Zoology 119 (2016) 113–118

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

Perch compliance and experience affect destination choice of brown tree snakes (*Boiga irregularis*)

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ARTICLE INFO

Article history:
Received 25 October 2015
Received in revised form
18 November 2015
Accepted 2 December 2015
Available online 4 December 2015

Keywords:
Arboreal locomotion
Arboreal snakes
Movement ecology
Perch choice

ABSTRACT

Arboreal animals often encounter branches with variable diameters that are highly correlated with stiffness, but how surface compliance affects the perch choice of animals is poorly understood. We used artificial branches to test the effects of different diameters and compliance on the choice between two destinations for twenty brown tree snakes as they bridged gaps. When both destinations were rigid, the diameters of the surfaces did not affect perch choice. However, with increased experience snakes developed a preference for a rigid, large-diameter perch compared to a compliant, small-diameter perch that collapsed under loads that were a small fraction of the weight of the snake. In hundreds of trials, with only one exception, the snakes proceeded to crawl entirely onto all rigid perches after first touching them, whereas the snakes commonly withdrew from the compliant perch even after touching it so lightly that it did not collapse. Hence, both tactile and visual cues appear to influence how these animals select a destination while crossing a gap. The preference for the rigid, large-diameter perch compared to the compliant, small-diameter perch developed mainly from short-term learning during three successive trials per testing session per individual. Furthermore, a preference for large diameters did not persist in the final treatment which used a rigid, large-diameter perch and a rigid, small-diameter perch. Hence, brown tree snakes appeared to be able to form short-term associations between the perch appearance and stiffness, the latter of which may have been determined via tactile sensory input.

1. Introduction

Variation in habitat structure commonly affects the biomechanical demands of animal locomotion, which can constrain where animals are able to go and affect the ease or speed of movement. However, if animals actively choose where they go, they may exploit an even smaller subset of the environment than what is physically accessible. Consequently, understanding the movement ecology of animals is facilitated by studying constraints on locomotion that arise both from biomechanical factors and the behavior of the animal.

Diverse animals live and move in arboreal habitats, and arboreal locomotion is well suited for studying potential interactions between biomechanical factors and choice of routes for two key reasons. First, compared to other habitats, the networks of branches in trees create discrete options from which an animal may choose. Second, the different diameters, inclines and spacings of branches have predictable biomechanical consequences, which have been well documented for a variety of vertebrates, including snakes. For example, on cylindrical surfaces with shallow inclines, animals must prevent toppling sideways, which is affected both by the diameter of the cylinder and the anatomy of the animal (Cartmill, 1985; Losos and Sinervo, 1989; Astley and Jayne, 2007). Pegs (mimicking secondary branches) along the top of narrow cylinders can impede the running of limbed animals (Hyams et al., 2012; Jones and Jayne, 2012). However, for elongate animals such as snakes that can weave between branches, secondary branches can help to prevent toppling (Astley and Jayne, 2009; Crotty and Jayne, 2015) or create shapes that enhance the gap-bridging performance of snakes (Jayne et al., 2014).

For natural vegetation many biomechanically important attributes of branches, such as diameter and length, are highly correlated with each other (Mattingly and Jayne, 2004). For example, thinner branches are also mechanically more compliant (possess decreased flexural stiffness) than thicker branches, and increased compliance can adversely affect some aspects of locomotor performance (Demes et al., 1995; Gilman and Irschick, 2013). Many

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http://dx.doi.org/10.1016/j.zool.2015.12.002
0944-2006/

species of arboreal snakes have convergently evolved light-weight bodies (Guyer and Donnelly, 1990; Lillywhite and Henderson, 1993; Pizzatto et al., 2007) that presumably facilitate moving on slender branches by reducing the amount of branch compliance and instability as well as reducing the possibility that branches break.

Other than one previous study that found that increased surface compliance increases the difficulty of gripping while climbing (Byrnes and Jayne, 2010), little is known regarding how branch compliance affects either the locomotion of snakes or where they choose to go. Some attributes of branches that are visually apparent do influence where snakes choose to go. For example, when bridging gaps snakes often prefer destinations that are larger or have shapes that help to prevent falling (Mansfield and Jayne, 2011; Jayne et al., 2014). However, none of these previous laboratory experiments tested preferences for destinations that had substantially different compliance. Hence, some of these previously observed preferences for larger perches could arise from some combination of preferences for destinations that: (i) are visually more conspicuous, (ii) present a larger target area that decreases the precision of movement needed to touch it (Jayne et al., 2014), or (iii) provide a more stable supporting surface.

Experience and learning could also potentially influence the choice of perches by animals. For example, if an animal moved onto a small branch that broke, this adverse experience could reduce the chance that the animal would subsequently choose a similar surface. Although the ability to learn is not as well studied in reptiles as in birds and mammals, reptiles including snakes are able to learn (Burghardt, 1977; Holtzman et al., 1999; Northcutt, 2013). Hence, if arboreal snakes could learn to associate smaller branches with increased compliance and decreased stability, then with experience snakes might be able to use visual cues to avoid surfaces that are highly compliant and unstable.

