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Spatial and reversal learning in congeneric lizards with different foraging strategies

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Environmental demands that require intensive search for mates, food and nest sites are correlated with efficient spatial memory in many mammalian and avian species. This convergence of evidence has led to the view that spatial memory, and the neurological structures associated with it, have been selected in niches that require memory for the location of goal objects. Whether such evolutionary demands are also correlated with nonspatial abilities that require flexible use of associations similar to those required for spatial memory has not been well studied. In addition, correlations between niche types and the use of spatial or nonspatial memory have not been investigated in nonmammalian, nonavian taxa. In this study, we investigated the relationship between foraging strategies and performance on two tasks, one spatial and the other nonspatial, in congeneric lizard species: *Acanthodactylus boskianus*, an active forager that collects clumped sedentary prey, and *Acanthodactylus scutellatus*, a sit-and-wait predator that collects distributed mobile prey. The two species did not differ in their performance of a spatial memory task, but *A. boskianus*, the active forager, performed better on the reversal of a visual discrimination, a nonspatial task. These findings question the generality of the spatial adaptation model for vertebrates. We present the pliancy hypothesis, which we developed to account for these results.

The role of ecology in selection for spatial abilities is currently a major topic in cognitive ethology. Numerous studies using mammalian and avian species have examined the relationship between ecology and spatial memory, either directly, through a variety of maze and food-retrieval tasks, or indirectly, by measuring the size of the hippocampus, which has been well established as the neural substrate integral for some aspect of spatial cognition (O'Keefe & Nadel 1978; Rudy & Sutherland 1995; Day & Schallert 1996; Eichenbaum 1996; Whishaw & Jarrad 1996). These studies have demonstrated enhanced spatial memory in species that must search intensively for resources; for example, species that cache food in scattered locations (Sherry & Duff 1996), lay eggs in distributed nest sites (Sherry et al. 1993), search widely for mates (Sherry et al. 1992; Galea et al. 1996) or that must navigate to specific home sites (Bingman 1992). Closely related species with less spatially demanding niches score comparatively lower on tests of spatial ability.

On first glance, the ecology–spatial ability relationship seems like the quintessential example of selection for behaviours adapted to a particular niche. The consistency of this relationship has led to the spatial adaptation theory (Gaulin 1992; Sherry et al. 1992), which suggests that correlations between spatial ability (and underlying neurological substrates) and spatially demanding niches are a consequence of selection for navigational demands (Gaulin 1992; Sherry et al. 1992). However, there is no evidence that spatial ability per se was the trait upon which selection acted. Rather, selection could have acted more generally, producing skills that allow animals to select appropriate behaviours efficiently based on flexible use of stored memories about associations in the environment. Flexibility of this type is crucial to spatial and many nonspatial tasks.

Skilled spatial abilities and skills in other tasks that require the animal to use environmental knowledge pliantly, such as reversal learning, nonspatial working memory and nonspatial, delayed nonmatching to sample (Gray & McNaughton 1983), transitivity, social transmission of food preferences and symmetry preference (Eichenbaum 1996), are equally affected by many experimental manipulations in rats and other common

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laboratory animals. Presumably this is because they share the same neurological substrate. In pigeons, lesioning of the hippocampus has also been shown to affect spatial navigation (Bingman 1992) as well as resulting in deficits in latent inhibition, and reversal (but not acquisition) of position and conditional discrimination (Good 1987). Although efficient spatial abilities seem to be selected for in a number of species, spatial skills could be the result of selection for behavioural flexibility supported by memory processes, of which spatial memory is only a subset. This possibility does not fit into the spatial adaptation model (Gaulin 1992; Sherry et al. 1992).

We investigated two lines of evidence that test the generality of the spatial adaptation model. First, we studied representatives of a nonmammalian, nonavian vertebrate group to determine whether spatial ability and intensive search behaviours are generally correlated in vertebrates, and thus phylogenetically conserved. Second, we used a nonspatial test that involves flexibility in associating awards with cues to determine whether general improvements in complex memory are correlated with intensive search behaviours in lizards.

We studied lizards with distinct foraging niches that should encourage differential adaptations for learning and memory. Actively foraging lizards move frequently and use intensive visual and olfactory search for hidden prey items, whereas sit-and-wait predators move less often and visually scan the habitat and ambush prey as it moves into capture range (Anderson & Karasov 1981). Although the detailed behaviours and strategies associated with prey capture and foraging in the wild have not been well documented, it has long been assumed that active foraging requires more mental capabilities than sit-and-wait predation (Regal 1978). We have adopted this assumption and further believe that it is logical to hypothesize, on the basis of differences in foraging strategy, that active foragers require more spatial skills.

Given that alternative strategies for locating mates, nests and food have driven selection for spatial abilities in mammals and birds, it is plausible that the relatively dichotomous foraging strategies of lizards (Anderson & Karasov 1981; Huey & Pianka 1981; Nagy et al. 1985; Pietruszka 1986; Perry et al. 1990; Cooper 1994) might select for distinct adaptations for spatial memory in lizard species. We tested lizards' spatial abilities in an adaptation of the Barne's maze (Bach et al. 1995), which required lizards to escape cool temperatures and open spaces by moving to the one heated rock in an array of eight rocks placed in sandy pits along the perimeter of a circular arena. This approach is similar to behavioural paradigms designed to test general spatial abilities in voles, pigeons and other species in which a resource that is intensively searched for in the wild is replaced with an arbitrary reward in a laboratory test; for example, the ability of an animal to locate mates in the wild is assessed by testing its ability to locate a food reward (Gaulin 1992). In our behavioural paradigm, the spatial adaptation model predicts that active-foraging lizards will perform better than those that are sit-and-wait predators, and that active foragers will favour the use of a spatial memory strategy to locate the hot rock. We also tested these lizards on a local cue version of the hot-rock maze as a control for differences in motor response and motivation. In the local cue version, lizards had to make only an operant response to approach the local cue, a single prominent visual cue spatially contiguous with the hot rock. The spatial adaptation model predicts no differences between active foragers and sit-and-wait predators on the local cue version of the hot-rock maze.

An alternative to the spatial adaptation model, which we will call the pliancy model, is that the ecological demands of active foraging may select for behavioural flexibility that is supported by memory of complex associations, but does not necessarily select for a predisposition to solve tasks using a spatial strategy. By pliancy we mean having the behavioural flexibility to encode complex relationships between stimuli and reinforcers, and to use this information to select adaptively a behavioural response strategy when stimuli, reinforcers or both change in unpredictable ways. Our definition of pliancy is somewhat similar to configuration learning (Rudy & Sutherland 1995), but refers more to an ability to select the most appropriate configurations in relation to reinforcers rather than to the existence of these configural associations themselves (Day & Schallert 1996). If pliancy can evolve without selection for predispositions to use distal cues to guide search in a spatial manner, we may find that active foraging species do not differ from sit-and-wait predators on the spatial task, but we would expect the active forager to be better at a nonspatial task that requires pliancy. Thus, on the basis of the pliancy model, we predicted that active foragers and sit-and-wait predators would acquire visual discrimination of a food reward in the same number of trials, but that the active forager would take fewer trials to learn a reversal of this discrimination. Reversal learning requires, in our terms, pliancy.

Given that the pliancy model suggests that spatial memory need not be directly selected for in species that actively forage, there is the distinct possibility that, regardless of foraging strategy, lizards may not solve the spatial task using spatial memory. There are numerous ways to solve navigation problems without reliance on flexible choice for stores of associations. For instance, many hymenopteran species are able to locate nest and food sites by storing viewpoint-dependent retinotopic images of landmarks surrounding the nest site when leaving, and comparing them to current retinal images when returning (Collett & Zeil 1996).

The manner in which reptiles perform close-range navigation, especially as it applies to a laboratory task, has not been investigated (with the exception of Holtzman et al. 1999). We do know that reptiles can solve other types of tasks that require pliancy, such as reversal of nonspatial discriminations (Grisham & Powers 1990). If we find a lack of evidence for spatial memory in lizards while identifying species differences in other tasks requiring pliancy, this would support the pliancy model for the vertebrate taxa, but the spatial adaptation model could still hold true for mammals and birds.

