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

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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.

Keywords: Arboreal locomotion; Arboreal snakes; Movement ecology; Perch choice

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 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, *Boiga 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.

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 5 cm, whereas destinations B and D had cylinders with diameters of 2.5 cm. With the exception of destination D, the perches were sufficiently rigid to not move appreciably when the snakes touched them. We made one perch (D) highly compliant by attaching a spring to the end of the cylinder farthest from the gap (Fig. 2E), and we adjusted the tension of this system as close as possible to the minimum required amount to keep the unloaded perch horizontal. Static loads placed on the end of the compliant perch indicated that a mass of 10 g was the threshold required to cause the compliant perch to collapse.

Quantitative published data are lacking for the sizes and compliance of branches used by brown tree snakes in their natural environment. However, while collecting these snakes in Guam the senior author observed them moving on a wide variety of surfaces ranging from highly flexible, green leaf stems with diameters as small as 2–3 mm up to a variety of woody branches with diameters of 30 mm and greater, for which no appreciable bending was observed as the snakes crawled on them.

2.3. Experimental procedures for choice tests

At the beginning of each trial we placed a snake on the end of the starting perch farthest from the gap and oriented towards the destination perches (Fig. 1). If the snake did not move spontaneously toward a destination perch after 15 s, we lightly tapped its tail to encourage movement. For the gap distances that we used, previous experiments with brown tree snakes and some other species of snakes found no evidence that odors possibly left behind from snakes crawling onto a destination biased subsequent preferences for a particular destination (Hoefer and Jayne, 2013). However, as added precautions against the possible influence of odors (as in Hoefer and Jayne, 2013) both destination perches were wiped with 70% ethanol in between successive trials for each individual, and halfway through the experiments the cylinders of all perches were covered with a new layer of the same type of duct tape as used in the original construction of the perches (see Section 2.2).

For each snake we conducted six trials using one particular pair of destinations (treatment) per day (Table 1). The first three trials within a testing session were done in rapid succession (usually 3–15 min), and after the snakes had rested for a minimum of 1 h we performed a second testing session with three more replicates during the same day. In the second set of trials the left–right positions of the two destination perches were reversed to reduce the possibility that any unintended cues or the overall location in the room might bias the preference for a particular destination. To reduce possible effects of experience during the first two treatments with different rigid perches (Table 1, days 1 and 2), the snakes were divided into two batches of 10 individuals that were exposed to the two treatments with rigid perches in the opposite order. For six days after the initial choice tests using only rigid perches, we performed tests to determine whether the snakes preferred a large rigid perch (Fig. 2A) to a thinner compliant perch (Fig. 2D) as well as whether experience might affect any such preferences. When the compliant

perch collapsed out of reach after the snake touched it, we (i) scored the compliant perch as being preferred, (ii) removed the snake from the apparatus, (iii) repositioned the compliant perch so that it was horizontal, and (iv) placed the snake back onto the apparatus to conduct the next trial. For those occasions when the compliant perch did not collapse after the first time it was touched, we still scored the compliant perch as being preferred for that trial, but we obtained some additional data by letting the trial continue until the snake either successfully crawled onto a perch or touched the compliant perch and caused it to collapse. After three days of testing the preference for perch A vs. D, we used one day for a preliminary analysis of the prior experiments, and then we continued the remainder of the tests on successive days (Table 1). On the last day of the experiments, we used perches A and B to test whether the snake had developed a persistent preference for a thicker perch compared to the thinner perch even when the thinner perch was no longer highly compliant (Table 1).

2.4. Data collection and analysis

For each individual and each treatment, we calculated preference (Pref1) as the percentage of trials in which the individual first touched a particular perch (Table 1). For all 180 values of Pref1, the values ($\pm$ SE) of skewness (-0.25 ± 0.18) and kurtosis (-0.33 ± 0.36) did not differ significantly from 0; hence, they did not deviate substantially from being normally distributed. We used one-tailed t-tests to determine if Pref1 for the most preferred perch within a given treatment was significantly ($P < 0.05$) greater than the value that reflected a random choice (50%). Although we were usually successful in obtaining three trials per session of testing for a given individual, occasionally the snakes refused to continue crossing the gap after the first or second trial within a session. Hence, some of the sample sizes for the number of trials per day

were slightly smaller than the number of sessions per day times the number of trials per session times the number of individuals ($2 \times 3 \times 20 = 120$). All of the mean values presented are given $\pm$ SEM.