We manipulated perch diameter and compliance independently to test whether either of these two factors affected the preferences for different destinations when brown tree snakes (*Boiga irregularis*) bridged gaps. We also tested whether or not increased experience with a rigid, large-diameter perch and a compliant, small-diameter perch affected either the perch preference or the behavior of the snakes. We hypothesized that the snakes might learn to avoid the small compliant perch with increased experience. We also hypothesized that a bias against a small compliant perch might persist even when the small perch was made rigid, thus showing the snakes learned to associate perch diameter and perch compliance.

2. Materials and methods

2.1. Experimental subjects

Our study species, *B. irregularis*, is highly arboreal, proficient at bridging gaps, and known to use certain differences in visual cues to choose between different perches when bridging gaps (Jayne and Riley, 2007; Jayne et al., 2014). We used 20 adult snakes (18 males, 2 females) that were captured in Guam (summer 2010 and 2011) and then housed at the University of Cincinnati, where all experiments were performed during summer 2014. The snakes were housed in individual cages with incandescent light bulbs that allowed them to regulate daytime body temperatures between 25 and 33 °C. We used snakes with overall sizes that were as similar as was practical to obtain. The snout–vent lengths (SVL) of the snakes averaged 143 cm and ranged from 124 cm to 153 cm, and their masses averaged 471 g and ranged from 345 g to 588 g.

The snakes were fasted for one week prior to the start of trials and not fed again until after the experiment. The body temperature of the snakes during all experiments was between 29 and 31 °C, which is within the field active temperature of this species (Anderson et al., 2005). We did not use any snakes when their eye scales were cloudy from ecdysis.

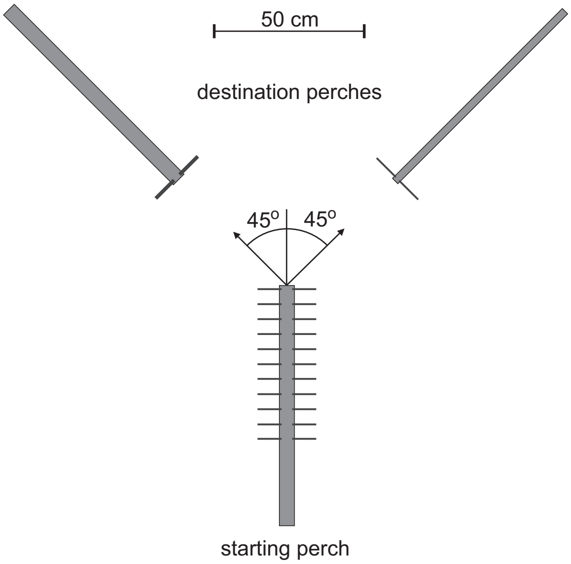

Fig. 1. A schematic overhead view of the arrangement of perches used in the choice tests. All three of the large cylinders containing pegs were in the same horizontal plane. The vertical cylinders that elevated the perches above the floor are not shown.

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 (MA214902-0; MA3500A-0).

2.2. Experimental apparatus

Similar to the choice tests performed in previous studies (Mansfield and Jayne, 2011), we used three 80 cm long perches arranged in a Y-shape that was in a horizontal plane and elevated 150 cm above the floor (Fig. 1). The end of each perch farthest from the gap was supported by a vertical cylinder with a diameter of 5 cm. We covered all three of the 80 cm long cylinders with Nashua 394 duct tape (Berry Plastics, Franklin, KY, USA), in order to create a uniform color and provide a surface texture that facilitated the ease of locomotion of the snakes, as described in more detail by Astley and Jayne (2007). To create a surface upon which the snakes crawled readily, the initial perch upon which the snakes were placed had a diameter of 5 cm, and two 50 cm long rows of pegs with a 6 mm diameter and a 10 cm length spaced at 5 cm intervals and oriented 45° relative to horizontal (Fig. 1). The distance of the gap between the starting perch and the destinations was 85% of the maximal gap distance predicted from the SVL of each snake based on the scaling equation of a previous study of gap-bridging performance of brown tree snakes (Jayne and Riley, 2007). We covered all walls of the experimental room with a white drop-cloth in order to create a uniform visual background.

All of the destination perches had a single pair of pegs, each of which was 45° relative to horizontal, perpendicular to the long axis of the cylinder, and 1 cm from the end of the cylinder nearest the starting perch. As seen in an end-on view of the destination, the pair of pegs created a V-shape with an overall width of 19 cm (Fig. 2). All of the pegs used as part of the destination perch were sufficiently rigid that we did not observe any bending when the snakes crawled on them. Destination perch A had pegs with a 12 mm diameter, whereas all other destinations had peg diameters of 6 mm (Fig. 2). Destination perches A and C had a cylinder diameter of