 0.001*	63 $\pm$ 6	0.022
10	G (b,b,w)	E (w,w,b)	w	64 $\pm$ 6	0.022	56 $\pm$ 7	0.176
11	A (b,b,b)	F (w,b,w)	w	67 $\pm$ 6	0.004	83 $\pm$ 4	< 0.001*
12	E (w,w,b)	B (w,w,w)	w	67 $\pm$ 6	0.009	70 $\pm$ 6	0.002*
13	A (b,b,b)	G (b,b,w)	w	66 $\pm$ 4	0.001*	55 $\pm$ 5	0.168
14	H (b,w,b)	F (w,b,w)	w	50 $\pm$ 6	0.999	70 $\pm$ 6	0.002*
15	F (w,b,w)	E (w,w,b)	w	53 $\pm$ 6	0.314	58 $\pm$ 7	0.125
16	A (b,b,b)	J (w,b,b)	w	60 $\pm$ 4	0.014	69 $\pm$ 5	0.001*
17	A (b,b,b)-10 cm	A (b,b,b)	w	69 $\pm$ 5	< 0.001*	71 $\pm$ 7	0.003
18	A (b,b,b)-10 cm	B (w,w,w)	w	74 $\pm$ 5	< 0.001*	58 $\pm$ 6	0.102
19	A (b,b,b) 0°	A (b,b,b) 90°	w	89 $\pm$ 4	< 0.001*	92 $\pm$ 3	< 0.001*
20	B (w,w,w) 0°	A (b,b,b) 90°	w	71 $\pm$ 5	< 0.001*	61 $\pm$ 6	0.041

and gap bridging, the starting perch was also covered with gray gaffer's tape, and it had two parallel rows of pegs placed at 10 cm intervals along the length of the perch (Fig. 1).

2.3. Experimental procedures for choice tests

To reduce possible confounding effects of prior experience, we divided individuals of each species into two batches, and each batch of snakes within a particular species experienced the treatments in a different randomized order. For different treatments, we also randomized the order of testing individuals within a batch. Prior to testing, we placed the snakes in a heated container until their body temperatures were 29–31 °C, which is within range of their field active body temperatures (Montgomery and Rand, 1978; Anderson et al., 2005). At the beginning of each trial, we placed the snake on the end of the starting perch farthest from the gap, and we orientated the snake towards the destinations while standing directly behind the starting perch. If the snake did not move within 10 s, we gently tapped or lifted the snake's tail to prompt it to move. Each trial concluded when the snake crawled onto a destination. After testing each snake three times in rapid succession for a particular treatment, the snakes rested for at least two hours before another bout of three trials in which the left-right position of the same pair of perches was reversed.

Previous studies found that possible olfactory cues from snakes repetitively crawling on the destinations did not influence choice with a gap distance $\geq$ 40 cm (Mansfield and Jayne, 2011; Hoefer and Jayne, 2013). However, as an added precaution to minimize a possible effect of olfactory cues, we cleaned each destination perch with paper towels dampened with 70% ethanol after each snake completed its set of three trials. Furthermore, we replaced the tape covering the destinations after each batch of snakes had completed three trials for a particular

