

Dorsal cortex volume in male side-blotched lizards, *Uta stansburiana*, is associated with different space use strategies

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Spatial abilities have been associated with many ecologically relevant behaviours such as territoriality, mate choice, navigation and acquisition of food resources. Differential demands on spatial abilities in birds and mammals affect the hippocampus, the region of the brain responsible for spatial processing. In some bird and mammal species, higher demands on spatial abilities are associated with larger hippocampal volumes. The medial and dorsal cortices are the putative reptilian homologues of the mammalian hippocampus, yet few studies have examined the relationship between these brain areas and differential spatial use strategies in reptiles. Furthermore, many studies in birds and mammals compare hippocampal attributes between species that use space differently, potentially confounding species-specific effects with effects due to differential behaviours in spatial use. Here, we investigated the relationship between spatial use strategies and medial and dorsal cortical volumes in males of the side-blotched lizard. In this species, males occur in three different morphs, each morph using different spatial niches: large territory holders, small territory holders and nonterritory holders with home ranges smaller than the territories of small territory holders. We found that large territory holders had larger dorsal cortical volumes relative to the remainder of the telencephalon compared with nonterritorial males, and that small territory holders were intermediate. These results suggest that some aspect of holding a large territory may place demands on spatial abilities, which is reflected in a brain region thought partially responsible for spatial processing.

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The ability to track the spatial distribution of resources has fitness ramifications in the contexts of territoriality, mate choice, navigation, acquisition of food resources and many other ecologically relevant behaviours (e.g. Brennan et al. 1990; Shettleworth 1990; Godard 1991; Menzel et al. 2000). Furthermore, differences in spatial ability and demands on spatial ability differentially affect brain anatomy, specifically reflected in the hippocampus, one of the brain regions thought to be important in spatial memory processing (O'Keefe & Nadel 1978; Morris et al. 1982). Animals that have a greater reliance on spatially relevant behaviours tend to have larger hippocampi (Krebs et al. 1989; Sherry et al. 1989; Jacobs & Spencer 1994; Healy & Krebs 1996; Lucas et al. 2004). Therefore, there appears to be a positive relationship between increased demands placed on spatial abilities and enlargement of the hippocampus.

Numerous studies have found a positive relationship between space use and hippocampal morphology. Interspecific comparisons

have found that species with higher demands on spatial abilities have larger hippocampal volumes than do closely related species that do not have such demands on spatial abilities. For example, differences in space use in relation to foraging behaviours are correlated with hippocampal volume; species that rely on spatially diverse resources or on spatial memory and/or engage in active foraging search patterns have larger hippocampi (Krebs et al. 1989; Sherry et al. 1989; Jacobs & Spencer 1994; Day et al. 1999; Lucas et al. 2004). Intraspecific differences in hippocampal formations have also been correlated with differential space use patterns. This pattern has been shown between the sexes and between populations that use space differently, especially when one group has a greater reliance on tracking spatially distributed resources than the other group. For example, male meadow voles, *Microtus pennsylvanicus*, have higher demands on spatial abilities as a result of patrolling large territories compared with females that reside in significantly smaller home ranges. This difference is reflected by a larger hippocampal volume in male meadow voles than in females (Jacobs et al. 1990). Similarly, in cottonmouth snakes, *Agkistrodon piscivorous*, males have larger home ranges than females, and this difference in home range size is positively related

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to the size of the putative reptilian hippocampal homologue (Roth et al. 2006). Also, nest-searching female brown-headed cowbirds, *Molothrus ater*, have larger hippocampi than do males, which do not search for host nests (Sherry et al. 1993). Black-capped chickadees, *Poecile atricapillus*, from northern populations, which live in harsh environments demanding heavier reliance on memory for food caches have larger hippocampal volumes than do chickadees from southern populations living in milder environments (Pravosudov & Clayton 2002; Roth & Pravosudov 2009). These studies suggest that a relationship exists between demands on spatial ability and the hippocampal architecture, where higher demands on spatial abilities appear to contribute to increases in hippocampal size.

Although there is support for the relationship between spatial ability demands and hippocampal volume, differences in hippocampal attributes could be related to greater genetic and other differences between species, rather than to differences in spatial use per se (e.g. Girvan & Braithwaite 1998). Therefore, a better relationship between hippocampal structure and differential space use could be elucidated by comparing individuals within the same species in the same population, where individuals use spatial niches differently. By doing so, effects on the hippocampal structure due to species-specific differences can potentially be minimized, outside of the effects of differential space use.