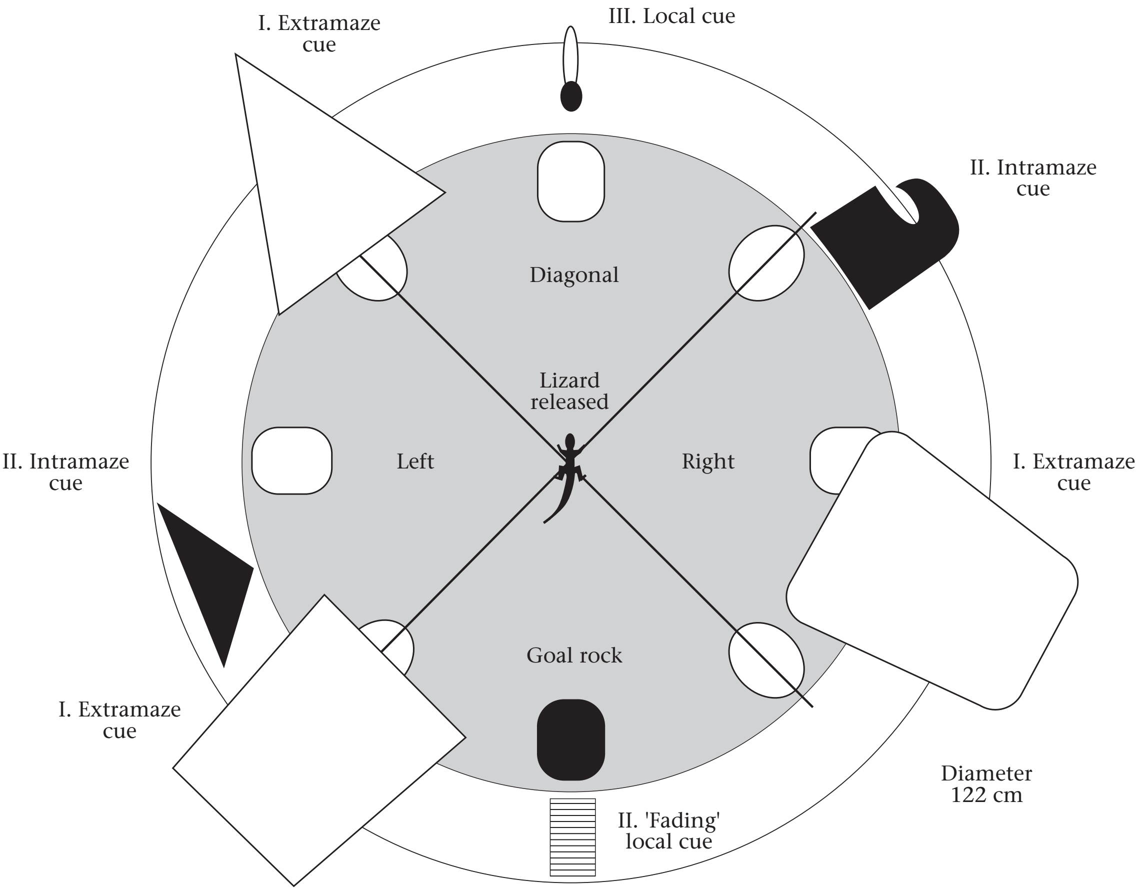

Figure 1. Illustration of cue sets used in three experiments in the hot-rock arena. I. In experiment 1, four extramaze cues were hung like flags over the arena, only three examples are shown due to space constraints. These cues were removed after 16 blocks of training. II. In experiment 2, intramaze cues were attached to the walls of the maze and a single local cue was attached directly behind the goal rock. The local cue was exchanged with smaller versions every three blocks and then removed after nine blocks of training. III. Each day in experiment 3, a randomly chosen rock was heated and cued by a red light.

EXPERIMENT 1: EXTRAMAZE SPATIAL CUES

Subjects

Congeneric desert-dwelling lacertids, *Acanthodactylus boskianus* (*N*=6) and *A. scutellatus* (*N*=9), males were used. Lizards were collected in the field in Israel (see Perry et al. 1990) by Y. L. Werner and colleagues (necessary permits obtained) from 22 April to 27 April 1995. Animals were maintained in the laboratories of Y. L. Werner and W. E. Cooper approximately 6 months prior to behavioural testing. In our laboratory, males were housed separately with zero (two *A. scutellatus*) to three females. Lizards that were housed alone behaved similarly in all experiments to those housed with females. The same lizards were used for all experiments.

Apparatus

We built a circular arena (1.5 m in diameter and 0.4 m in height) and covered the walls with solid, coloured contact paper in an attempt to provide a homogenous field. The floor was 1.25-cm thick plywood. Along the perimeter of the arena, we placed eight sandy pits containing insulated hot rocks (4 × 10 cm, Junior Sizzle Stones by Tetra Terrafuna®) spaced at regular intervals. We denied the lizards access to all but one pit by covering the sandy floor with a foam-core board, on the surface of which we glued artificial plastic turf. We cut eight holes in the foam core board/artificial turf covering. We barred entrance to seven of the holes using removable Plexiglas windows. The insulated hot rocks (heat gradient negligible, 2 cm horizontal, 3 cm vertical) were heated by internal coils and reached a substrate temperature between 39 and 45°C, approximating the lizards' mean active body temperatures of about 39°C (Duvdevani & Borut 1974). All rocks could be heated, but only one rock was heated during a particular training trial. We made four distal extramaze cues of poster board of varying colour and irregular shapes, approximately 50 × 75 cm, and suspended them over the arena from a horizontal, 60-cm length of PVC pipe (2.53 cm in diameter) connected at a right angle to a vertical 90-cm long (5.06 cm in diameter) PVC pipe that was embedded in a tub of cement (20 cm in diameter). The poles were placed approximately 10 cm from the arena walls so that the cues hung a maximum of 15 cm inside the arena. We also positioned the cues such that no cue hung directly over the goal (Fig. 1, extramaze cues).

During testing, we placed the lizards in tubular holding cages (30 cm in height, 15 cm in diameter), heated between trials by lamps to between 29 and 32°C. To release lizards into the centre of the arena, we inverted the holding cage and lifted the cage by a handle on the bottom, releasing the hinged top and freeing the lizard. We videotaped each lizard's performance from above and monitored it on-line from another room to minimize observer effects.

Procedures

Acquisition

On first trials only, we placed each lizard directly on the heated goal rock for 3 min. All other trials began when we released a lizard from the holding cage into the centre of the arena, and ended when the lizard located the goal. We conducted one block of three acquisition trials daily for 20 days. After day 16, we removed the distal extramaze cues.

We defined latency to the goal as the time beginning with the first head movements of a lizard and ending when a lizard located the pit containing the goal. In early acquisition trials, lizards frequently spent time motionless or dashed from the holding cage and then remained motionless from a few seconds to several minutes. We did not include this time in final measures of latency. If a lizard remained motionless for 10 min, we captured it, placed it on the goal for 3 min, recorded latency as 10+ min, and ended the trial.

Once on the goal, lizards rarely moved prior to the termination of the 3-min reinforcement period. If a lizard touched the goal but moved away in less than 1 min, we did not record latency until it returned to the goal and stayed 1 min or more. In some circumstances, a lizard would lie next to the pit rather than climbing into the pit. If the lizard stayed within 3 cm of the pit for the 3-min reinforcing time, we recorded latency as the time from release until the lizard was within 3 cm of the pit. If the lizard did not locate or lie next to the goal 10 min after movement began, we placed it in the pit containing the heated rock for 3 min, recorded latency as 10+ min, and ended the trial.

We traced the lizard's movements on a scaled map of the arena and measured path distance using Sigma Plot software and a bit-map pad. We defined learning as a decrease across trials in one or more of the following: latency, total distance travelled, and the percentage of total distance travelled in nongoal quadrants.

After each trial, we captured the lizard and returned it to its holding cage. Between trials, we wiped the plastic artificial turf floor covering with alcohol to minimize olfactory cues, rotated the floor covering and exchanged the Plexiglas windows, such that the last open hole was now covered with a window, and a hole that had been covered with a window was now open and aligned with the sandy pit containing the goal. Because we rotated the floor between trials, there was no stable relationship between texture patterns on the turf and the location of the goal. After a single trial for each lizard, we tested a different lizard. We tested lizards in squads of three or four lizards, thus intertrial intervals ranged from about 6 to 20 min depending on the performance of intervening lizards.

Probe trials

Although a decline in latency across trials implies learning to locate the goal, it does not necessarily indicate a spatial search strategy using the distal cues. To assess differences in spatial and nonspatial strategies, we used a probe trial typical of the those used in studies of spatial learning (Morris 1981). At the completion of training, we allowed all rocks to cool, and turned the wall of the maze 180° so that any features on the maze wall or the goal rock that could have been used as local feature cues would now indicate that the goal was diagonally opposite its original location. Distal cues remained in the same spatial location in relation to the previously correct location of the goal and the room. For this experiment, objects in the room served as the remaining distal cues for the probe trial, because experimenter-supplied distal cues, as mentioned previously, had been removed after block 16 (day 16) to determine whether the lizards were attending to these cues.

We released a lizard into the maze and allowed it to explore for 10 min. We recorded the time a lizard took to reach the location of the previously heated rock, and the time taken to reach the location that was 180° from the originally heated rock. In addition, we recorded the percentage of total distance traversed in four evenly divided quadrants; goal, diagonal, right and left (with reference to the goal quadrant) during the first 3 min of search (Fig. 1). Because lizards were finding the goal in approximately 3 min during the last trials of acquisition, we used this period to observe search patterns.

If a lizard learned the spatial location of the goal using distal cues, latency to the goal for the last block of acquisition should not differ from latency to the goal on the first probe trial, and a greater percentage of the total path distance should be in the previously rewarded goal quadrant than in other quadrants of the maze. If a lizard had used local feature cues on the walls of the maze or the rock to guide it to the goal, it would show a preference for searching in the diagonal quadrant of the maze, as the maze had been rotated 180° from the original position. A lizard that had learned to find the reward by trial and error or praxis (rules for motor patterns such as 'search towards wall'), lizards would not show a preference for any quadrant of the maze during the probe trial. If lizards used some combination of local feature cues and distal cues, there should be individual preferences for maze quadrants but no group preference for the originally rewarded quadrant, or the diagonal quadrant.

Results and Discussion

Acquisition

We used a two-way repeated measures analysis of variance (ANOVA, species × block) to analyse acquisition effects of latency for blocks 1–20 (Fig. 2), distance, the percentage of total distance in the goal quadrant (Fig. 3)