To gain insights into whether contact with the compliant perch biased subsequent choices within a testing session, we calculated one additional quantity (Table 1: D, then A). For both of the testing sessions within each of the six days of tests using the rigid (A) and compliant perch (D), we determined the frequency of snakes choosing perch A in the trial immediately after the first trial in which snakes chose perch D (frequency = $(\# \text{ D, then A})/(\# \text{ D, then A} + \# \text{ D, then D})$). In some testing sessions the snakes did not choose the compliant perch in either of the first two trials within a session, which resulted in fewer total cases per day than the number of individuals times the number of testing sessions per day ($20 \times 2 = 40$).

3. Results

For both of the treatments involving only rigid destination perches, no significant preferences occurred either for perch A vs. C or for A vs. B (Table 1). Hence, neither cylinder diameter nor peg diameter alone was sufficient to affect the choice between different destinations.

Furthermore, for these two treatments, whenever snakes touched a destination, they proceeded to cross the gap and crawl entirely onto the destination perch.

For the first day of testing with the rigid, thick perch (A) and the thin, compliant perch (D), the snakes lacked a significant preference for either perch (Table 1). However, after more experience on subsequent days, the snakes developed a significant preference for the thick, rigid destination compared to the thin, compliant destination (Table 1).

During all of the trials from the six days of tests using perches A and D (Fig. 3), the snakes never touched the rigid perch more than once within a single trial. Furthermore, for the 412 trials in which the snake touched the rigid perch first, we only observed one case in which the snake withdrew its body rather than proceeding to bridge the gap and crawl completely onto the rigid destination perch (Fig. 3). In 33% of the 296 trials in which the snake first touched the compliant perch, the compliant perch collapsed completely and was out of reach of the snake, which ended the trial (Fig. 3). However, for the 197 cases in which the compliant perch was touched first but did not collapse out of reach of the snake, the snake withdrew its body into the gap and then subsequently touched either the rigid ($n = 112$) or the compliant ($n = 85$) perch (Fig. 3). The snakes touched the compliant perch two, three or more than three times within a trial in 85, 34 and 7 cases, respectively. Hence, the gap-bridging behavior of the brown tree snakes often was not a simple all-or-none behavior in which snakes crawled continuously until they either successfully bridged a gap or the destination perch had a mechanical failure. As the amount of experience increased from the first to the last day of tests with the compliant and rigid perches, the probability of the snakes touching the rigid perch in the trial immediately following one in which the compliant perch was touched increased from 46 to 67% (Table 1).

For the last choice test, the snakes lacked a significant preference for either the thick (A) or the thin (B) rigid perches (Table 1). Thus, even though the snakes developed a significant preference for the thick, rigid perch (A) compared to the thin, compliant perch (D), the snakes lacked a persistent preference for the thick compared to the thin destination perch when they did not differ in compliance.

4. Discussion

Snakes can use visual cues to select between different destinations when bridging gaps (Mansfield and Jayne, 2011; Jayne et al., 2014), and our results suggest that both tactile cues and experience can also influence where arboreal snakes go. Because tactile information is not available to the snakes until they touch the destination, visual cues are key for influencing the initial choice and approaching the destination. A subsequent use of tactile cues seems likely because the snakes often withdrew after touching the compliant perch, but they usually continued to crawl completely onto all of the rigid perches (Fig. 3).

The most common visual attribute of perches that significantly affects choice of snakes is overall width (Mansfield and Jayne, 2011; Jayne et al., 2014). When snakes bridge gaps, they initially touch destinations from above. Consequently, their common preference for a greater overall width is probably beneficial because they will have a larger target that requires less precise motor control to touch (Mansfield and Jayne, 2011; Jayne et al., 2014). In addition to keeping the overall width of all of our destinations constant, all of our perches had a similar V-shape (Fig. 2) that was well suited for preventing the sort of sideways slipping that can occur when snakes bridge gaps to cylinders without pegs (Jayne et al., 2014).

Objects can be visually more conspicuous either when they are larger in one dimension, such as overall width, or when they have a greater projected area. Despite having the same overall width and similar overall shape, the projected area of perch A (Fig. 2A) in our experiments was approximately four times that of the destinations with narrow cylinders and narrow pegs (Fig. 2B and D), and yet we observed no preferences between these as long as both perches were rigid. In previous experiments brown tree snakes also lacked a significant preference when presented with a large diameter (8.9 cm) cylinder completely lacking pegs and with a much larger projected area (62 cm^2) compared to that of a small diameter (2.7 cm) cylinder with a V-shaped pair of pegs (12

cm²) with the same overall width as the large cylinder (Jayne et al., 2014). Collectively, these findings for brown tree snakes suggest that differences in projected area usually do not influence perch preferences unless some additional attributes of the perches vary.