Therefore, the goal of our study was two-fold: (1) to isolate the effects of differential space use on brain attributes, while controlling for species and population differences and (2) to determine whether the volumes of the putative reptilian hippocampal homologues (medial and dorsal cortices; Butler 1976; Rodríguez et al. 2002a; Salas et al. 2003) are related to the differential use of space, as has been shown in the hippocampal structures in mammals and birds. Concisely, we wanted to relate space use with particular brain regions known to be involved with spatial processing. To this end, we used the male side-blotched lizard as our model species.

In this species, males within the same population are found in one of three morphs, where each morph appears to use space differently (Sinervo & Lively 1996; Sinervo et al. 2000, 2006). The orange morph occupies and defends large territories ($\sim 40 \text{ m}^2$), the blue morph occupies and defends smaller territories ($\sim 23 \text{ m}^2$) while the yellow morph does not hold or defend a territory and its home range is smaller than the territories of the other two morphs ($\sim 20 \text{ m}^2$) (Sinervo & Lively 1996; Zamudio & Sinervo 2000; Sinervo et al. 2000, 2006; Calsbeek & Sinervo 2002). As has been shown with other studies linking hippocampal volume and aspects of ecological space use (Jacobs et al. 1990; Day et al. 1999; Roth et al. 2006), permanent territory patrol and defence probably cause increased demands on spatial use, memory and processing. Furthermore, large territory holders should have greater demands on spatial use, memory and processing compared with smaller territory holders. We predicted, based on the patterns of territoriality and space use of the three morphs, that the orange morph would have the largest medial and dorsal cortical volumes relative to the rest of the telencephalon because of the increased demand on spatial abilities related to holding and patrolling a large territory. We expected that the yellow morph would have the smallest relative medial and dorsal cortical volumes, as yellow males do not hold or defend territories. Finally, we predicted the blue morph would have intermediate medial and dorsal cortical volumes relative to the orange and yellow morphs, as these males do hold territories but their territories are smaller than those held by orange males.

METHODS

We collected nine orange males, eight blue males and seven yellow males in March of 2008 from the Los Baños Grandes area, Merced County, California, U.S.A. Lizards were transported

individually in plastic containers ($15.24 \times 10.16 \times 10.16 \text{ cm}$) to the University of Nevada, Reno (travel time $\approx 3.5 \text{ h}$). Upon arrival, individuals were immediately anaesthetized with a lethal overdose of Nembutal (0.05 ml of 50 mg/ml Nembutal). The lizards were transcardially perfused with 0.1 M phosphate buffered saline for 10 min followed by a 15–20 min perfusion of 4% paraformaldehyde in 0.1 M phosphate buffer. Brains were extracted and postfixed in 4% paraformaldehyde for 24 h before cryoprotection. Brains were cryoprotected in 15% sucrose, then 30% sucrose, and finally flash-frozen on dry ice. Brains were stored at -80°C until sliced. Brains were sliced on a cryostat (Leica CM 3050S; -20°C) in the coronal plane every $40 \mu\text{m}$. Every section was mounted and Nissl-stained with thionin. Slides were coded, and thus, tissue slices were measured blind to morph type.

Identification of the brain areas responsible for spatial processing in reptiles is, at present, equivocal. However, two main areas, the medial and dorsal cortex, have been identified in several studies as important in spatial processing, in that lesions to either cortical region can impair spatial abilities (Grisham & Powers 1990; Petrillo et al. 1994; Reiman-Avigan & Schade-Powers 1995; Rodríguez et al. 2002a, b; López et al. 2003). Thus, both areas were measured and analysed separately in this study. The goal of our study was to determine whether differential space use specifically affects the medial and dorsal cortical volumes, but not the rest of the brain; therefore, we used the remainder of the telencephalon (i.e. telencephalon minus medial and dorsal cortical volumes) as a control area (Krebs et al. 1989; Clayton 2001; Pravosudov & Clayton 2002; Roth et al. 2006).

