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The role of visual cues in learning escape behaviour in the little brown skink (*Scincella lateralis*)

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Abstract

Many small animals escape predators by running under an escape retreat such as a rock, log, or pile of leaves. Rapid escape to a retreat would be facilitated if the animal already learned the location of the retreat before it ever had to flee from a predator. One way a small animal might do this is to attend to a prominent 'local cue', that is, a visual cue that is part of, or contiguous with, the retreat. I tested the hypothesis that a small lizard commonly known as the little brown skink, *Scincella lateralis*, can use a local visual cue to learn an escape behaviour. Little brown skinks were presented with two retreats side-by side in an observation chamber. One retreat was backed with a vertical striped cue and the other backed with a horizontal striped cue. Each lizard was induced to run from one end of the observation tank to the opposite end with the two retreats; the retreat that each lizard chose for escape was recorded through a series of 15 trials conducted over three days. Half of the lizards were trained to escape to the vertical cue retreat; half were trained to escape to the horizontal cue retreat. About one-third of little brown skinks met the learning criterion of escaping to the correct retreat in five consecutive trials. However, significantly more of the vertical cue lizards met the learning criterion than did horizontal cue lizards. Also, the vertical cue lizards escaped to the correct retreat significantly more often than expected by chance. Furthermore, even the horizontal cue lizards showed a preference for escaping to the vertical cue retreat. This suggests little brown skinks can use a local visual cue to learn an escape behaviour, but only if it a vertical cue. This may be related to the use of a vertical cue to obtain positional information to locate a retreat or perhaps to the tendency of this forest species to attend to abundant vertical cues in its habitat.

Keywords

learning, visual cue, lizard, Scincidae, escape behaviour, refuge.

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1. Introduction

Small animals are under constant threat of predatory attack leading them to evolve a diverse array of antipredator behaviours and morphologies. One of the most common antipredator behaviours employed by small animals is rapid flight to a retreat within which the animal is safe from a pursuing predator. Successful escape to a retreat is a remarkably complex behaviour requiring a potential prey animal to correctly assess a threat, choose a proper retreat, and flee to that retreat in time to escape the predator. Understanding the myriad factors that influence escape behaviour has been the goal of escape behaviour theory (Ydenberg & Dill, 1986; Cooper & Frederick, 2007).

One group of animals that has been especially useful in the study of escape behaviours is diurnal lizards (Cooper, 1999, 2003, 2008; Martin & Lopez, 2000, 2003). This is because most species of lizards are small, typically escape by fleeing, and react to a stalking human in the field the same way as they react to a large predator (Cooper & Frederick, 2007 and references therein). Studies have shown that small lizards often flee to retreats, such as crevices or bushes, within which they are relatively safe from predators (Cooper, 1997, 1998, 2003). Some of these studies have shown that lizards flee to a retreat in a direct path without stopping, presumably to decrease the likelihood of being overtaken by the pursuing predator (Cooper, 1997, 1998). Rapid, direct flight to a retreat would be most effective if the lizard already knew the location of the retreat before it had to flee. Anecdotal observations suggest that this may be the case for some lizard species (Martin & Lopez, 2003; Paulissen, 2008).

The only means by which a lizard could know the location of an escape retreat prior to fleeing to it would be if the lizard had previously committed the retreat's location to memory by spatial learning. A number of studies have demonstrated that lizards and their phylogenetic relatives the snakes (collectively the 'squamates') can learn to flee to a retreat to escape a simulated predatory attack (Paulissen, 2008, 2011; Amiel & Shine, 2012; Noble et al., 2012) or can learn to escape to a refuge to avoid being exposed in an open arena (Holtzman et al., 1999; Stone et al., 2000; Day et al., 2003; LaDage et al., 2012). Less well known are the environmental features to which squamates attend that help them learn and remember where a retreat or refuge is located. Studies in which lizards escaped from an open, exposed arena where they were not in immediate danger have suggested that 'distal cues', features outside the test arena and not directly associated with the goal, are used by squamates to help them learn and remember the location of a refuge (Holtzman et al., 1999; Stone et al., 2000; LaDage et al., 2012). However, small squamates that are confronted by a predator may only have a few seconds to reach an escape retreat before they are caught, and so may not have time to scan for distal environment cues located some distance away from the escape retreat. It seems more likely that in such circumstances that a small squamate would look for and orient toward a prominent local cue that is part of, or contiguous with, an escape retreat to reduce the time the animal is exposed to the predator. If this is true, then it should be possible to train small squamates to escape to a 'correct' retreat that is labelled by a local cue.