Overall, our finding of no preferences among our different rigid perches with constant overall width agrees well with the findings in previous studies, but it is intriguing that with experience the snakes began to avoid the compliant perch with small diameter as the experiments progressed. In our experiments all of the brown tree snakes simply crawled steadily across the gap until they touched the destination, and we used gap distances substantially less than the upper limit that these snakes can span (Jayne and Riley, 2007). Indeed, the large number of times the compliant destination did not collapse when touched further supports the notion that the snakes in our experiments could easily support their suspended weight and hence transfer their weight very gradually when crawling onto a destination across a gap. Furthermore, rather than emerging only after the snakes repeatedly experienced the compliant perch, the behavior of gradually transferring weight to the destination was common the first time the snakes encountered the compliant perch as indicated by the large proportion of times the compliant perch did not collapse when first touched by the snakes (Fig. 3).

When gap distances are very large, brown tree snakes often use lunging behaviors that involve (i) pausing before reaching the destination, (ii) rearing up and back, (iii) assuming postures similar to those involved in striking behaviors, and (iv) subsequently lunging rapidly forward and downward towards the destination (Jayne and Riley, 2007; Jayne et al., 2014). Unlike the low-speed crawling across gaps observed in our study, lunges are never stopped and reversed, and lunging snakes hit the destination quite forcefully (Jayne and Riley, 2007; Jayne et al., 2014). Hence, for high-speed lunges the snakes probably rely solely on visual cues rather than the

sequential use of visual and tactile cues suggested by our observation of low-speed crawling across gaps. A common feature of the motor control of very rapid movements is that events more closely resemble an all-or-none response after initiation rather than being modified by the animal integrating sensory feedback acquired while performing the behavior (Lock and Collett, 1979). Although the visual acuity of snakes is not well documented, many arboreal snakes have large eyes with a large amount of binocular overlap compared to their terrestrial counterparts (Lillywhite and Henderson, 1993; Caprette et al., 2004), which suggest an important role of vision for many snakes that live and move in arboreal environments with considerable three-dimensional and visual complexity. However, brown tree snakes have very strong nocturnal tendencies (Rodda et al., 1999). Although the exact amount of light needed by any species of snake to use visual cues to choose and go to different destinations is not known, some information suggests that at least some arboreal snakes can move quite well without any visual information. For example, one of the snakes that was collected in Guam and used in our experiments was in a cave, and many brown tree snakes were captured moving on very slender branches (< 5 mm diameter) on overcast nights when neither the moon nor any stars were visible. In laboratory experiments with complete darkness, boa constrictors readily explore and bridge gaps considerable distances away from an elevated surface that is supporting them (Jayne et al., 2012). Hence, brown tree snakes and some snake species probably can use either vision or touch exclusively as well as a sequential use of these two sensory modalities depending on variation in (i) gap distance, (ii) speed and type of movement, and (iii) the amount of light. Perhaps olfaction could become increasingly important for snakes locating or choosing perches when crossing gaps in the dark, but no olfactory cues seem likely to be causally related to either perch size or compliance, which were the focus of our study.

The effect of experience on perch choice in our experiments was statistically significant but rather subtle. As the experiments progressed, the bias of snakes for the rigid perch arose largely from being more likely to choose the rigid perch after a trial within a bout of testing in which they touched the compliant perch (Table 1). Since the locations of the different perches were constant within each bout of three successive tests, spatial memory and spatial learning could have been involved, and previous studies suggest that this type of learning allows some snakes and lizards to find shelters more readily as familiarity with their environment increases (Holtzman et al., 1999; Day et al., 2003; LaDage et al., 2012; Carazo et al., 2014).