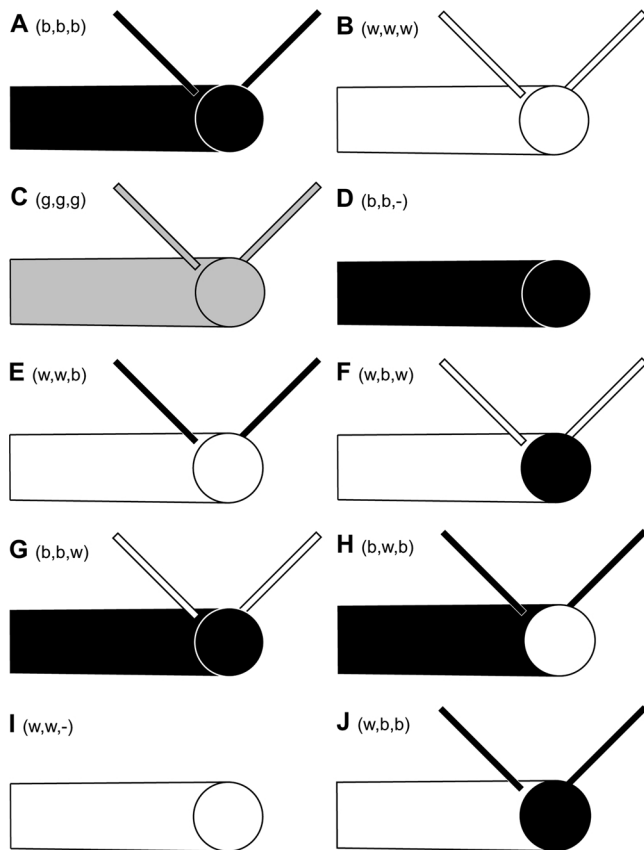


Fig. 2. Schematic views of the destinations showing the manipulations of destination intensity and structure. The text in parentheses indicates the abbreviations used in Table 1 for when the sides of the cylinder, the end of the cylinder, and the pegs had intensities of black (b), gray (g) and white (w) and when pegs were absent (-).

treatment.

2.4. Data collection and analysis

For each individual and each treatment, we calculated preference as the percentage of the six trials when a snake selected a particular destination. For each species we then calculated the mean value of preference (Pref1) for a particular treatment (n = the number of individuals). We then used a one-tailed t test to determine if Pref1 for the destination that was chosen most often was significantly ($p < 0.05$) greater than the value expected for randomly choosing between the two alternative perches (50%). To facilitate evaluating the effects of making multiple comparisons, as suggested by (Moran, 2003), we provide exact, uncorrected p values (Table 1). However, we also performed a table-wide sequential Bonferroni correction (Rice, 1989) that divided 0.05 by the rank order of the p values for all 40 comparisons.

3. Results

When both destinations were black, the snakes of both species preferred the destination with attributes that enhanced the ease of crossing a gap. For example, for equal gap distance and yaw angles of 45°, the snakes had a significant preference for the destination with pegs rather than the one without pegs (Table 1, tmt 6). For yaw angles of 45°, the snakes also had a significant preference for the destination with a gap distance that was shorter by 10 cm (Fig. 1B; Table 1, tmt 17). Finally, the snakes also had a highly significant preference for the destination along a straight trajectory rather than the alternative with 90° yaw angle (Fig. 1C; Table 1, tmt 19).

For the three treatments with a white background and for which each destination had pegs, a yaw angle of 45°, and a uniform intensity, snakes of both species had a significant preference for the darker destination (Table 1, tmt 1-3). When one destination was black and the other was gray (Table 1, tmt 2) the preference for the darker destination was not as strong as when one of the destinations was white (Table 1, tmt 1,3).

In four of the remaining eight treatments with a white background and both destinations having pegs and a yaw angle of 45° (Table 1, tmt 9-16), both species had significant and similar preferences. These uniform preferences included: 1) a black rather than a white cylinder (tmt 9), 2) an all black destination rather than one with only a black end (tmt 11), 3) black pegs rather than white pegs when both cylinders were white (tmt 12), and 4) an all-black destination rather than one with only a black end and pegs (tmt 16). Thus, for destinations with combinations of black and white, the snakes commonly preferred the destination that had a greater amount of black.

When the background was black, the brown tree snakes unexpectedly continued to have a significant preference for an all-black rather than an all-white destination (Table 1, tmt 4). However, the boa constrictors had a significant preference for the all-white rather than the all-black destination when the background was black.