This study tests this hypothesis by studying learning of an escape behaviour in the little brown skink lizard, *Scincella lateralis* (formerly *Lygosoma laterale*; Squamata: Scincidae). This is a small species that escapes its predators by running a short distance (10–100 cm; pers. observ.) then rapidly escaping into a hole under a pile of leaves, a rock, a log, or other cover object (Smith, 1997; pers. observ.). It has been shown to be capable of learning to escape to under one particular 'correct' retreat in previous spatial learning studies (Paulissen, 2008, 2011). The specific aims of this study are (1) to determine if little brown skinks can be trained to escape to a specific, 'correct' retreat labelled by a prominent local visual cue, and (2) to determine if the type of cue makes a difference in escape behaviour learning.

2. Materials and methods

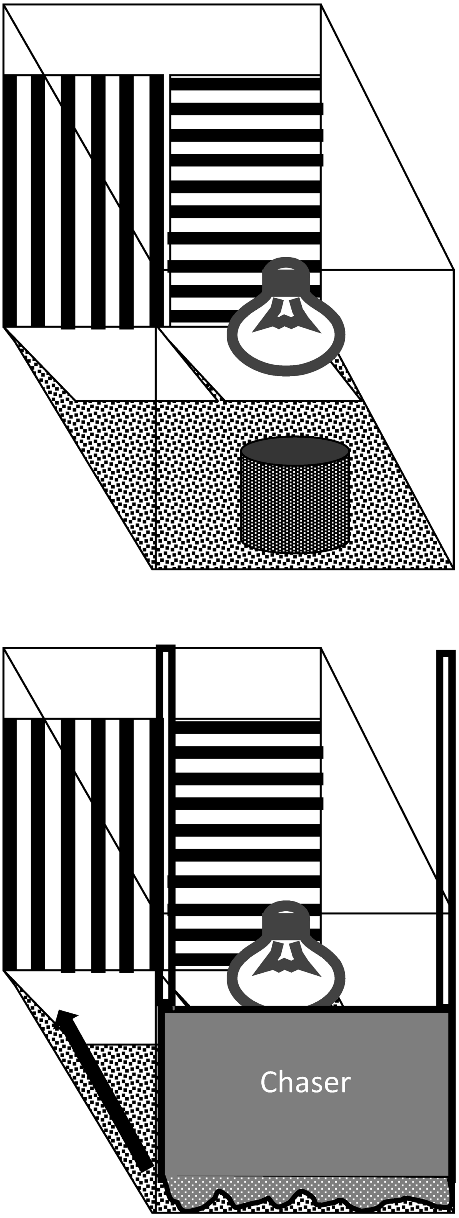
2.1. Study animals and captive maintenance

The little brown skink, *Scincella lateralis*, is a small, terrestrial, arthropodivorous lizard that inhabits forest habitats in the southeastern USA (Conant & Collins, 1998). The average snout–vent length (SVL) of adult males from the areas where this study was conducted is 42.3 mm; the average SVL of adult females is slightly larger at 45.5 mm (Becker & Paulissen, 2012). It is most common in deciduous forests with a dense leaf litter within which it prowls for food and under which it retreats from predators and bad weather. Adult little brown skinks were captured by hand from oak-hickory forests in Cherokee county in northeastern Oklahoma, USA. The lizards used in this study were caught between mid-May and late September 2010–2013; this period constitutes the bulk of the activity season in Oklahoma. All lizards were measured, weighed, sexed (by eversion of the hemipenes of males) and housed individually in 300 × 130 × 70 mm clear plastic boxes. Each box had a double layer of paper towel on its floor and a one quarter arc of a 10 cm long cardboard tube for a retreat. Each lizard was provided 6–8 mealworms from a laboratory culture each day; a 30 mm diameter water dish was filled with dechlorinated water daily. Light and heat for each box was provided by 60 W standard light bulbs run off timers set to a 12:12 L:D photoperiod. Lizards were usually tested within one week of capture and were released at their capture sites when testing was complete.