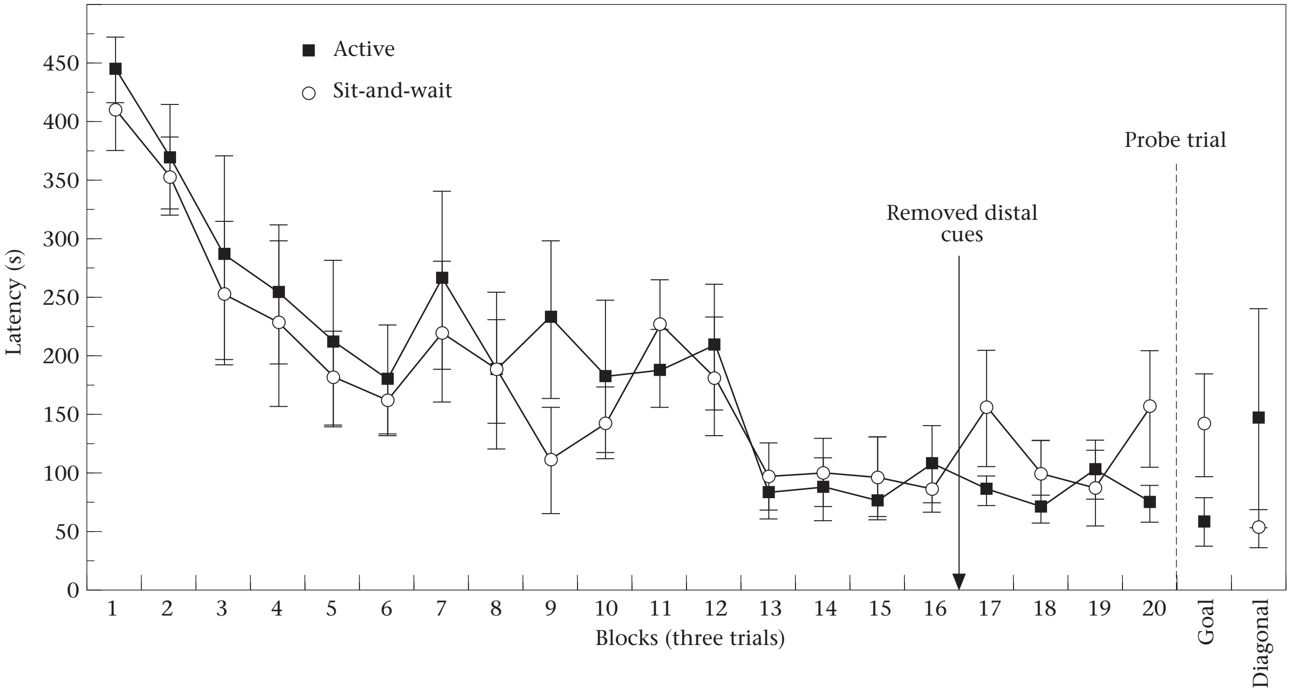

Figure 2. Mean latency from release to the goal in experiment 1 for the active foragers and the sit-and-wait predators across 20 blocks of training. The arrow on the *Y* axis shows when the distal extramaze cues were removed; there was no significant increase in latency. The dashed line indicates when the maze was rotated 180°. Latency to reach the original location of the goal and the rock diagonally opposite the original location are shown.

and speed (cm/s) for blocks 14–20, and to analyse the effect of removing the distal cues after block 16 on latency, distance and the percentage of total distance in the goal quadrant. For all statistical tests in this paper, $\alpha=0.05$, and all values are reported to nearest threshold significance, with a minimum value of 0.001. All *t* tests are two-tailed.

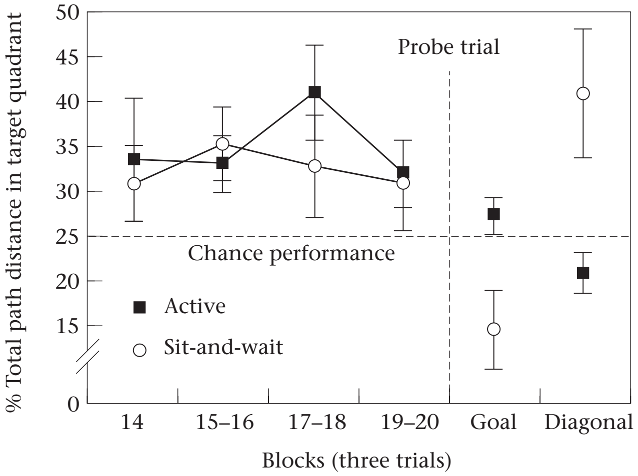

Figure 3. The mean percentage of total path distance covered in the goal quadrant during acquisition, and in the goal quadrant and the quadrant diagonally opposite the goal quadrant on the probe trial for experiment 1. Distal extramaze cues were available up to block 16. The maze was rotated 180° during the probe trial. Distance measurements were analysed for blocks 14–20 only. Blocks were averaged to reduce variability in the presentation, but statistics were done on single blocks of three trials each. The horizontal line indicates chance performance of 25% of total path distance in each quadrant. The vertical dashed line separates the training trials from the probe trial.

Although both groups showed improvements in latency to locate the goal (block effect: $F_{19,247}=9.6$, $P<0.001$; trend linear analysis: $F_{1,247}=133.9$, $P<0.001$), there were no differences between species during acquisition for measurements of latency ($F_{1,13}=0.06$, NS), distance ($F_{1,13}=1.4$, NS), percentage of total distance in the goal quadrant ($F_{1,13}=0.06$, NS) or speed ($F_{1,13}=1.1$, NS), and no interactions (latency: $F_{19,247}=0.51$, NS; distance: $F_{6,78}=0.64$, NS; percentage of total distance: $F_{6,78}=0.9$, NS; speed: $F_{6,78}=0.45$, NS). Only latency was measured throughout training in experiment 1, the other dependent measures were scored only on blocks 14–20 at the end of training. There was no significant improvement during these last trials of training for measurements of distance ($F_{6,78}=0.65$, NS), percentage of total distance ($F_{6,78}=1.3$, NS), or speed ($F_{6,78}=0.23$, NS). Lizards apparently did not use distal extramaze cues to navigate to the goal because there were no significant differences for either species between the block of training prior to removal of the distal cues and performance on the first block after the distal cues had been removed for any of the dependent measures (Fig. 2, blocks 16–17). We analysed comparisons between blocks 16 and 17 with separate two-way ANOVAs (species × block). *F* values (all nonsignificant) were as follows: latency (species effect: $F_{1,13}=0.4$; block effect: $F_{1,13}=0.27$; interaction: $F_{1,13}=1.2$); distance (species effect: $F_{1,13}=0.23$; block effect:

$F_{1,13}$=0.01; interaction: $F_{1,13}$=0.97); percentage of distance in goal quadrant (species effect: $F_{1,13}$=3.7; block effect: $F_{1,13}$=0.06; interaction: $F_{1,13}$=0.01); speed (species effect: $F_{1,13}$=0.92; block effect: $F_{1,13}$=0.0001; interaction: $F_{1,13}$=0.07).

We suspect that lizards do not typically attend to stationary objects above their heads, and therefore, were not using the experimenter-supplied distal cues. Under similar conditions, rats will orient their heads towards distal visual cues at choice points displaying 'vicarious trial-and-error' (VTE) head movements, which decrease as the rats learn to distinguish among cues and no longer needs to examine both incorrect and correct choices (Amsel 1993). Because the arena walls were 40 cm high, lizards could not have attended to cues directly in their line of sight, but could have used as cues objects on the ceiling and objects high in the room on the opposite side of the arena from their position. Lizards' VTEs did not suggest they used distal cues. Although the lizards showed lateral VTEs, they did not have a vertical component to their VTEs, nor was the head turned to the side so that one eye oriented vertically, as was done when motion occurred above their heads at the same level as the distal cues.

Probe trials

Results of the probe trials suggested that the lizards had not developed a spatial strategy. Given that the lizards did not respond to removal of the distal cues, we did not expect that they would indicate use of a spatial strategy by searching for the goal in its original location. They could, however, have been attending to the cues in the room and on the ceiling to guide spatial search. The results suggest this was not the case. Lizards did not appear to be using any distal cues outside the arena.

We analysed species difference in latency to reach three focal locations, the goal rock on the last trial of training, the goal rock during the probe trial, or the rock diagonally opposite the goal rock during the probe trial, using a two-way repeated measures ANOVA (species × focal location). There was no species difference in latency to arrive at the focal locations (ANOVA: $F_{1,13}$=0.65, NS). There was also no effect of focal location; for both species, the time taken to reach the three focal locations did not differ (ANOVA: $F_{2,26}$=0.89, NS) and there was no species × focal location interaction (ANOVA: $F_{2,26}$=2.4, NS).

Results of a two-way repeated measures ANOVA analysing species differences in the percentage of total path distance travelled in the three target quadrants revealed no species effect (species × target quadrant: $F_{1,13}$=1, NS); thus, there was no difference between species in the distance travelled in the goal quadrant on the last trial of training, in the goal quadrant on the probe trial and in the diagonal quadrant on the probe trial. There was also no difference across species in the percentage of total path distance travelled in the target quadrants ($F_{2,26}$=1.5, NS). The interaction between species and target quadrant was significant ($F_{2,26}$=4.5, $P<0.02$; Fig. 3). We performed one-way repeated measures ANOVAs, followed by least square means analysis (with alphas corrected for multiple comparisons), for each species to analyse this effect further. The sit-and-wait predator had a biased search pattern ($F_{2,16}$=4.6, $P<0.05$). The percentage of total path distance travelled in the goal quadrant on the last trial of training did not differ significantly from the percentage of total path distance travelled in the goal quadrant (t_8=0.91, NS) or the diagonal quadrant (t_8=2, NS) during the probe trial, but there was a significant preference for searching in the diagonal quadrant over the goal quadrant on the probe trial (t_8=3, $P<0.05$), suggesting that these lizards had used slight aberrations on the walls of the maze to guide search during acquisition. A bias for the diagonal quadrant rather than the goal quadrant was not present during acquisition. For the active forager, there was no difference between the percentage of total path distance travelled in the three target quadrants ($F_{2,10}$=2.1, NS), suggesting that the active forager was not using distal cues or local cues for search. The active foragers appeared to be using a combination of trial-and-error search and random paths. This result was not predicted but was not surprising given that the distal cues provided by the experimenter were apparently useless to the lizards.