In several cases the preference for a darker destination with a white background was so strong that it overrode or lessened the preference for a mechanically advantageous destination. For example, the brown tree snakes retained a significant preference for a black destination even when it was farther away than a white destination (Table 1, tmt 18), and the boa constrictors in this treatment no longer preferred the closer destination when it was white. In the presence of a black destination without pegs, neither of the species continued to prefer the mechanically advantageous white destination with pegs (Table 1, tmt 5). Furthermore, in both species the presence of a black destination with a yaw angle of 90°, decreased the preference for the mechanically advantageous white destination that was straight ahead (tmt 20).

4. Discussion

The ability of diverse animals to travel along non-random paths is widespread (Kabadayi et al., 2018), and it implies some ability to sense cues in the environment to facilitate the orientation of movements. However, the visual cues involved in path choice are minimally understood for most animals compared to the role of vision in systems such as mate choice, the interactions between animals, and interactions between pollinators and plants (van der Kooi et al., 2019). More specifically, understanding the role of vision for path choice of snakes remains rudimentary, although numerous studies of snakes have documented the role of olfactory (Burghardt, 1967) and visual cues (Drummond, 1985) for making choices during predatory behavior, especially for species with specialized infrared receptors (Buning, 1983). Given that size, distance, orientation, color, and contrast can convey important information in many other contexts such as species and sex recognition (Agrawal and Dickinson, 2019), dominance and territorial interactions (Chunco et al., 2007), and feeding of diverse animals (Ewert, 1982; van der Kooi et al., 2019), one could reasonably expect some of these same visual cues to be important for path choice, especially if they are correlated to the biomechanical demands for moving.

Snakes probably evolved from a burrowing ancestor in which a functional eye was nearly lost but subsequently re-elaborated as snakes diversified (Caprette et al., 2004), and this has led to a common assumption that the visual acuity of snakes is poor compared to that of lizards. However, the limited experimental data indicate that the visual acuity of snakes is reasonably good considering the size of their eye (Rumpff, 1979; Baker et al., 2007), although their ability to perceive colors is probably reduced compared to lizards (Simoes et al., 2015).

Visual cues, such as distance, location, size, and shape, can facilitate

choosing the destination that is most mechanically beneficial when bridging gaps. For example, snakes bridging gaps prefer locations that are closer and along straighter trajectories, and these preferences reduce torques that tend to make the body of the snake buckle or topple sideways (Mansfield and Jayne, 2011; Hoefer and Jayne, 2013). Snakes also prefer wider destination perches (Mansfield and Jayne, 2011; Jayne et al., 2014), which create larger targets and thus require less precise motor control (Jayne et al., 2014). The preference of brown tree snakes for destinations with a V-shaped rather than an inverted V-shape formed by a pair of pegs at the end of the perch reduces the chance slipping off the side of the destination (Jayne et al., 2014). Brown tree snakes may also have a short-term ability to learn to avoid small diameter perches that are extremely compliant compared to thick perches with negligible bending (Mauro and Jayne, 2016).

Some additional preferences during gap bridging suggest a primacy for structural variation where snakes make first contact rather than structural variation that enhances the crawling of snakes once they are on the destination. For example, the preference for a perch with a V-shaped pair of pegs rather than a pegless cylinder decreases as the pegs are farther from the gap (Mansfield and Jayne, 2011). The preference for a larger diameter pegless cylinder and the lack of a consistent preference for pegs along the top-center of the destination (Mansfield and Jayne, 2011; Jayne et al., 2014) further suggest the primacy of factors that facilitate making first contact without falling off.

A possible confounding factor regarding preferences for mechanically beneficial objects is that increased apparent size (as a result of being closer), increased cylinder diameter, the presence of pegs, and increased peg length also all probably make a destination visually more conspicuous. For example, in common with snakes bridging gaps, arboreal lizards running on connected networks of perches also prefer branches with larger diameter (Mattingly and Jayne, 2005). One possible explanation for this preference of lizards is that their running speeds are enhanced by larger cylinder diameter (Losos and Irschick, 1996), but of course a larger cylinder is probably also visually more conspicuous. Hence, manipulating the contrast of destinations can facilitate disentangling some of the potential effects of being visually more conspicuous from those that affect the mechanical demands.