2.2. *Experimental apparatus and testing*

Trials were conducted in a 50 cm long × 25 cm wide × 32.5 cm high glass chamber (Figure 1). The substrate was a mix of topsoil and sand approximating the soil of oak-hickory forests in northeastern Oklahoma. Two 12.5 × 12.5 cm cardboard retreats were placed side-by-side at the back of the chamber; together they covered the entire width of the back end of the chamber's floor. A shallow trough about two lizard body lengths wide was dug into the substrate in front of each retreat facing toward the front of the tank to make it easier for a lizard to escape under a retreat. The vertical wall behind each retreat displayed a 12 cm wide by 20.5 cm tall cue card with a pattern of 12.5 mm wide black stripes alternating with 19 mm wide dark green stripes. Two cue cards were used, one with vertical stripes, the other with horizontal stripes. During trials, one of the cue cards was behind one of the cardboard retreats and the other cue card was behind the second cardboard retreat (Figure 1). The position of the cue cards was the same for every trial conducted on a lizard. The two 50 cm long sides of the chamber were lined with plain green paper the same colour as the green bars of the cue cards. The front of the chamber held a movable 24.75 cm by 20 cm tall grey cardboard 'chaser'

Figure 1. Schematic of test chamber used in spatial learning trials on little brown skinks (*Scincella lateralis*). A single lizard was confined in the opaque cylinder under the heat lamp for 2 min (top panel). Then the cylinder was removed and the lizard was chased toward the back end of the chamber using a cardboard 'chaser' which consisted of a flat piece of cardboard with a burlap 'skirt' on the bottom and two rods that served as hand grips (bottom panel). The direction the chaser was moved is indicated by the arrow. The lizard 'escaped' under one of the two flat cardboard retreats: either the one backed by the vertical striped cue card or the one backed by the horizontal striped cue card. Prior to the first trial, one of these two retreats had been designated the 'correct' retreat for the lizard (see Materials and methods).


Chaser

with a 3 cm burlap skirt taped across its bottom. A 60 Watt (120 V) heat lamp was suspended 14 cm above the substrate just behind the chaser and an opaque plastic cylinder was placed just under the heat lamp (Figure 1).

Prior to a lizard's first trial, one of the two retreats (either the one backed by the vertical striped cue card, hereafter the vertical cue retreat, or the one backed by the horizontal striped cue card, hereafter the horizontal cue retreat) was designated via coin-flip as the 'correct' retreat for that lizard. To begin a trial, a single lizard was confined in the opaque cylinder on the substrate under the heat lamp for 2 min; this was to allow it to warm to a body temperature of 32–33°C, which is the temperature at which little brown skink running speed is maximized (Smith, 1997). At the end of the 2 min, I moved to a position directly in front of the cylinder (so that my body, the cylinder, and the retreats at the far end of the observation tank were in a straight line) then I raised the cylinder straight up so the lizard was free to run on the substrate toward whichever of the two cardboard retreats it chose without being biased by my position or movements. To induce the lizard to run toward the retreats, the cardboard 'chaser' was advanced at a practiced pace from the front of the observation tank toward the back end of the tank where the retreats were located. The lizard always ran toward the retreats in advance of the chaser, the chaser's burlap skirt preventing the lizard from doubling back toward the front of the tank. Since the cardboard chaser spanned the width of the chamber, advancing it while holding it parallel to the back of the chamber did not bias the lizard toward either the left or the right retreat. Lizards reached the retreats within 6–7 s (mean $\pm$ SD $= 6.7 \pm 4.72$ s) of being released. Once a lizard reached the retreats, it 'escaped' to under one of the two cardboard retreats — either the vertical cue retreat or the horizontal cue retreat. If the lizard escaped to its correct retreat, it was left undisturbed for 5 min to reinforce its correct choice (5 min was chosen because it had been found to be sufficient to facilitate learning in previous studies of *Scincella lateralis*: Paulissen, 2008, 2011). Such trials were scored as correct choice trials. If the lizard escaped to the incorrect retreat, the chaser was returned to the front of the chamber, then both retreats were raised and the lizard was gently returned to the start position; then the chaser was advanced to 're-chase' the lizard to induce it to run toward the two retreats again. This was repeated as many times as needed until the lizard finally chose the correct retreat, at which time it was left undisturbed for 5 min. These trials were scored as incorrect choice trials. After the 5 min reinforcement period, the lizard was removed from the chamber and placed back in its plastic box till the next trial. The cardboard retreats and chaser were removed from the chamber and the substrate was thoroughly mixed to disperse odours. The retreats, chaser, and opaque cylinder were then replaced to set up for another trial.