We measured the volume of the medial cortex, the dorsal cortex and the remainder of the telencephalon using standard stereological techniques; all volumes were estimated with standard stereological methods (Stereoinvestigator, Microbrightfield, Inc., Williston, VT, U.S.A.; microscope, Leica M4000B). We optimized our measuring scheme such that our coefficient of error was less than 0.05 for both the medial and dorsal cortices. We measured the volume of the medial and dorsal cortices by using every third section (average of 12.52 sections per brain) and the volume of the remainder of the telencephalon by using every fourth section (telencephalon volume minus medial and dorsal cortical volumes). Medial and dorsal cortical volumes and telencephalon volume were measured in their entirety and estimated with the Cavalieri procedure (Gundersen & Jensen 1987). Medial and dorsal cortical volumes were measured with a $200 \mu\text{m}$ grid; telencephalon volume was measured with a $300 \mu\text{m}$ grid. The left and right hemispheres were both measured for all volumes and then added to produce the given values. There were no significant differences between left and right medial and dorsal cortical volumes or telencephalon volumes.

Statistics

The data were log-transformed to conform to the assumptions for parametric analyses, and Levene's test on transformed data found no difference in variances between the morphs (dorsal cortex: $F_{2,21} = 3.694$, $P = 0.051$; medial cortex: $F_{2,21} = 0.003$, $P \approx 1.0$). We tested for differences in telencephalon volume among the three types of morphs with general linear models (GLM) with snout-vent length as the covariate. By doing so, we verified that morph type had no effect on telencephalon volume, when controlled for snout-vent length. We then tested our a priori predictions for separate differences in relative dorsal and medial cortical volumes using GLM, with telencephalon volume as a covariate, followed by planned comparisons (Fisher's least significant difference). We considered all results to be statistically significant if $\alpha \leq 0.05$.

Because our a priori predictions were directional, in that orange morphs should have larger medial and cortical volumes relative to the rest of the telencephalon than yellow morphs, while blue morphs should be intermediate, we also used an ordered heterogeneity test (Rice & Gaines 1994a, b). This test incorporates the complement of the probability from the nondirectional heterogeneity test ($P_c = 1 - \text{ANOVA } P \text{ value}$) and the rank order from a Spearman rank correlation (r_s) to permit testing of order within the context of a heterogeneity test (test statistic: $r_s P_c$) (Rice & Gaines 1994a, b).

RESULTS

Telencephalon volume relative to snout–vent length (SVL) did not differ significantly between orange, blue and yellow morphs ($F_{2,20} = 0.701$, $P = 0.508$; SVL covariate: $F_{1,20} = 2.925$, $P = 0.011$; Figs 1, 2, 3). Morph type also did not have a significant association with medial cortex volume relative to the rest of the telencephalon ($F_{2,20} = 1.097$, $P = 0.353$; telencephalon covariate: $F_{1,20} = 9.292$, $P = 0.006$; Fig. 4). However, morph type did have a significant association with relative dorsal cortex volume ($F_{2,20} = 3.557$, $P = 0.048$; Fig. 5; telencephalon covariate: $F_{1,20} = 20.258$, $P < 0.001$). Yellow males had significantly smaller relative dorsal cortices than orange males (Fisher's LSD test: $P = 0.017$) while blue males showed a trend towards larger dorsal cortices compared with yellow males ($P = 0.07$). However, there were no differences in relative dorsal cortical volumes between orange and blue males ($P = 0.55$).

Finally, the ordered heterogeneity test indicated that morph type, incorporating predicted directionality of morph effects, was significantly associated with relative dorsal cortex volume ($r_s P_c = 0.953$, $P < 0.001$). These results show that orange males had larger dorsal cortices relative to the rest of the telencephalon than yellow males, whereas blue males were intermediate between the orange and yellow males. Interestingly, relative medial cortex volume followed the same trend as the dorsal cortex, and mean values for the three morphs showed perfect negative correlation with space use ($r_s = 1.0$; Fig. 4), although the ordered heterogeneity test was marginally non-significant ($r_s P_c = 0.647$, $0.05 < P < 0.1$).

DISCUSSION

We found that the dorsal cortex volume relative to the rest of the telencephalon in male side-blotched lizards differs depending on male morph type. Orange males, which hold large territories and occupy the largest home ranges, had relatively larger dorsal cortical volumes compared with yellow males, which do not hold territories and have the smallest home ranges of the three morphs compared. Blue males that hold territories and occupy home ranges that are smaller than those of orange males but larger than the home ranges of yellow males had intermediate relative dorsal cortical volumes compared with those of orange and yellow males. Yellow males, which do not hold territories and have the smallest home ranges compared with orange or blue males, had the smallest dorsal cortical volumes.