Preferred quadrant analyses

For each lizard, the preferred quadrant was the quadrant that had the greatest percentage of total path distance during the probe trial. Because individual differences in which quadrant is preferred can obscure group differences, and because preference for any particular quadrant indicates deviation from random or trial-and-error search patterns, we analysed species differences in the percentage of total distance travelled in the preferred quadrant. We included three target quadrants in a repeated measures ANOVA: (1) the percentage of total distance in the preferred quadrant on the probe trial (preferred quadrant), (2) the average percentage of total path distance in the three nonpreferred quadrants during the probe trial (other quadrants), and (3) the percentage of total path distance in the goal quadrant on the last trial of acquisition (last quadrant). We ran a two-way repeated measures ANOVA (species × target quadrant). There was no species difference ($F_{1,13}$=0.004, NS) and only a marginal interaction ($F_{2,26}$=2.6, $P<0.1$). There was an overall effect for target quadrant ($F_{2,26}$=10.8, $P<0.001$; Fig. 4). However, the pattern of results seen in one-way repeated measures ANOVAs of individual species effects, followed by least squares means analysis with alpha corrected for multiple comparisons, did not suggest that the lizards were using the same strategy to guide search during the probe trial as they had used to guide search during acquisition. If lizards were using the same strategy to guide them to the preferred quadrant and to reach the goal during acquisition, the percentage of total path distance in the last quadrant should have differed from the other quadrants but not from the percentage of total distance in the preferred quadrant. Similarly, the percentage of total path distance in the preferred quadrant and the other quadrants should have differed from each other. This pattern would suggest that, despite the lack of a group tendency to use distal spatial cues preferentially, individual lizards were searching a particular quadrant in

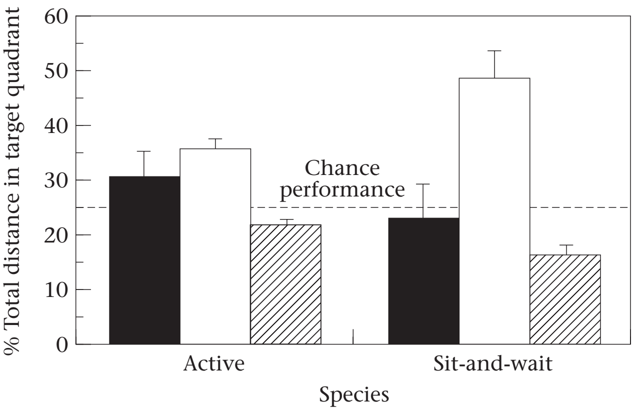

Figure 4. Preferred quadrant analysis for experiment 1. Last (■): the percentage of total path distance in the goal quadrant on the last trial of training; Preferred (□): the percentage of total path distance in the quadrant searched the most by individual lizards during the probe trial; Other (▨): the average percentage of total path distance in the three nonpreferred quadrants for individual lizards during the probe trial. No distal cues other than objects in the room were available during the last trial of training or the probe trial. The maze was turned 180° during the probe trial.

a manner similar to search in the goal quadrant at the end of training. Preferential search suggests an expectation of reward in an individual lizard's preferred quadrant and thus some memory for place.

This was not the case for either the active forager or the sit-and-wait predator. For the active forager, the percentage of total path distance in the preferred quadrant differed significantly from the percentage of total path distance in the other quadrants. In addition, the percentage of total path distance in the last quadrant did not differ significantly from that in the preferred quadrant. However, the percentage of total path distance in the last quadrant did not differ significantly from that in the other quadrants. Because performance on the last trial of training did not differ significantly from the other quadrants, active foragers appeared to have wandered randomly during the probe trial. For the sit-and-wait predator, the percentage of total distance in the preferred quadrant differed significantly from the percentage of total path distance in the other quadrants (t_8=4.2, P<0.01) but it also differed significantly from the last quadrant (t_8=3.3, P<0.05), and performance on the last quadrant was similar to the other quadrants (t_8=0.85, NS). Thus, search was not random during the probe trial. The sit-and-wait lizards had a significant preference for one quadrant on the probe trial. However, their performance on the probe trial was unlike that on the last trial of training, suggesting that the lizards were not using similar search behaviours during acquisition and the probe trial.

The contrast between the last quadrant and the preferred quadrant for sit-and-wait lizards was accentuated by the unusual performance of this group on the last quadrant. The sit-and-wait lizards were typically searching the goal quadrant at values above chance in the last seven trials of training (Fig. 3), but declined to below chance search of the goal quadrant in the last trial of training (last quadrant). Still, the sit-and-wait lizards did concentrate search during the probe trial in the quadrant diagonally opposite the trained quadrant, and thus, appeared to be more inclined to use the local cues as a guide to the goal. Six of the nine sit-and-wait lizards had a moderate to strong preference for the diagonal quadrant during the probe trial (33–73% of total distance), two others appeared to search randomly, the last preferred the right quadrant (57%).

As expected, the sit-and-wait predator did not use distal cues for navigation and appeared to use instead local features for navigation. Unexpectedly, the active foraging lizards as a group did not use local or spatial cues preferentially, and individual lizards appeared to search randomly in the four quadrants. Placement of distal cues outside the maze made complete tests of the hypotheses in experiment 1 difficult as the lizards appeared not to attend to these cues.

EXPERIMENT 2: INTRAMAZE DISTAL CUES

Experiment 1 demonstrated that neither lizard species responded spatially to extramaze distal cues. After a week-long break, we began testing again with spatial cues placed inside the maze.

Subjects

Subjects were *A. boskianus* (*N*=6) and *A. scutellatus* (*N*=9) males.

Apparatus

The same circular arena used in experiment 1 was used for experiment 2. We positioned two prominent intramaze cues (Fig. 1, intramaze cues) such that direct approach or avoidance of either one would not lead to contact with the goal. Although these distal cues were intramaze cues, like extramaze distal cues, they cue the goal indirectly and provide information about the spatial arrangement of the arena but do not otherwise provide local information about the goal.

Procedures

Acquisition

Basic procedures were the same as for experiment 1. In the present experiment, we conducted one block of three acquisition trials daily for 12 days. We were concerned that prior experience with a lack of useful distal cues in experiment 1 may have encouraged the lizards to navigate using praxis and trial-and-error search. To discourage these behaviours, and to promote use of experimenter-supplied cues, we used a shaping procedure similar in concept to one that has helped rats with drug- (Day & Schallert 1996) and lesion- (L. B. Day, M. Weisend, R. J. Sutherland, T. Schallert, unpublished data) induced hippocampal deficits and impaired spatial abilities to select efficient spatial strategies. In addition to the two intramaze distal cues, we placed a prominent local cue (10 × 45 cm) directly behind the goal for five blocks. This cue was reduced in size (10 × 28 cm) before block 6, and

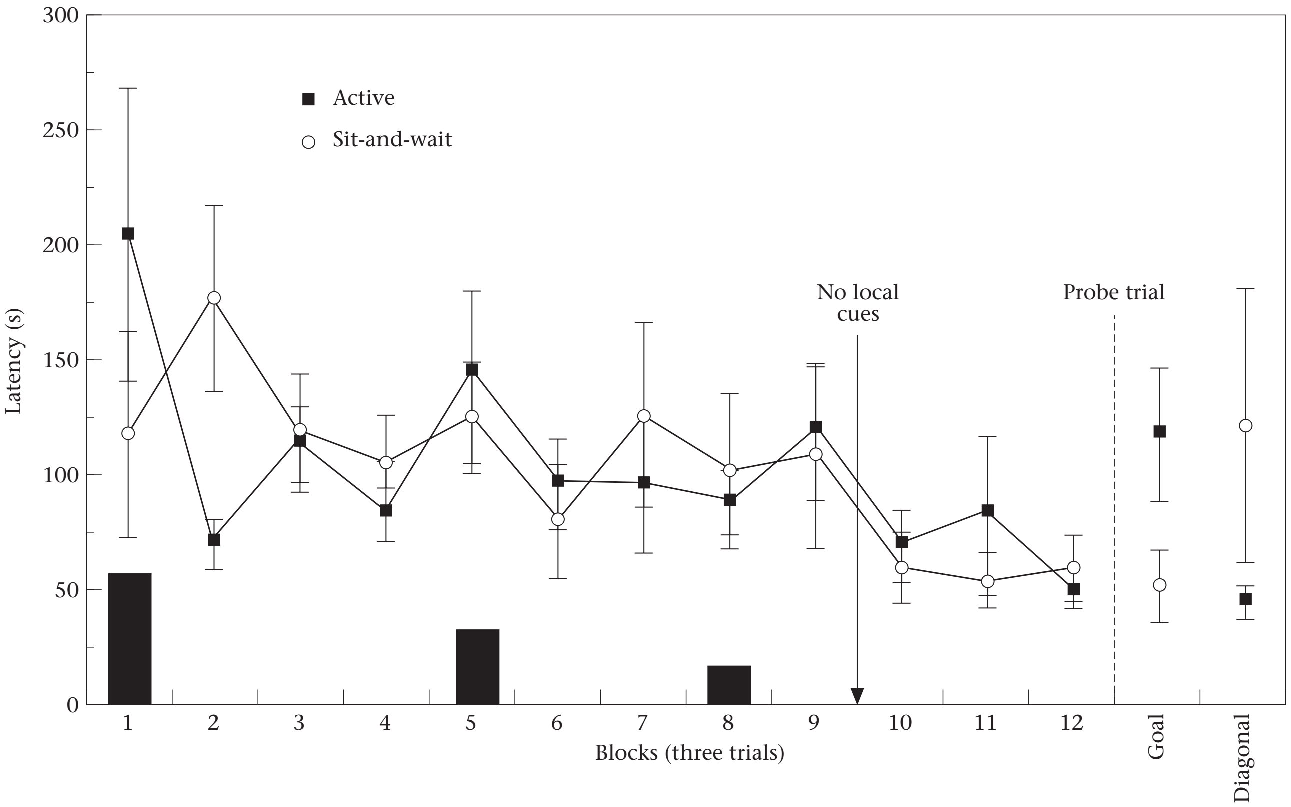

Figure 5. Mean latency from release to the goal in experiment 2 for the active foragers and the sit-and-wait predators across 12 blocks of training. The rectangles on the *Y* axis represent reductions and the arrow represents the removal of the fading local cue; there was no significant increase in latency following the removal of the local cue. The dashed line indicates when the maze was rotated 180° for the probe trial. The distal intramaze cues remained in the same location, relative to the room, during the probe trial and during training. Latency to reach the original location of the goal and the rock diagonally opposite the original location during the probe are shown.

again (10 × 15 cm) before block 8, and then removed before block 10. We conducted the remaining three blocks without the local cue.

Probe trials

Probe trials were the same as for experiment 1. We removed the distal cues from the arena walls prior to wall rotation and then reattached the cues such that they remained in the same location relative to the room.