A total of 15 trials were conducted on each lizard, five on each of three consecutive days. Each lizard had a rest period of at least 40 min between successive trials to recover from the exertion of running. A total of 32 lizards (18 males, 14 females) were used; 16 (7 males, 9 females) were designated as vertical cue retreat lizards and 16 (11 males, 5 females) were designated as horizontal cue retreat lizards. The positions of the vertical and horizontal cue cards were fixed for each lizard but alternated among lizards so that for 16 lizards the vertical cue card was behind the left retreat and the horizontal cue card was behind the right, and for 16 lizards the positions of the cue cards were reversed. This was done to check for the possibility of side bias (see Discussion).

2.3. Data analysis

When a lizard was chased down the chamber by the chaser, it had a choice of escaping to the vertical cue retreat or the horizontal cue retreat. One of these two retreats was designated as the correct retreat for that lizard prior to the first trial; thus if a lizard chose a retreat at random, it had a 50% chance of choosing its correct retreat during a trial. A 'learning criterion' to score if the lizard had learned which retreat was the correct one was set as the lizard making the correct choice in at least five consecutive trials (since the probability of doing so at random are $0.5^5 = 0.03125$, which is less than 0.05). I used Fisher's exact tests to compare the number of lizards that met the learning criterion for (1) lizards whose correct retreat was the one with the vertical cue versus those whose correct retreat was the one with the horizontal cue; (2) lizards whose correct retreat was on the left versus those whose correct retreat was on the right regardless of cue; and (3) males versus females. To provide a more complete picture of lizard performance during the 15 trials, I scored the following for each lizard: (1) the number of trials in which the lizard made the correct choice; (2) the maximum number of consecutive trials in which the lizard made the correct choice; (3) the maximum number of consecutive trials in which the lizard made the incorrect choice, and (4) the mean number of re-chases conducted per incorrect choice trial. Statistical comparisons between groups were made using two-sample t-tests. To test for a bias in retreat selection between vertical cue and horizontal cue lizards, I compared the number of trials (out of 15) in which lizards made the correct choice to the number expected if the lizards chose retreats at random (7.5 trials) using a one-sample t-test. All statistics were run on MYSTAT 12 for Windows (Systat, 2007).

3. Results

Only 11 of the 32 little brown skinks (34.4%) met the learning criterion of making the correct choice in five consecutive trials. There was no significant difference in the proportion of males versus females that met the learning criterion (Table 1). Similarly, there was no significant difference in the proportion of lizards whose correct retreat was on the left versus those whose correct retreat was on the right that met the learning criterion (Table 1). However, a significantly greater proportion of vertical cue lizards met the learning criterion than did horizontal cue lizards (Table 1). Further analysis showed the vertical cue lizards made the correct choice in a significantly greater number of trials, made the correct choice in significantly more consecutive trials, and made the incorrect choice in significantly fewer consecutive trials than did the horizontal cue lizards (Table 2). However, the mean number of rechases per incorrect choice trial did not differ between vertical cue versus horizontal cue lizards (Table 2). Finally, the vertical cue lizards made the

Table 1.
Number of little brown skinks that did and did not meet the learning criterion of making the correct choice in at least five consecutive trials broken down by sex, position of the correct retreat and stripe pattern of the cue card of the correct retreat.

	Did meet learning criterion	Did not meet learning criterion	p
Sex			
Male	8		0.266
Female	3	11	
Position of correct retreat			
Left side	7	9	0.458
Right side	4	12	
Cue of correct retreat			
Vertical	10	6	0.002
Horizontal	1	15	

The p-value of Fisher's exact test (two-tail) is given.