As predicted, differences in spatial use tactics through territoriality/home range sizes among the morphs were reflected in an area of the brain thought partially responsible for spatial processing (i.e. the dorsal cortex). Males that hold large territories and occupy large home ranges presumably have increased demands on spatial ability because of the increased processing of spatial information, whereas males that do not hold territories, have smaller home ranges and are more philopatric, as in the yellow morph (Zamudio & Sinervo 2000; Sinervo et al. 2006), probably have comparatively lower demands on processing spatial information. This difference

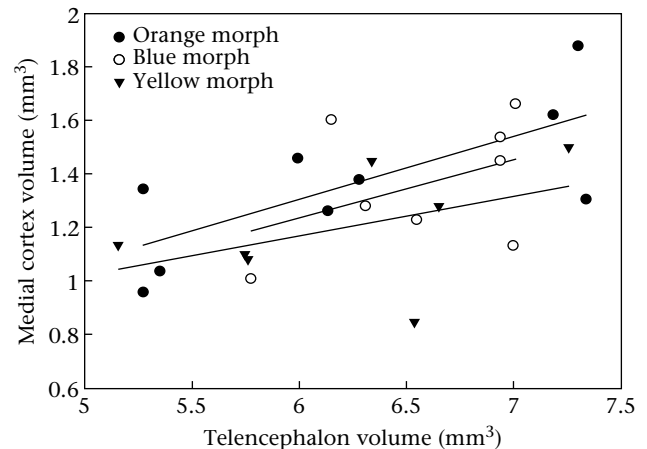


Figure 1. Relationship between telencephalon volume and medial cortex volume in three morphs of male side-blotched lizards.

appears to be reflected in the relative volume of the dorsal cortex, as an increase in demands on spatial abilities relates to a larger dorsal cortex relative to the rest of the telencephalon. Such differentiation among morphs in relative dorsal cortical volume may result from flexible differential space use strategies or could be genetically determined, but our study does not allow discrimination between these two explanations because the animals in this study were free ranging.

We did not, however, find statistically significant differences between morphs in medial cortex volume. This result does not fully coincide with a previous study in lizards, in which both dorsal and medial cortical volumes positively correlated with an increase in foraging activity (Day et al. 1999). Other studies have found that lesions to the medial cortex do result in spatial learning deficits in turtles (Rodríguez et al. 2002a, b; López et al. 2003). Ultimately, the scarcity of information on the importance of the dorsal cortex and the medial cortex in spatial processing in reptiles, as well as the paucity of studies relating spatial memory, ecology and dorsal and medial cortical volumes in reptiles precludes meaningful comparisons across studies. Although our results were not statistically significant, medial cortex volume did show the same pattern as that found for dorsal cortex volume (Figs 4, 5). A larger sample size may potentially clarify the variance surrounding dorsal cortex volumes

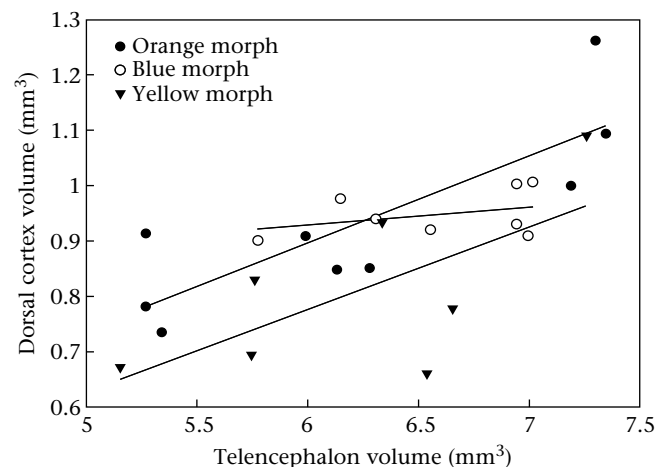


Figure 2. Relationship between telencephalon volume and dorsal cortex volume in three morphs of male side-blotched lizards.