Results and Discussion

Acquisition

Analyses were carried out as for experiment 1. There were no species differences during acquisition nor any interactions with species for latency (species effect: $F_{1,13}$=0.01, NS; interaction: $F_{11,143}$=1.3, NS), distance (species effect: $F_{1,13}$=0.04, NS; interaction: $F_{11,143}$=0.08, NS), the percentage of total distance in the goal quadrant (species effect: $F_{1,13}$=0.1, NS; interaction: $F_{11,143}$=1.7, NS), or speed (species effect: $F_{1,13}$=0.8, NS; interaction: $F_{11,143}$=1.1, NS). Both species learned to navigate to the goal across blocks as shown by the decrease in latency to the goal ($F_{11,143}$=2.6, P<0.01; trend linear: $F_{1,143}$=19.3, P<0.001; Fig. 5), decreased distance to the goal ($F_{11,143}$=2.8, P<0.01; trend linear: $F_{1,143}$=23.5, P<0.001), and an increase in the percentage of the total distance in the goal quadrant ($F_{11,143}$=2.5, P<0.01; trend linear: $F_{1,143}$=14.9, P<0.001; Fig. 6). Speed did not change across blocks ($F_{11,143}$=0.64, NS). We analysed the lizards reaction to removal of the local cue designed to shape goal-directed behaviour using a two-way repeated measures ANOVA (species × block). There was no significant impairment in performance for any of the dependent measures when the local cue used for shaping was removed between block 9 and 10 (Figs 5 and 6). *F* values for this analysis were as follows: latency (species effect: $F_{1,13}$=0.09; block effect: $F_{1,13}$=3; interaction: $F_{1,13}$=0.0001); distance (species effect: $F_{1,13}$=0.001; block effect: $F_{1,13}$=2.5; interaction: $F_{1,13}$=0.02); the percentage of total distance in the goal quadrant (species effect: $F_{1,13}$=0.83; block effect: $F_{1,13}$=1.9; interaction: $F_{1,13}$=0.02); speed (species effect: $F_{1,13}$=2.7; block effect: $F_{1,13}$=0.1; interaction: $F_{1,13}$=0.29).

Probe trial

Analyses were the same as for experiment 1. There were no significant differences between the species and no interactions between species and blocks for measurements of latency to the two focal locations (species effect: $F_{1,13}$=0.08, NS; interaction: $F_{2,26}$=2.08, NS) or the percentage of total path distance in the three target

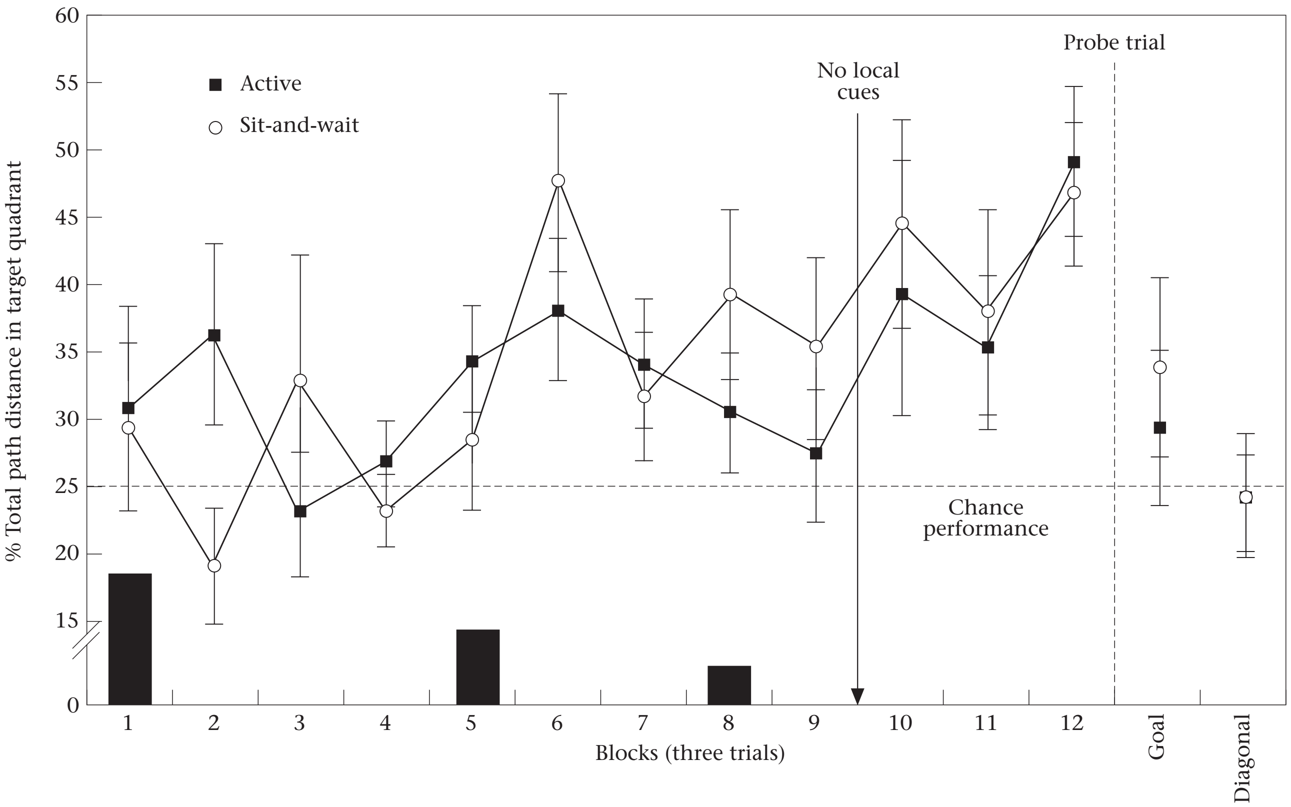

Figure 6. The mean percentage of total path distance covered in the goal quadrant during acquisition and in the goal quadrant and the quadrant diagonally opposite the goal quadrant on the probe trial in experiment 2. The rectangles on the *Y* axis represent reduction, and the arrow represents the removal of the fading local cue; there was no significant decrease in total path distance covered in the goal quadrant following removal of the local cue. The maze was rotated 180° during the probe trial, while distal intramaze cues remained in the same location, relative to the room, during the probe trial and during training. The horizontal line indicates chance performance of 25% of total path distance in a quadrant. The vertical dashed line separates the training trials from the probe trial.

quadrants (species effect: $F_{1,13}$=0.07, NS; interaction: $F_{2,26}$=0.18, NS). There was no significant difference between latency to arrive at the goal rock on the last trial of training, the goal rock during the probe trial, and the diagonal rock during the probe trial ($F_{2,26}$=0.48, NS) (Figs 5 and 6). A greater amount of the total path distance was covered in the goal quadrant on the last trial of training than in either the goal quadrant or the diagonal quadrant during the probe trial ($F_{2,26}$=7.7, P<0.001). This result as well as the preferred quadrant analysis (below) suggests that lizards did not respond to either local cues or distal cues preferentially.

Preferred quadrant analysis

There were also no species differences ($F_{1,13}$=0.03, NS), or interactions ($F_{2,26}$=0.07, NS) using the preferred quadrant analyses as in experiment 1 (Fig. 7). However, individuals of both species did prefer one particular quadrant of the maze during the probe trial ($F_{1,13}$=30, P<0.001) and this pattern of performance suggests the use of a strategy consistent with the strategy used in training.

Results of one-way ANOVAs for each species, followed by least mean squares analysis (with alpha corrected for multiple comparisons), revealed that there was no difference between the percentage of total distance travelled in the last quadrant and in the preferred quadrant, but that there was a significant difference in the distance travelled in each of these quadrants when compared to the other quadrants for both species. Least square means results (active forager: last quadrant versus other quadrants: t_5=5.6, P<0.001; preferred quadrant versus other quadrants: t_5=4.2, P<0.01; last quadrant versus preferred quadrant: t_5=1.38, NS; sit-and-wait predator: last quadrants versus other quadrants: t_8=4.6, P<0.001; preferred quadrants versus other quadrants: t_8=3.9, P<0.01; last quadrant versus preferred quadrant: t_5=0.69, NS). Examination of the individual lizards' distributions of the percentage of path distance travelled in each quadrant confirmed that 10 of the 15 lizards had a strong preference for one quadrant (average 48% in preferred quadrant). Thus, the lizards' behaviour suggested the expectation of the goal in a specific location, but their navigation strategy was not specifically tapped by the probe trials we conducted.

When environmental cues can be used as spatial cues or local cues, mammalian species tend to use cues spatially (McNaughton 1996). In studies with birds, black-capped chickadees, *Parus atricapillus*, have been shown to use spatial cues over feature cues when both cue types are available, while dark-eyed juncos, *Junco hyemalis*, used spatial cues and feature cues about equally

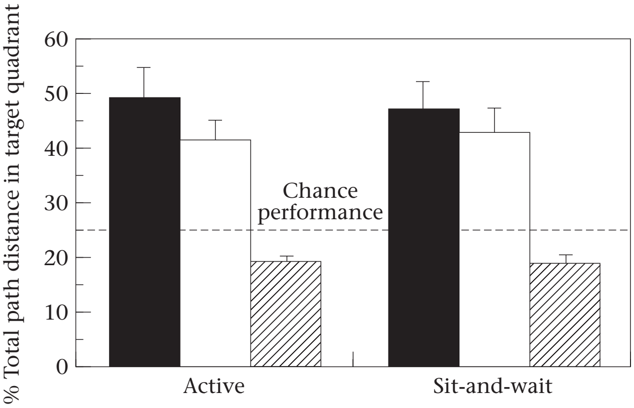

Figure 7. Preferred quadrant analysis for experiment 2. Last (■): the percentage of total path distance travelled in the goal quadrant on the last trial of training; Preferred (□): the percentage of total path distance travelled in the quadrant searched the most for each lizard during the probe trial; Other (▨): the average percentage of total path distance of the three nonpreferred quadrants during the probe trial. Distal intramaze cues were in the same spatial location, relative to the room, during the last trial of training and during the probe trial, but the maze was rotated 180° for the probe trial.