Table 2.
Comparison of performance parameters of vertical cue versus horizontal cue lizards in 15 trials.

	Vertical cue lizards	Horizontal cue lizards	p (t-test)
Total number of trials lizards made correct choice	9.3 ± 2.82	6.3 ± 2.24	0.003
Number of consecutive trials lizards made correct choice	5.2 ± 2.94	2.5 ± 1.46	0.003
Number of consecutive trials lizards made incorrect choice	2.4 ± 1.50	4.2 ± 1.59	0.003
Number of re-chases per incorrect trial	2.2 ± 0.66	2.4 ± 0.77	0.458

Numbers are mean ± SD. The p-value for a two-sample t-test (two-tail) is given ($N = 16$).

correct choice in significantly more trials than expected by chance (mean ± SD = 9.25 ± 2.817 trials; one sample $t = 2.484$, df = 15, $p = 0.025$). The horizontal cue lizards chose the correct retreat in fewer trials than expected by chance, though the difference narrowly failed to reach statistical significance (mean ± SD = 6.31 ± 2.243 trials; one sample $t = -2.118$, df = 15, $p = 0.051$). This means that the horizontal cue lizards chose the (incorrect) vertical retreat in 8.7 out of 15 trials on average (Table 2: 15–6.3 trials horizontal cue lizards made the correct choice = 8.7 trials the horizontal cue lizards made the incorrect choice of escaping to the vertical cue retreat). Taken together, these results indicate little brown skinks can use a visual cue to learn an escape behaviour, but only if the cue is a vertically striped one.

4. Discussion

The purpose of this study was to determine if little brown skinks could use a prominent local visual cue to learn an escape behaviour. The answer is yes, if the visual cue identifying the correct retreat is a vertically striped one (Table 1). This suggests that a lizard that escapes a predator by running to a previously identified refuge is able to use local visual cues associated with the refuge to facilitate its escape. Doing so would allow fleeing a lizard to reach a refuge quicker and more directly than if the lizard had to search for the location of a refuge each time it fled from a predator. Presumably, this increases the likelihood of the lizard making a successful escape.

An unexpected result of this study was that it was easier for little brown skinks to learn the escape behaviour when the escape retreat was associated with a vertical cue than when it was associated with a horizontal cue. Most of the vertical cue lizards met the learning criterion whereas only 1 of 16 horizontal cue lizards did so (Table 1). Furthermore, analysis of performances suggests the horizontal cue lizards were not as proficient at learning from their training as were the vertical cue lizards. When a lizard made an incorrect choice during a trial, it was gently returned to the start position in the observation tank and re-chased toward the retreats; this was repeated until the lizard escaped to the correct retreat. Although horizontal cue lizards made incorrect choices in more trials than did vertical cue lizards, the number of re-chases per incorrect trial that horizontal cue lizards required before they finally escaped to the correct retreat was the same as what the vertical cue lizards required (Table 2). When a horizontal cue lizard made an incorrect choice during a trial, it was able to correct its choice as quickly during the trial as a vertical cue lizard. However, the horizontal cue lizards generally failed to make the correct choice in trials after an incorrect choice trial as indicated by the frequency with which horizontal cue lizards followed one incorrect choice trial with another incorrect choice trial (Table 2: mean number of consecutive trials lizards made incorrect choice). This suggests they were less able to transfer training from an incorrect choice trial to subsequent trials than vertical cue lizards, further suggesting that it was harder for little brown skinks to learn an escape behaviour associated with a horizontal cue than a vertical cue.

Why this should be is unknown, but the results of this study hint at two possible hypotheses.

