Animal Behaviour 88 (2014) 233–241

Contents lists available at ScienceDirect

Animal Behaviour

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

Hit or miss: branch structure affects perch choice, behaviour, distance and accuracy of brown tree snakes bridging gaps

Bruce C. Jayne [a,*], Andrew M. Lehmkuhl [a], Michael A. Riley [b]

[a] *Department of Biological Sciences, University of Cincinnati, Cincinnati, OH, U.S.A.*
[b] *Department of Psychology, University of Cincinnati, Cincinnati, OH, U.S.A.*

ARTICLE INFO

Article history:
Received 2 September 2013
Initial acceptance 11 October 2013
Final acceptance 7 November 2013
Available online 11 January 2014
MS. number: A13-00721

Keywords:
arboreal
Boiga irregularis
Fitts's law
habitat structure
locomotion
performance

The effects of branch size, shape and orientation on arboreal animals' movement across gaps or their choice of destinations when doing so are poorly understood compared to the well-documented effects of habitat structure on the locomotor behaviours and maximal speeds of animals moving on solid surfaces. Some highly arboreal species of snakes, such as the brown tree snake, *Boiga irregularis*, cross gaps using either a slow-speed crawling or a high-speed lunging behaviour. We expected that wider destination perches would enhance either the speed or maximal distance crossed while bridging a gap, because reaching and touching larger objects requires less precise motor control. Thus, for *B. irregularis*, we tested whether branch size and shape affected perch preference, maximal distance and the behaviour used to bridge gaps. The snakes usually preferred wider destination perches, some of which significantly increased both maximal distance and the amount of high-speed lunging, which contributed to maximal distance. Cylinders with pegs that simulated secondary branches enhanced lunging success rate across gaps compared to cylinders without pegs. The use of high-speed lunges revealed trade-offs between the speed and the accuracy of head placement when first contacting the destination perch on the far side of a gap. Thus, the structure of destination perches on the far side of a void can have important consequences for what destination is chosen, the distance of the gap that is crossed and how the void is traversed.

The locomotor performance of many species of squamate reptiles has been a useful model system for gaining insights into how the interrelationships among behaviour, anatomy, physiological capacity and environmental structure affect and limit what animals do (Arnold, 1983; Irschick & Garland, 2001). The major focus in previous studies of the effects of environmental structure on the locomotor behaviours of animals has been on the surfaces that the animals contact and use to generate propulsive force. However, especially for arboreal animals, the voids between the surfaces that support animals also have great ecological relevance for where animals go and how they get there (Temerin & Cant, 1983).

The behaviours used to cross gaps often vary with the body plan of animals. One strategy of crossing gaps is simply to reach from one branch to another, and the limbs of primates (Cannon & Leighton, 1994; Fleagle & Mittermeier, 1980; Thorpe, Holder, & Crompton, 2009) and the elongate bodies of snakes seem well suited for doing this (Lillywhite, LaFrentz, Lin, & Tu, 2000). Limbed animals such as treefrogs (Emerson, 1991), lizards (Gillis, Bonvini, & Irschick, 2009; McGuire, 2003), squirrels (Essner, 2002) and primates (Demes, Jungers, Gross, & Fleagle, 1995) also commonly cross gaps by leaping and occasionally gliding. Some specialized arboreal species of snakes, such as gliding snakes (Socha, 2011) and brown tree snakes, *Boiga irregularis* (Byrnes & Jayne, 2012; Jayne & Riley, 2007) occasionally cross gaps by lunging rapidly.