Another possibility is that the brown tree snake transiently learned to associate perch diameter with compliance (or its adverse effects) during our experiments, and associative learning has been found for some squamate reptiles, at least for some tasks involved with feeding (Punzo and Madragon, 2002; Shanbhag et al., 2010; Clark et al., 2014). We used a compliant perch with cylinder and peg diameters one-half of those used in the rigid perch for the following reasons related to associative learning. First, in natural environments thinner branches are usually more compliant and more likely to break than thicker branches, and hence visual cues are associated with important biomechanical properties. Second, we wanted differences in the diameters of the perches sufficiently large so that they could probably be perceived by the brown tree snakes, and it seemed likely given that brown tree snakes can discriminate between destinations with only 1.5-fold differences in overall width (Jayne et al., 2014). The acquired bias for the rigid perch was consistent with learning an association between diameter and compliance. However, the lack of a preference for the large-diameter rigid perch compared to the small-diameter rigid perch in the last experiment indicated that any association that might have been made between compliance and diameter did not persist, despite some previously demonstrated capacities of

reptiles to retain learned behaviors for long periods of time (Davis and Burghardt, 2007; Lillywhite et al., 2015). When a learned behavior is not performed in a novel setting, this weakens the case that true associative learning has occurred (Paulissen, 2008). Some field observations in Guam (Fritts and Chiszar, 1999) very tentatively suggested that some brown tree snakes might be able to learn to avoid traps as experience increased with this presumably negative stimulus, but overall the ability of snakes to learn remains minimally studied and understood.

The diverse body plans and behaviors of animals involved in traversing gaps in arboreal environments can affect the consequences of an unsuccessful attempt as well as the sensory modalities that may be most useful for deciding how to cross a gap. For example, primates rely heavily on vision and commonly leap across gaps, but unsuccessful attempts to cross gaps or a destination that breaks can have catastrophic effects such as broken bones and death (Currey, 2002; Strier, 2011). Regardless of whether the destination for the snakes in our study collapsed, snakes never fell while attempting to crawl across a gap. However, failed lunges seem likely to increase the probability of perch collapse and falling and thus might create a more negative stimulus than what was experienced by the snakes in our study when the destination collapsed suddenly. Such reduced costs associated with failed attempts by snakes in turn may diminish the importance of either initially avoiding or learning to avoid unstable or fragile destinations, and simply using trial and error along with tactile feedback to gauge the sturdiness of the destination could be a reasonably effective strategy in these circumstances. Although the current paucity of data limits our ability to generalize, they do hint at further insights that could be gained from more comparative studies regarding the predictive value of arboreal habitat structure and the role of active choice in determining where animals go. Perhaps, the use of reaching rather than

ballistic behaviors and having the ability to grip or stick to surfaces rather than relying only on balance affect the selectivity of destinations by the diverse animals that cross gaps in arboreal environments.

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Figure Captions

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.

Fig. 2. Schematic diagrams of the different destination perches used in the choice tests. (A–D) End-on views of the perches used in the study. (A) A thick cylinder with thick pegs. (B) A thin cylinder with thin pegs. (C) A thick cylinder with thin pegs. (D) Perch D had the same dimensions as perch B, but only a small external load was required to collapse perch D as a result of the spring-loaded joint (E) where the horizontal cylinder was attached to a vertical cylinder that elevated the destination above the floor.

Fig. 3. A summary of the order in which snakes touched perches during all of the choice tests involving the large rigid perch (Fig. 2A) and the small compliant perch (Fig. 2D). The trials were terminated either after the snake successfully bridged to the destination perch or after the snake touched the compliant perch and caused it to collapse. Snakes never successfully bridged to the compliant perch.

Table 1

Results of the choice tests. See Fig. 2 for the shapes of the different destination perches. Pref1 is the mean $\pm$ SEM percentage of trials in which destination 1 was chosen ($n = 20$ individuals). The t-test determined whether Pref1 $> 50\%$, and * indicates a significant preference. The column at the right is the percentage of trials in which a snake touched the rigid perch (A) in the trial immediately following the first trial within a session in which the compliant perch (D) was chosen.

Test Day	Destination perch		Pref1	<i>t</i>	<i>P</i>	D, then A
	1	2				
1 or 2	A	C	55.0 $\pm$ 5.6%	0.90	0.1896	
2 or 1	B	A	50.8 $\pm$ 5.2	0.16	0.4372	
3	A	D	51.8 $\pm$ 5.1%	0.34	0.3673	46% ($n = 28$)
4	A	D	58.7 $\pm$ 5.4%	1.59	0.0637	40% ($n = 25$)
5	A	D	58.3 $\pm$ 3.1%	2.70	0.0070*	62% ($n = 29$)
7	A	D	58.3 $\pm$ 3.1%	2.70	0.0070*	54% ($n = 28$)
8	A	D	58.3 $\pm$ 3.9%	2.13	0.0234*	64% ($n = 28$)
9	A	D	62.5 $\pm$ 4.8%	2.59	0.0089*	67% ($n = 24$)
10	B	A	54.2 $\pm$ 5.1%	0.82	0.2126	

Fig. 1

Fig. 2

Fig. 3