(Brodbeck & Shettleworth 1995). Neither of these two bird species, however, makes a preponderance of choices to extraneous stimuli that are not reliably cued by either spatial or feature cues (Brodbeck & Shettleworth 1995). Unlike mammals or birds, our lizards did not choose local feature cues (diagonal quadrant) or spatial cues (goal quadrant) preferentially. Although we cannot expect the lizards to categorize stimuli in any arbitrary manner set up by an experimenter, the distinction between feature cues and spatial cues is common to many species. However, it has recently been noted by Strasser & Bingman (1996) that homing pigeons, at least when trained to receive food rewards in the laboratory, appear to encode the environment holistically rather than by dissociation of specific cue types, such as the colour identifying the food site, nearby landmarks and geometric cues. Although specific tests still need to be carried out, we believe that lizards may use holistic encoding of the environment similar to the way in which pigeons apparently solved Strasser & Bingman's (1996) task. Because the lizards in our study chose a specific quadrant to search in during the probe trials, we suggest that the lizards were affected by the dissociation of local feature cues and spatial cues such that their search was guided by a mismatch of the environmental configuration between acquisition and probe trials. The altered environmental configuration may have led to concentrated search in a random quadrant.

EXPERIMENT 3: LOCAL CUES

Subjects

Subjects were *A. boskianus* (N=5) and *A. scutellatus* (N=9) males.

Apparatus and Procedures

We used the arena and basic test procedures described in experiment 1 and 2 to test operant conditioning to a local visual cue. Each day, we randomly chose a rock to be used as the heated goal rock. A small red light hung over the chosen hot rock to cue the goal. We conducted one block of three trials daily for 12 days. We recorded latency to the goal as for the previous experiments.

Results and Discussion

Contrary to expectations, there was a species difference in latency to reach the goal. The active forager had longer latencies to reach the goal than did the sit-and-wait predator ($F_{1,12}$=5.13; P<0.05; Fig. 8). The decline in latency across blocks suggests that both species learned the task ($F_{11,132}$=6.04, P<0.001; trend linear: $F_{1,132}$=28.3, P<0.001). There was no block × species interaction ($F_{11,132}$=0.79, NS).

The superior performance of the sit-and-wait predator may be due to their greater reliance on vision for prey capture (Anderson & Karasov 1981; Cooper 1994). Whether the species difference was based on peripheral sensory differences or differences in some aspect of acquiring the association is unclear. Whatever the reason for this species difference in visual cue tracking, this result does not affect the interpretations of experiments 1 and 2 because neither latency nor speed differed between the species when spatial cues were used.

EXPERIMENT 4: REVERSAL OF VISUAL DISCRIMINATION

Spatial learning is not the only type of memory that may evolve in an environment that demands memory for aspects of place. We hypothesized that active foragers would be adept at complex nonspatial tasks that require pliancy. We predicted that active foragers would take fewer trials to acquire a reversal of a visual discrimination than sit-and-wait predators. They should not differ on acquisition of the original visual discrimination, as this task requires only simple stimulus–response associations.

Subjects

Subjects were *A. boskianus* (N=6) and *A. scutellatus* (N=9) males.

Apparatus

Prior investigations have demonstrated that other lacertid lizards (*Lacerta viridis, L. agilis*) can discriminate colours (Wagner 1932; Benes 1969), shapes (Luczynska 1935), brightness and differences in acuity (Burghardt 1977). As we placed more emphasis on discrimination learning than the ability to discriminate particular stimuli, we created two stimuli that varied on the dimensions of colour (yellow versus blue), shape (circle versus square), and stripe pattern (vertical versus horizontal).

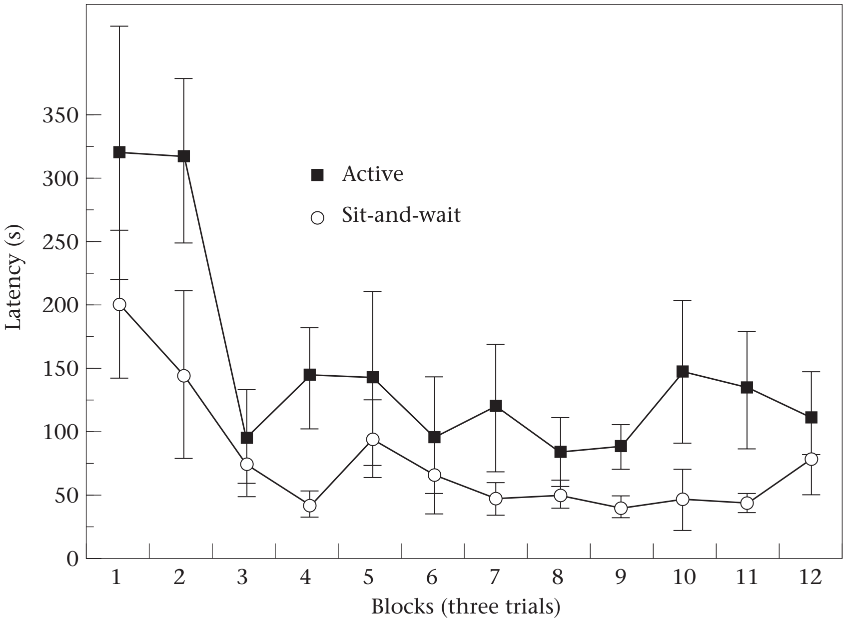

Figure 8. Mean latency from release to goal when a prominent local cue was hung over a randomly chosen hot rock each day.

Thus, we used a yellow circle with black vertical stripes (YCV) that was 6.5 cm in diameter and a blue square with black horizontal stripes (BSH) that was 5 × 7 cm. We used the fork method of Wagner (1932) to present the stimuli. Each stimulus disk was attached to one tine of a two-tine fork such that the disk faced the other tine. On the nondisk tine, we placed either a positive reinforcer (a mealworm), or a negative reinforcer (a mealworm soaked in 10 mg salt and 252 mg quinine/100 ml water). The fork was offered to the lizard such that the mealworm was backed by the stimulus disk (Fig. 9).

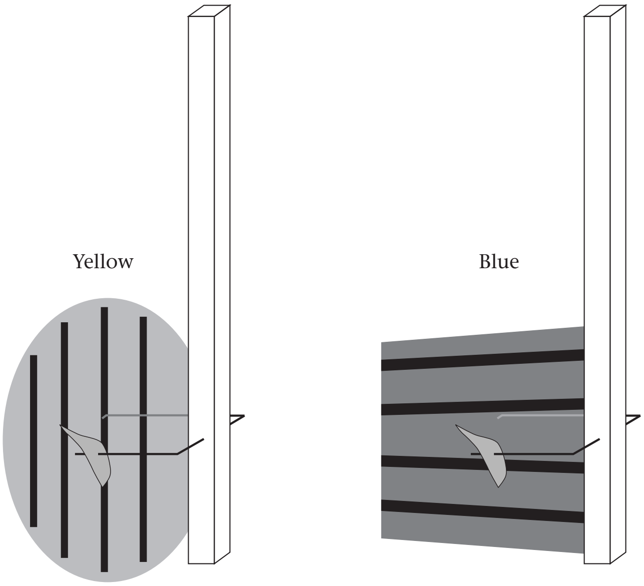

Figure 9. Discrimination apparatus. Each fork held a stimulus disk on one tine and a mealworm on the other tine. Forks were presented simultaneously to the lizards that had to choose which fork had the palatable mealworm (soaked in water), and which had the unpalatable mealworm (soaked in water with quinine and salt).

Procedures

In taste preference tests, lizards ate more of the positive reinforcers than the negative reinforcers (palatable: $\bar{X} \pm \mathrm{SE}=7.8 \pm 1.9$; unpalatable: $\bar{X} \pm \mathrm{SE}=2.4 \pm 0.7$; $t_{12}=3$; $P<0.01$). For 20 days prior to acquisition, all lizards were given four successive presentations of the negative or positive stimuli in random order with the constraint that two positive presentations and two negative presentations were given per day. After familiarization with successive presentations of the stimuli, we began simultaneous presentation.

For half of the lizards, the YCV stimulus was positive, and for the other half of the lizards, the BSH stimulus was positive. We confined the lizard being tested to an area (30 × 15 cm) of the home cage with an opaque Plexiglas divider. We presented the negative and positive stimuli simultaneously for four trials a day. We altered the left–right position of the positive stimuli randomly so that position was irrelevant to acquiring the discrimination. A trial began when the experimenter inserted both forks into the cage. If the lizard had not sampled (tongue-flicked or bitten) either the positive or the negative mealworm within 2 min, the experimenter removed both stimuli and recorded the trial as a no response trial. When the lizard ate, tongue-flicked, or bit one of the mealworms, the experimenter recorded whether the sampled mealworm was a positive or negative reinforcer. We recorded the trial as correct if the positive mealworm was sampled first, regardless of which mealworm was swallowed. We allowed the lizard to sample the mealworms ad libitum during a 2-min period. If the lizard pulled one of the mealworms off the apparatus but did not eat it by the end of the 2-min period, we removed the mealworm from the cage. As soon as the lizard pulled a mealworm off either fork, we withdrew both stimuli from the cage. Lizards were given four trials per day until they reached a

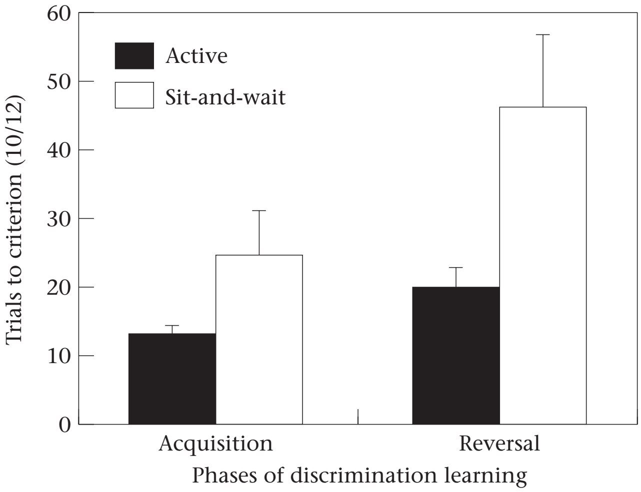

Figure 10. Mean trials to a criterion of 10 out of 12 correct responses for acquisition and reversal of the visual discrimination.

criterion of 10 correct responses out of 12 response trials with no limit on the number of days it took to complete 12 response trials. When a lizard reached criterion on the visual discrimination, the positive and negative reinforcers were associated with the opposite stimulus disk. We conducted these reversal trials as for the original acquisition. Criterion for acquisition of the reversal was 10 correct responses out of 12 response trials.