The first hypothesis concerns positional information a lizard may gain from a vertical, but not a horizontal, cue. A study by Day et al. (2003) on the teiid lizard *Cnemidophorus inornatus* (now *Aspidoscelis inornata*: Reeder et al., 2002) required lizards to choose one of two shaded refuges to escape excessive heat. In one experiment, the two refuges were painted different colours and striping patterns; in a second experiment the two refuges were visually identical and lizards had only the position of the refuge on the right or left side of a divider to guide their choice. Lizards using the position cues took fewer trials to reach the learning criterion and made correct choices significantly more often than lizards which had the colour and striping patterns of the refuges from which to learn. Day et al. (2003) concluded position cues are easier to learn than visual cues, at least when the goal is a refuge. In my study, little brown skinks may have obtained positional information from the vertical stripes of the vertical cue card to help them orient to the retreat. The stripes of the vertical cue card ran from the centre of the observation tank to the left side of the tank when the vertical cue card was behind the left retreat (as in Figure 1), and from the centre of the observation tank to the right side of the tank when the cue card was behind the right retreat. If the little brown skinks fixated on one of the vertical stripes then escaped under a portion of the cardboard retreat just to the left or to the right of that vertical stripe, they should escape to the retreat backed by the vertical cue card more often than they escape to under the retreat backed by the horizontal cue card. This is exactly what happened: little brown skinks trained to the vertical cue escaped to the vertical cue retreat significantly more often than expected by chance and the little brown skinks trained to the horizontal cue escaped to the horizontal retreat less often than expected by chance, indicating they also preferred to escape to the vertical cue retreat (though the difference narrowly failed to reach statistical significance). The fact that little brown skinks learn escape behaviour associated with a vertical cue better than one associated with a horizontal cue may be less about the orientation of the stripes *per se* and more about the ease with which little brown skinks use position relative to a vertical cue to learn where an escape retreat is located. Given that *A. inornata* also preferentially responds to position over a visual cues (Day et al., 2003), it is possible that position relative to some prominent environmental feature may be the most important cue to which lizards attend when learning where escape retreats are located.

The second hypothesis accounting for why little brown skinks may learn escape behaviours associated with vertical cues more easily than horizontal cues is that the little brown skink sensory system is biased toward perceiving vertical cues and/or forming associations between vertical cues and features of their environment, at least compared to the response to horizontal cues. While it is not surprising that lizards trained to escape to the vertical cue retreat chose that retreat in significantly more trials than expected by chance, it is informative that the lizards trained to escape to the horizontal cue retreat still chose the vertical retreat in 8.7 out of 15 trials on average (a result that narrowly failed to reach statistical significance), suggesting that even that the horizontal cue lizards preferred to escape to the vertical cue retreat despite their training to the contrary. It is possible that the little brown skink visual system is simply better able to perceive vertical cues than horizontal ones. To the human eye, the forest habitat occupied by little brown skinks presents an overwhelming density of vertically oriented visual cues in the form of trees ranging in size from thin sticks no wider than the stripes on the vertical cue card to large tree trunks up 50 cm in diameter, whereas the density of horizontally aligned logs and sticks is substantially lower. It, therefore, makes evolutionary sense that the little brown skink would pay special attention to vertical tree trunks and use them as visual cues to help them navigate as they move through their habitat because these cues are very abundant and will not move during a skink's lifetime (unless the tree falls).

Since the two retreats to which little brown skinks had to escape under were side by side in the observation chamber (Figure 1) and the position (left or right) of the correct retreat was constant for each lizard, it is possible that the 11 lizards that met the learning criterion did so in reaction to position of the correct retreat rather than to the pattern of stripes *per se*. However, this is unlikely to have been the case for several reasons. There were 16 vertical cue lizards and 16 horizontal cue lizards; for both groups, the correct retreat was on the left side for 8 of the 16 lizards and was on the right side for 8 of the 16 lizards so the experimental design was balanced. If position of the correct retreat were more important than the striping pattern of the cue cards, then the proportions of vertical cue lizards that met the learning criterion would be the same as the proportion of horizontal cue lizards that did so, but this was not the case (Table 1). Considering only the vertical cue lizards (which were significantly better at meeting the learning criterion than horizontal cue lizards), if the position of the correct retreat was important, then there should be a difference in the proportion of 'left vertical' cue versus 'right vertical' cue lizards that met the learning criterion. Again this was not the case: there was no significant difference in the proportion of left vertical cue versus right vertical cue lizards that met the Learning Criterion (left vertical cue: 6 of 8; right vertical cue: 4 of 8; Fisher's exact test $p = 0.608$).