When the structural attributes of both destinations were the same, the following four observed trends in preferences were consistent with both of our study species preferring to go to the object with higher contrast relative to the background. First, when the background was white and each destination had uniform intensity, both species preferred the black rather than the white, the gray rather than the white, and the black rather than the gray destination. Second, the preference for the darker destination weakened when the alternatives were black and gray compared to black and white. Third, when the snakes had a significant preference between destinations with variable amounts of black, they preferred the greater amount of black. Fourth, the boa constrictors preferred the white rather than the black destination when the background was black.

An unexpected result was that, unlike the boa constrictors, the brown tree snakes preferred the black destination even when the background was black. This suggests that a lower intensity by itself may be sufficient to elicit a preference in some circumstances and that high contrast between an object and the background is not necessary to elicit a preference in brown tree snakes. Although this preference for the black rather than the white perch against a black background was significant, it was not as strong as for the black versus the white perch in front of a white background. Furthermore, brown tree snakes had a stronger preference for black versus white rather than for either black versus gray or for gray versus white perches. Consequently, for brown tree snakes, increased contrast also may increase the strength of preferences even though contrast by itself may not be sufficient to elicit a preference.

Additional results suggest that the brown tree snakes had a stronger sensory bias for dark objects than the boa constrictors. First, the brown

tree snakes had a significant preference for certain dark objects rather than a more mechanically beneficial white destination (tmt 18), whereas boa constrictors lacked a significant preference for either of these alternatives. Second, boa constrictors were not as responsive as brown tree snakes to variable proportions of black and white within a destination (tmt 10, 13).

As with previously documented preferences for mechanical factors, the strength of many of the observed preferences was proportional to the magnitude of the differences between destinations. For example, the strength of preference increases when the disparity between the destinations increases for: 1) lengths of pegs, 2) cylinder diameter, 3) gap distance, 4) location of the first pair of pegs, and 5) turning angle within a horizontal plane (Mansfield and Jayne, 2011; Hoefer and Jayne, 2013; Jayne et al., 2014). Similarly, the snakes in our study had some stronger preferences for objects with uniform intensity and greater contrast as well as for destinations with greater amounts of amount of black.

Additional insights regarding the strength of preferences and whether preference for intensity trumps preference for mechanical factors, or vice versa, can be gained by further examining certain interactive effects. For example, when the destination with pegs was white and the pegless destination was black, the preference for a destination with pegs was eliminated (tmt 5). By contrast, the preference for going straight to a white perch rather than to a black perch requiring a right angle turn shows how a large mechanical disparity can supersede the bias for a dark, high-contrast object, but the preference for going straight rather than turning was less when the straight-ahead destination was white rather than black (tmt 20 vs. 19). Thus, an effect of intensity or high contrast also persisted, but it was not sufficient to completely override a stronger preference for the large mechanical benefits of the alternative. Because a right angle turns maximizes the mechanical demands of bridging gaps in horizontal plane (Byrnes and Jayne, 2012), we would predict that at some point for turns less severe than 90° the snakes would actually favor turning towards a darker perch rather than going straight ahead to a lighter destination.

The above precedent for a large difference in mechanical demands diminishing the importance of object intensity leads to some additional predictions. Our experiments only varied gap distance by 10 cm, and our standardized gap distances were only approximately 70% of the expected maximal gap bridging ability of our subjects. Hence, we would expect that the preference of both species for the closer object rather than the darker object could be restored either by using gap distances with much larger disparities or that are closer to the limit of gap bridging ability.