Results and Discussion

We used the number of trials to criterion for the original discrimination and the reversal as dependent measures. All lizards reached criterion on the original discrimination, and all but one lizard was able to acquire the reversal. One of the sit-and-wait predators was eliminated from the study due to low response. One of the active foragers was given the wrong response contingency for several days in a row and was also eliminated. Because of small sample sizes and heterogeneity of variance between groups, as confirmed by *F* test (acquisition: F_3=0.03, $P<0.01$; reversal: F_3=0.04, $P<0.01$), we used a Mann–Whitney *U* test for all comparisons. Whether the YVC or the BHS was initially positive had no effect on the ability to discriminate between rewarding and nonrewarding stimuli (acquisition: active forager: blue first: $\bar{X}\pm$SE=13.5 ± 3.5; yellow first: $\bar{X}\pm$SE=12.5 ± 0.5; sit-and-wait: blue first: $\bar{X}\pm$SE=22.3 ± 9.7; yellow first: $\bar{X}\pm$SE=27.3 ± 9.8; *U*=13.5, N_1=4, N_2=8, NS); reversal: active forager: blue first $\bar{X}\pm$SE=17 ± 6; yellow first: $\bar{X}\pm$SE=22 ± 1; sit-and-wait: blue first: $\bar{X}\pm$SE=52.5 ± 18.1; yellow first $\bar{X}\pm$SE=40 ± 12.5; *U*=15, N_1=4, N_2=8, NS). As predicted on the basis of foraging ecology, the species did not differ in the number of trials to criterion during acquisition (*U*=0.5, N_1=4, N_2=8, NS), but the active forager completed the reversal in fewer trials to criterion than the sit-and-wait predator (*U*=4, N_1=4, N_2=8, $P<0.05$; Fig. 10).

Differences in the types of memory demands experienced by sit-and-wait predators versus active foragers may influence the ability to acquire the reversal. An active forager that collects immobile prey may be prepared to learn that the cues that signal reward will change either as a patch is depleted in the short term, or based on changes in prey availability in the long run. Sit-and-wait predators, on the other hand, collect active prey and may learn that particular visual signals that are properties of the prey items themselves consistently signal the reward value of prey. Although, differences between sit-and-wait predators and active foragers in their willingness to respond to rewards with rapid approach may have influenced latencies in the locally cued version of the hot-rock maze, differential motivation or speed to respond cannot explain species differences in this experiment because there were no differences between species on the acquisition of the discrimination.

GENERAL DISCUSSION

The behaviour of our lizards did not support the spatial adaptation model for animals that must search intensively for resources. Lizards were capable of improvement in performance on two spatial tasks, but active foragers were not better at acquisition of the spatial tasks as the spatial adaptation model would predict. Similarly, active foraging lizards did not use a more efficient spatial strategy than sit-and-wait predators to solve the task when useful distal cues were available, as demonstrated by the probe trial in experiment 2. In addition, neither species solved the arena tasks using spatial cues preferentially in experiment 1 or experiment 2.

The species did differ in their ability to solve a second pliancy-dependent task, the reversal of a visual discrimination, as shown in experiment 4. The demands of intensive search experienced by the active forager appear to influence performance on a nonspatial pliancy-dependent task, but not a spatial task in the lizards studied. This pattern of results conforms to the pliancy model. If this pattern is found to generalize to other nonspatial tasks, other lizard species, and other reptiles, it suggests that the habit of preferentially using distal cues to guide spatial search evolved as a secondary specialization of adaptations for pliancy in some species of birds and mammals. Adaptations for other pliant forms of memory that develop in intensive-search niches might, on the other hand, be part of a general vertebrate pattern.

We cannot rule out the possibility that we found no difference between our lizards species because we lack a complete understanding of the detailed behaviours of active foragers and sit-and-wait predators in the wild. If spatial navigation is not necessary in active foragers, the spatial adaptation model would not predict its existence in these species. Perhaps active foraging lizards do not use distal cues for systematic search of locations that typically contain immobile prey, but search opportunistically for prey and retrace paths to home burrows when foraging activity ceases. These behaviours would not require spatial navigation. Perhaps sit-and-wait predators, rather than recognizing waiting places by local cues, have preferences for successful sites and use distal cues or even celestial cues to navigate to these sites each day, a behaviour that would require spatial skills. We know that both lizards species we tested retreat to burrows when chased (Gad Perry, unpublished data). Whether they recognize or recall the locations of burrows is unknown. However, based on what we do know about the general foraging behaviours of these species, we do believe that active foraging requires more mental capabilities than sit-and-wait predation, and thus more pliancy. Regardless of detailed differences between the species, it appears that neither species can transfer any spatial abilities they may have to a laboratory task that requires similar capabilities.

Not only were there no species differences in the spatial task, but the manner in which the lizards learned the spatial task was very different from that seen in mammals and birds under most conditions. In addition to the fact that they did not use spatial or local cues preferentially (similar to recent demonstrations with pigeons; Strasser & Bingman 1996), they rarely approached the goal directly even in the locally cued version of the spatial maze, and revisited incorrect rocks many times in succession. Like lizards, snakes in a spatial maze maintain high rates of visiting locations that do not lead to a goal, and show interindividual variation in the cues they use to guide them to the goal (Holtzman, in press; Holtzman et al. 1999). However, most of the snakes in Holtzman's (in press) studies apparently used a distal intramaze cue to reach a goal to a greater extent than did our lizards. We cannot discount the possibility that Holtzman's task is more ecologically relevant to the snakes than ours was to the lizards, and that our lizards might show enhanced spatial ability in a different task. However, our results demonstrate that spatial memory, if it exists in reptiles, may not be as easily or as flexibly evoked in laboratory settings as it can in mammals and birds. In addition, we show that the lizards' performance in a spatial task contains unusual elements, such as the high error rate and the high individual variability of the lizards in their overall perfomance and in the cues they used to solve the spatial task.

We believe the novel behaviours of lizards suggest fundamental differences in the way that mammals, birds and reptiles navigate to rewards. Our study contains the first tests of lizard spatial ability and as such can give only a glance at the strategies typically used by lizards to navigate to a goal. We suggest that they code the environment as a configuration, which is sufficient for many tasks requiring pliancy, but that they do not have the neural mechanisms to categorize or choose the most efficient cue types when these cues are dissociated.

Encoding the environment as a configuration of cues may be sufficient for navigation in an environment explored on a daily basis, where large dissociation between local and distal cues do not occur. Perhaps preference for spatial cues is not necessary except in animals, like some seed-storing birds, that cache extensively and must remember these locations over long periods when local features of the environment are apt to vary (Sherry & Duff 1996). This would not explain, however, why a mammal such as the male meadow vole, *Microtus pennsylvanicus*, which searches a large home range for females, is adept at using distal spatial cues (Galea et al. 1996). The relation of a female's burrow to surrounding brush and distant horizons is not apt to change drastically during the breeding period. Perhaps mammals, which typically lack the ability to use magnetic and celestial cues and do not have the advantage of a bird's eye view of landmarks, necessarily rely heavily on memory for geometric arrangement of distal cues to correct errors in path integration accumulated by imperfect estimation of rotation and distance by vestibular and motor systems (Benhamou & Poucet 1996; McNaughton 1996).

Many mammals and birds appear to be well prepared to take advantage of distal visual cues (Benhamou & Poucet 1996; McNaughton 1996). Perhaps lizards cannot efficiently store and retrieve complex associations between cues that are visual, and were thus at a disadvantage in our spatial task. The spatial adaptation model would still have some support if active foragers show skilled navigation when species-relevant cue types are provided. For example, the lizards may be more prepared to take advantage of olfactory cues or cues provided by moving stimuli.

Arguments based on general abilities to deal with particular cue types cannot be extended to explain the differences between the active forager and the sit-and-wait predator on the reversal of the visual discrimination. Despite any disadvantages in sensory or memory capacities, all but one of the lizards acquired the reversal of a visual discrimination. Past studies have shown that lizards can acquire serial reversals and get better with each reversal (Vance & Richardson 1966; Grisham & Powers 1990). Thus, an inability to do tasks that are thought to require memory for complex associations in mammals cannot explain our results. We might, however, be able to explain these differences on the basis of species-specific traits rather than general rules about the evolution of intensive foragers.

Hampton & Shettleworth (1996) found, as we did, that ecology does not always predict behaviours in tasks requiring pliancy. Unlike our example, however, Hampton & Shettleworth (1996) found that the more spatial of two pliancy-dependent tasks was correlated with intensive search behaviour. In trying to explain these differences, they examined the specific memory requirements of the tasks and suggested how each of these might conform to the species-specific tendencies of their caching and noncaching birds if not to intensive foragers in general.

The ability of the active forager in the reversal task may be due to the specific manner in which these animals forage rather than to a general excellence in complex memory tasks. The reversal of a discrimination requires inhibition of a previously rewarded response. Active foragers that search for patchy distributions of immobile prey might be more prepared than sit-and-wait predators to alter response contingencies even after receiving substantial reward, that is, after depleting a patch. Test of similar species pairs on these and a variety of other pliancy-dependent tasks should verify whether abilities are more closely related to differences in memory ability in general or to species-specific peculiarities tied more resolutely to specific adaptations for active foraging.

Similarly, specific adaptations for active foraging might explain the unexpected superior performance of the sit-and-wait species on the locally cued task. A number of possible differences can be ruled out. The locally cued task is meant as a control for motor and motivation components of the spatial task. Given that there were no differences in latency to the goal on the spatial task, the spatial version ended up serving as a control for motor and motivation components of the locally cued task. Differences between the species in their ability to approach a reward cannot explain the differences in latency observed. The sit-and-wait species may be more accustomed to associating visual cues with reward, whereas the active forager often uses chemosensory cues (Cooper 1994). However, the species did not differ on the spatial task or the acquisition of the visual discrimination task suggesting that sensory biases were not relevant to differences between the species on the visual cue task. Reactions to local visual cues associated with reward rather than sensory biases associated with such cues might explain the species differences. Prey pursuit for sit-and-wait predators is dependent on assessment of food value to a greater extent than for active foragers. Active foragers show partial preferences, approaching a prey item on one occasion and ignoring it on another occasion, regardless of the distance of the prey from the lizard. Sit-and-wait predators' preference patterns obey a zero–one rule, where a prey item ignored at a close distance is consistently ignored at a greater distance as well (S. Shafir & J. Roughgarden, unpublished data). These differences between sit-and-wait predators' and active foragers' decision-making rules about when to approach a reward of a known value might have influenced latency to the goal in our study. Whatever the explanation for the unexpected differences in the local cue version of the hot-rock arena, the results of this study highlight the need to consider various aspects of a species' ecology when choosing behavioural tests and model species.