Arboreal locomotion is affected also by structural variation of branches, including the diameter, length, orientation and spacing of branches (Cartmill, 1985; Mattingly & Jayne, 2005). Hence, animals moving on and between branches frequently encounter discrete options with important functional consequences. For example, limbed animals such as anole lizards often can run faster on cylinders with larger diameters and they often choose surfaces that enhance their speed (Jones & Jayne, 2012; Losos & Irschick, 1996; Mattingly & Jayne, 2005). By contrast, large diameters are detrimental to the speeds of arboreal snake locomotion (Astley & Jayne, 2007; Jayne & Herrmann, 2011). Thus, an intriguing finding for rat snakes (*Pantherophis* spp.) is that they prefer to cross gaps to a destination perch with a larger diameter (Mansfield & Jayne, 2011). Despite these previous data on perch choice, gap-bridging performance and how perch structure affects the crawling of snakes, whether branch structure affects either the gap-bridging ability or behaviour of any species of snake has not been previously studied.

Numerous studies on human movement and reaching likely have implications for predicting how variation in branch structure may affect the choice of destination perches, performance and

* Correspondence: B. C. Jayne, Department of Biological Sciences, University of Cincinnati, P.O. Box 210006, Cincinnati, OH 45221-0006, U.S.A.
E-mail address: bruce.jayne@uc.edu (B. C. Jayne).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.12.002

behaviours used when bridging gaps. For example, the variability of human movement increases with the amount of force produced (Harris & Wolpert, 1998), and greater forces are often required for greater speed. This can create a trade-off between speed and accuracy for movements such as reaching (Meyer, Abrams, Kornblum, Wright, & Smith, 1988). Hence, to move accurately, more difficult movements must be slowed down, and this relation between movement time (speed) and accuracy is termed Fitts's law (Fitts, 1954). Fitts's law is well established in humans and holds true for reaching movements of the few species of primates that have been studied (Fagot & Paleressompoulle, 2009; Ojakangas & Ebner, 1991; Roy, Paulignan, Meunier, & Boussaoud, 2002). The route choice and gap-bridging of arboreal snakes could be similarly influenced by the interplay between speed and accuracy described for a variety of other systems (Chittka, Skorupski, & Raine, 2009). Namely, larger destination perches should require less precise motor control and allow for faster movements.

In this study we manipulated the size, shape and orientation of simulated branches to test for their effects on perch choice when crossing a gap as well as how these factors affect the behaviour and gap-bridging performance (Gap_{max}) of brown tree snakes. We hypothesized that the snakes would prefer destination perches that conveyed some benefit either for crossing the gap or for crawling on the perch (see Methods for more specific descriptions of the destination perches and their predicted effects on perch choice and gap-bridging performance). Alternatively, if supporting the weight of the portion of the body crossing the gap is the only factor limiting performance, then the attributes of the destination perch should be irrelevant to Gap_{max}. However, the rapid lunging behaviour of snakes can overcome some of the limitations imposed by crossing gaps slowly (Byrnes & Jayne, 2012; Jayne & Riley, 2007). Consequently, variation in the destination perches that increases the use of lunging could increase Gap_{max}, and a more rapid behaviour seems more likely when a destination perch is larger. Finally, if the abilities of snakes to touch and attain a purchase on a perch are important, then destination perches with features such as a wider horizontal area or a shape that reduces slipping could enhance performance.

METHODS

Experimental Subjects

We studied a highly arboreal species of snake (brown tree snakes, *B. irregularis*). All individuals (of unknown age) were captured in Guam (permits: U.S. Fish and Wildlife Service MA214902, MA35300A-0; Guam Department of Agriculture COO-027-10, COO-031-11) and had been in captivity for 1–2 years at the University of Cincinnati before the experiments were performed. The snout–vent lengths (SVL) and masses of the snakes ranged from 113 to 137 cm and from 261 to 456 g, respectively. To allow their use for future experiments, all of the snakes remained alive at the conclusion of these experiments, which precluded performing the dissections needed to definitively determine the sex of different individuals. The captive snakes were housed individually in cages (57 × 59 × 26 cm) with incandescent light bulbs that allowed the snakes to thermoregulate their body temperature behaviourally from 25 to 33 °C. Water in bowls within the cages was continuously available, and the snakes were fed large dead mice every 2–3 weeks. All procedures and animal care were in accordance with guidelines by the Institutional Animal Care and Use Committee of the University of Cincinnati (Protocol 07-01-08-01).