Although a more conspicuous object need not necessarily be an attractant to an animal, dark objects with high contrast were very strong attractants for both of our phylogenetically distant study species (Figueroa et al., 2016), and this may result from some combination of the following factors. Increasing contrast is a very general mechanism for eliciting more attention from the visual systems of diverse animal species (Ingle et al., 1978), and many of the preferences that we observed could result from this widespread property of animal visual systems that extends well beyond snakes and even beyond vertebrates. However, dark objects may also have additional importance to snakes for some of the following reasons. For example, snakes evolved from a burrowing ancestor (Caprette et al., 2004), and snakes are often quite secretive and very adept at finding and hiding under objects and in crevices or burrows (Greene, 1997). Both of our study species are not exclusively nocturnal, but they do have strong nocturnal tendencies (Greene, 1983; Rodda et al., 1999a), as do many other species of snakes. Hence, one interesting area of future work would be testing whether or not nocturnal species are more likely to be attracted to dark objects and dark places under well-lit conditions than diurnal snakes. It would also be interesting to determine whether or not a preference for either darker or contrasting objects would vary with different levels of light.

The time available for the snakes to make a decision in our experiments appears much longer than in some other systems. For example, the entire escape response and the determination of the escape trajectory in fishes commonly occurs in only a fraction of a second and without any pausing (Foreman and Eaton, 1993). Tests of route choice of anole lizards in the laboratory often lasted less than 3 s from the release of the lizard until it reached a bifurcation after running 1 m, and if any pauses occurred, they were usually only a fraction of a second (Mattingly and Jayne, 2005). Although we did not systematically quantify the time of trials in our experiments, many trials were completed within 10 - 60 s, some lasted a few minutes, and pauses lasting more than a second were common. We assume that our presence behind the snake and touching it provided some aversive stimulus. However, subjectively both species usually appeared to be moving well below their maximal speeds of arboreal locomotion (Jayne et al., 2015). Hence, our study system appears to be very far from an all-or-none, maximal speed escape response. Perhaps future work detailing the time course and path traveled by the head could provide more insights into whether increased contrast decreases the time course of events and increases the directness of the path traveled.

An additional interesting but unresolved issue is why boa constrictors preferred the white perch and brown tree snakes preferred the black perch when the background was dark. Testing more species could quickly resolve whether this observed difference reflects some fundamental difference between Henophidian and Caenophidian snakes. Both of our study species have strong nocturnal tendencies (Greene, 1983; Rodda et al., 1999a) and vertically elliptic pupils, but nuances such as the exact amounts of time they spend in the dark or bright light are not well known. Despite young boa constrictors often occurring in trees (Greene, 1983), boa constrictors are not considered an arboreal specialist, and they are rather stout and have relatively short tails compared to highly arboreal relatives in the genus *Corallus* (Pizzatto et al., 2007). By contrast, brown tree snakes are considered arboreal specialists based on their ecology (Rodda et al., 1999a) and anatomical specializations including a slender build and muscles with long tendons, both of which have evolved convergently many times in arboreal Caenophidian snakes (Jayne, 1982). Nonetheless, it is presently difficult to imagine how any of these differences between our study species might be causally related to the relatively few differences that we did observe in preferences for different destinations.

Although we expected that the intensity and contrast of destinations could influence where snakes choose to go, an overriding preference for intensity leading to a mechanically maladaptive choice was not anticipated. However, apparently maladaptive preferences are a recurrent finding for studies that have investigated the existence and consequences of sensory bias. Two classic examples of this are female preferences for mate choice in certain fish (Basolo, 1990) and frogs (Ryan et al., 1990). To the best of our knowledge, our results are the first to show how a sensory bias for color or contrast can result in counterintuitive choices that could impede movement (by increasing slipping or requiring greater muscular force to oppose greater buckling forces associated with larger gap distances).

The conspicuous sensory bias of brown tree snakes for darker objects may have useful implications for the management of this highly invasive species, which has had devastating ecological and economic consequences for the island of Guam (Rodda et al., 1999). For example, trapping this species might be facilitated if traps and objects providing access to the traps are dark in order to attract the snakes. Alternatively, light colors might enhance the effectiveness of structures intended to be barriers or reduce the attractiveness of infrastructure associated with nest boxes and electrical systems.

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Declaration of Competing Interest

None.

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