The data from our experiments alone are insufficient to draw conclusions about the evolution of spatial and complex nonspatial memories in niches that require intensive search. The relationship between foraging strategy and spatial ability could be validated by inclusion of a greater number of species and the addition of other nonspatial pliancy-dependent tasks. However, the current work lays much of the groundwork for future tests of the pliancy hypothesis. Our study is the first test of spatial abilities designed to investigate strategies used to locate places in the environment using a pair of species that display different foraging strategies. In addition, to our knowledge, only one other group of investigators has compared the relationship of species ecology to performance of both spatial and nonspatial pliancy-dependent tasks between the same species pair for both tasks in one series of experiments (Hampton & Shettleworth 1996). Without more information about strategies used by lizards to solve spatial tasks and their ability to solve other complex memory tasks, the nature of representations that allow for navigation behaviour of lizards in the wild and in laboratory will be unclear, and the relationship of these abilities to the evolution of spatial memory and the underlying neurological substrate will be unresolved.

The idea that the evolution of adaptations for spatial ability is promoted in niches that demand intensive search has been tested in mammals and birds that must search for food, mates and other resources. The ability of the spatial adaptation model to explain these various behaviours in diverse species has helped uphold this standard model in the face of contrary examples (Clayton 1995; Volman et al. 1997). Reptilian species with various forms of intensive search might be suitable models to uphold the pliancy hypothesis. One promising model for further research with lizards would be to look at female defence polygyny, where females are a concentrated resource and males attempt to encompass as many females in their territories as possible. This type of mating system has been shown to create sexual dimorphism within home ranges in mammals (Gaulin 1992) and lizards (Rand 1992), and may contribute to differences in spatial ability between the sexes. In addition, in some species, some male morphs are capable of holding territories, while other morphs are not, and thus there may be variation between male morphs' spatial abilities as well. If the pliancy model is correct, we would expect male morphs with large territories to be better at nonspatial pliancy-dependent tasks than females or male morphs with smaller territories. Spatial abilities should be equivalent between the three groups.

If such experiments corroborate our results, we may have to accept that the pliancy model is most appropriate for reptiles. In fact, spatial memory as a navigation strategy might not exist in reptiles at all. However, the spatial adaptation model could still hold true for nonreptilian vertebrates. It is possible that preferential use of distal spatial cues as an adaptation to niches demanding intensive search might be restricted to birds and mammals.

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References

Amsel, A. 1993. Hippocampal function in the rat: cognitive mapping or vicarious trial and error? *Hippocampus*, **3,** 251–256.

Anderson, R. A. & Karasov, W. H. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia*, **49,** 67–72.

Bach, M. E., Hawkins, R. D., Osman, M., Kandel, E. R. & Mayford, M. 1995. Impairment of spatial but not contextual memory in CaMKII mutant mice with a selective loss of hippocampal LTP in the range of the theta frequency. *Cell*, **81,** 905–915.

Benes, E. S. 1969. Behavioral evidence for color discrimination by the whiptail lizard, *Cnemidophorus tigris*. *Copeia*, **4,** 707–722.

Benhamou, S. & Poucet, B. 1996. A comparative analysis of spatial memory processes. *Behavioural Processes*, **35,** 113–126.

Bingman, V. P. 1992. The importance of comparative studies and ecological validity for understanding hippocampal structure and cognitive function. *Hippocampus*, **2,** 213–220.

Brodbeck, D. R. & Shettleworth, S. J. 1995. Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. *Journal of Experimental Psychology: Animal Behavior Processes*, **21,** 64–77.

Burghardt, G. 1977. Learning processes in reptiles. In: *Biology of the Reptilia* (Ed. by C. Gans & T. W. Tinkle), pp. 555–681. New York: Academic Press.

Clayton, N. S. 1995. Development of memory and the hippocampus: comparison of food-storing and nonstoring birds on a one-trial associative memory task. *Journal of Neuroscience*, **15,** 2796–2807.

Collett, T. S. & Zeil, J. 1996. Flights of learning. *Current Directions in Psychological Science*, **5,** 149–155.

Cooper, W. E. 1994. Prey chemical discrimination, foraging mode, and phylogeny. In: *Lizard Ecology: Historical and Experimental Perspectives* (Ed. by L. J. Vitt & E. Pianka), pp. 99–121. Princeton, New Jersey: Princeton University Press.

Day, L. B. & Schallert, T. 1996. Anticholinergic effects on acquisition of place learning in the Morris water task: spatial mapping deficit or inability to inhibit nonplace strategies? *Behavioral Neuroscience*, **110,** 998–1005.

Duvdevani, I. & Borut, A. 1974. Mean body temperature and heat absorption in four species of *Acanthodactylus* lizards (Lacertidae). *Herpetologica*, **30,** 176–181.

Eichenbaum, H. 1996. Is the rodent hippocampus just for 'place'? *Current Opinion in Neurobiology*, **6,** 187–195.

Galea, L. A. M., Kavaliers, M. & Ossenkopp, K.-P. 1996. Sexually dimorphic spatial learning in meadow voles *Microtus Pennsylvanicus* and deer mice *Peromyscus maniculatus*. *Journal of Experimental Biology*, **199,** 195–200.

Gaulin, S. 1992. Evolution of sex differences in spatial ability. *Yearbook of Physical Anthropology*, **35,** 125–151.

Good, M. 1987. The effects of hippocampal-area parahippocampalis lesions on discrimination learning in the pigeon. *Behavioural Brain Research*, **26,** 171–184.

Gray, J. A. & McNaughton, N. 1983. Comparison between behavioural effects of septal and hippocampal lesions: a review. *Neuroscience and Biobehavioral Reviews*, **7,** 119–188.

Grisham, W. & Powers, A. S. 1990. Effects of dorsal and medial cortex lesions on reversals in turtles. *Physiology and Behavior*, **47,** 43–49.

Hampton, R. R. & Shettleworth, S. J. 1996. Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behavioral Neuroscience*, **110,** 946–964.

Holtzman, D. In press. From slither to hither: orientation and spatial learning in snakes. *Integrative Biology*.

Holtzman, D., Harris, T. W., Aranguren, G. & Bostock, E. 1999. Spatial learning of an escape task by young corn snakes (*Elaphe guttata guttata*). *Animal Behaviour*, **57,** 51–60.

Huey, R. B. & Pianka, E. R. 1981. Ecological consequences of foraging mode. *Ecology*, **62,** 991–999.

Luczynska, H. 1935. Uber den formensin und das gedachtnis fur optische eindrucke bei eidechsen. *Bulletin of the International Academy of Political Science Letters, Series B, Science and Nature*, **2,** 325–342.

McNaughton, B. 1996. Cognitive cartography. *Nature*, **381,** 368–369.

Morris, R. G. M. 1981. Spatial localization does not require the presence of local cues. *Learning and Motivation*, **12,** 239–260.

Nagy, K. A., Huey, R. B. & Bennett, A. F. 1985. Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology*, **65,** 588–596.

O'Keefe, J. & Nadel, L. 1978. *The Hippocampus as a Cognitive Map*. Oxford: Clarendon Press.

Perry, G., Lampl, I., Lerner, A., Rothenstein, D., Shani, E., Sivan, N. & Werner, Y. L. 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphibia-Reptilia*, **11,** 373–384.

Pietruszka, R. D. 1986. Search tactics of desert lizards: how polarized are they? *Animal Behaviour*, **34,** 1742–1758.

Rand, M. S. 1992. Behavioral function and hormonal control of polymorphic sexual coloration in the lizard *Sceloporus undulatus erythrocheilus*. Ph.D. thesis, University of Colorado.

Regal, P. J. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. In: *Behavior and Neurology of Lizards* (Ed. by N. Greenberg & P. D. MacLean), pp. 183–202. Rockville, Maryland: National Institute of Mental Health.

Rudy, J. W. & Sutherland, R. J. 1995. Configural association theory and the hippocampal formation: an appraisal and reconfiguration. *Hippocampus*, **5,** 375–389.

Sherry, D. F. & Duff, S. J. 1996. Behavioural and neural bases of orientation in food-storing birds. *Journal of Experimental Biology*, **199,** 165–172.

Sherry, D. F., Jacobs, L. F. & Gaulin, S. J. 1992. Spatial memory and adaptive specialization of the hippocampus. *Trends in Neuroscience*, **15,** 298–303.

Sherry, D. F., Forbes, M. R. L., Khurgel, M. & Ivy, G. O. 1993. Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. *Proceedings of the National Academy of Sciences USA*, **90,** 7839–7843.

Strasser, R. & Bingman, V. 1996. The relative importance of location and feature cues for homing pigeon (*Columba livia*) goal recognition. *Journal of Comparative Psychology*, **110,** 77–87.

Vance, V. & Richardson, A. M. 1966. Reversal learning in desert iguanas, *Dipsosaurus dorsalis*. *American Zoologist*, **6,** 543.

Volman, S. F., Grubb, T. C. & Schuett, K. C. 1997. Relative hippocampal volume in relation to food-storing behavior in four species of woodpeckers. *Brain Behavior and Evolution*, **49,** 110–120.

Wagner, H. 1932. Uber den farbensinn der eidechsen. *Zeitschrift für vergleichende Physiologie*, **18,** 387–392.

Whishaw, I. Q. & Jarrad, L. E. 1996. Evidence for extrahippocampal involvement in place learning and hippocampal involvement in path integration. *Hippocampus*, **6,** 513–524.