Finally, if little brown skinks as a species have an innate side bias to escape to either the left or to the right, then the proportion of lizards that met the learning criterion should be greater for correct retreats on whichever is the preferred side compared to those on the opposite side regardless of cue. Yet there was no significant difference in the proportion of left versus right lizards that met the learning criterion (Table 1), suggesting no innate side bias exists. Though final confirmation of lack of side bias requires switching the positions of the cue cards during the trials, something that was not done during this study, the data that were collected give no indication that side bias affected the results of this study.

This study suggests that the specific features of a visual cue are important in determining whether or not little brown skinks can use that cue to help them learn and remember the location of a goal. If this result holds true for lizards in general, then spatial learning in lizards, and by extension other small animals, is more complicated than previously supposed. Future work should focus on the specific pattern, color, and shape of the cue as well as the precise position of the goal relative to the cue. It will require a great deal of study of a variety of animals before a complete understanding of the spatial learning is attained.

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References

Amiel, J.J. & Shine, R. (2012). Hotter nests produce smarter young lizards. — Biol. Lett. 8: 372-374.

Becker, B.M. & Paulissen, M.A. (2012). Sexual dimorphism in head size in the little brown skink (*Scincella lateralis*). — Herpetol. Conserv. Biol. 7: 109-114.

Conant, R. & Collins, J.T. (1998). A field guide to reptiles and amphibians of Eastern and Central North America. — Houghton Mifflin, Boston, MA.

Cooper, W.E. (1997). Escaping by a refuging prey, the broad-headed skink (*Eumeces laticeps*). — Can. J. Zool. 75: 943-947.

Cooper, W.E. (1998). Effects of refuge and conspicuousness on escape behaviour by the broad-headed skink (*Eumeces laticeps*). — Amphib.-Rept. 19: 103-108.

Cooper, W.E. (1999). Escape behaviour by prey blocked from entering the nearest refuge. — Can. J. Zool. 77: 671-674.

Cooper, W.E. (2003). Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. — Ethology 109: 617-626.

Cooper, W.E. (2008). Visual monitoring of predators: occurrence, cost and benefit for escape. — Anim. Behav. 76: 1365-1372.

Cooper, W.E. & Frederick, W.G. (2007). Optimal flight initiation distance. — J. Theor. Biol. 244: 59-67.

Day, L.B., Ismail, N. & Wilczynski, W. (2003). Use of position and feature cues in discrimination learning by a whiptail lizards (*Cnemidophorus inornatus*). — J. Comp. Psychol. 117: 440-448.

Holtzman, D.A., Harris, T.W., Aranguren, G. & Bostock, E. (1999). Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. — Anim. Behav. 57: 51-60.

LaDage, L.D., Roth, T.C., Cerjanic, A.M., Sinervo, B. & Pravosudov, V.V. (2012). Spatial memory: are lizards really deficient? — Biol. Lett. 8: 939-942.

Martin, J. & Lopez, P. (2000). Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decision of the lizard *Psammodromus algirus*. — Can. J. Zool. 78: 265-270.

Martin, J. & Lopez, P. (2003). Changes in the escape responses of the lizards *Acanthodactylus erythrurus* under persistent predatory attacks. — Copeia: 408-413.

Noble, D.W.A., Carazo, P. & Whiting, M.J. (2012). Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions. — Biol. Lett. 8: 946-948.

Paulissen, M.A. (2008). Spatial learning in the little brown skink, *Scincella lateralis*: the importance of experience. — Anim. Behav. 76: 135-141.

Paulissen, M.A. (2011). Geographic variation in learning of escape behavior in the little brown skink (*Scincella lateralis*). — J. Ethol. 29: 493-497.

Reeder, T.W., Cole, C.J. & Dessauer, H.C. (2002). Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. — Am. Museum Novitates 3365: 1-61.

Smith, D.G. (1997). Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. — Behav. Ecol. 8: 622-629.

Stone, A., Ford, N.B. & Holtzman, D.A. (2000). Spatial learning and shelter selection by juvenile spotted pythons, *Anterisia maculosus*. — J. Herpetol. 34: 575-587.

Systat (2007). MYSTAT Version 12 for Windows. — SYSTAT Software, Chicago, IL.

Ydenberg, R.C. & Dill, L.M. (1986). The economics of fleeing from predators. — Adv. Stud. Behav. 16: 229-249.