General Experimental Procedures

Before using the snakes for experiments, they were placed individually in cloth bags within a heated chamber so their body temperatures were between 29 and 31 °C, which is within the range of the field-active body temperatures of this species (Anderson et al., 2005). We did not perform experiments with any snakes when their eyes were cloudy because of the early stages of ecdysis.

During all experiments the experimenter stood directly behind the initial perch and released the snake headfirst towards the gap between perches (Fig. 1). The snakes often spontaneously crawled towards the gap and crossed it, but sometimes we had to lightly touch the tail of a snake to initiate moving. To minimize possible confounding effects of time and experience, the snakes were subdivided into two groups of equal size, each of which experienced the treatments in different randomized order.

We covered the primary cylindrical surfaces on which the snakes crawled with Nashua 394 duct tape (Berry Plastics, Franklin, MA, U.S.A.) to provide a standardized colour and a texture that facilitates snake locomotion (Astley & Jayne, 2007). We use the term 'perch' to refer collectively to the primary cylindrical surface and all of the associated 6 mm diameter wooden pegs (Figs 1, 2). To provide uniform visual backgrounds, we covered the walls of the experimental room with white cloth.

Choice tests

Overall, the procedures used for the choice tests followed those of previous studies of arboreal snakes including brown tree snakes (Hoefer & Jayne, 2013; Mansfield & Jayne, 2011). We tested whether different sizes and shapes of destination perches on the far side of a 40 cm gap were associated with biased selection between a pair of destination perches 45° to the left and right of the initial perch (Fig. 1a). In all choice tests the initial perch was a 49 mm diameter cylinder that was 80 cm long and had 12 pairs of 10 cm pegs that were spaced 5 cm apart and inclined 45° relative to the horizontal (Figs 1a, 2h). With only two exceptions (Fig. 2j, l), whenever pegs were present, the peg nearest the gap was 1 cm from the edge of the gap (Figs 1, 2). Whichever destination perch the snake first crawled onto after crossing the gap was scored as the preferred destination perch for a particular trial.

The destination perches had different sizes, shapes and attributes that are either known to affect the crawling speeds of arboreal snakes (Astley & Jayne, 2007; Jayne & Herrmann, 2011) or seemed likely to affect the ease of the snake touching and not slipping off the destination perch (Mansfield & Jayne, 2011). Snakes bridging horizontal gaps usually approach the destination perch from above and make first contact near the top centre edge of the destination perch (Jayne & Riley, 2007). Hence, the shape and size of the destination perch in the *Z* dimension (Fig. 1b) at this location are likely to be particularly important.

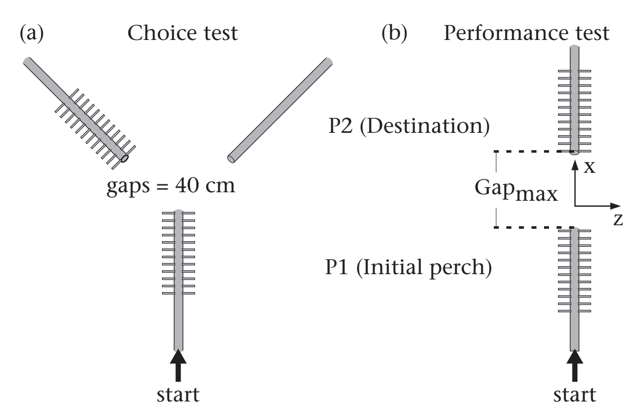

Figure 1. Overhead views of the experimental apparatus used for the tests of (a) perch choice and (b) maximum gap-bridging ability in brown tree snakes. The choice and performance tests used several types of perches (Fig. 2) not shown in this figure.