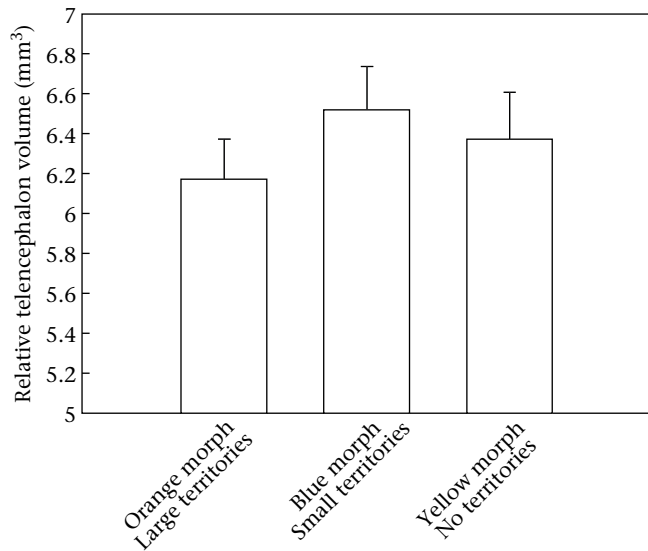


Figure 3. Relative telencephalon volume \pm SE (least squares means from the model with snout-vent length as the covariate) across three male morph types.

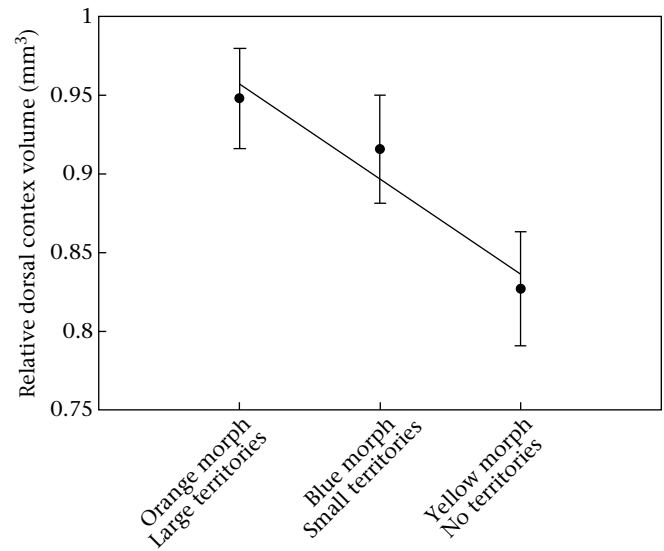


Figure 5. Relative dorsal cortex volume \pm SE (least squares means from the model with telencephalon volume as the covariate) across three male morph types. $N = 9$ orange males, 8 blue males and 7 yellow males.

found in this study, which may lend support to the notion that the medial cortex, as well as the dorsal cortex, are involved in spatial processing.

To our knowledge this is the first study to show differences in brain anatomy relating to differential behavioural tactics of space use within the same species in a single population of reptiles. The relationship between brain volume and ecology within the same species in a population has also been shown in the paper wasp *Polistes dominulus*, where the volumes of brain areas dealing with vision and olfaction in queens differ depending on whether the queen is solitary or with other queens (Ehmer et al. 2001). Accounting for species and population differences may be important when these differences confound the relationship between differences in space use and brain anatomy. For instance, hippocampal architecture may be influenced by differential genetic

architecture, diet, mating system, ontogeny or dispersal/migration patterns that occur between or within species (e.g. Healy et al. 1998; Hutcheon et al. 2002; Pravosudov et al. 2006). In an interspecific comparison on lizards, Perry & Garland (2002) found that diet affects home range size, while other studies found that different foraging strategies affect hippocampal attributes (Jacobs & Spencer 1994; Day et al. 1999). Although we do not know conclusively whether diet or foraging strategy differs between morphs of the side-blotched lizard, these factors may also potentially lead to differences in brain attributes because of differential space use. Evidence also suggests that differences in mating systems may have different effects on hippocampal attributes (Jacobs et al. 1990) and, although all three morphs of side-blotched lizards are polygamous, there are differences in rates of mate acquisition among the morphs. These differences may also lead to differences in hippocampal attributes. Regardless, we suggest that it may be advantageous to use model species that can potentially control for specific effects that may not be related to space use, especially if these variables may influence hippocampal attributes, as differences in the hippocampal formation may be shaped by differences between species or populations outside of differential spatial processing.

Similarly, sex differences in hippocampal anatomy and function are affected by differences in gonadal hormones (e.g. Williams et al. 1990; Roof & Havens 1992; Madeira & Leiberman 1995), outside of effects due to differential space use. While we did use individuals of the same sex in our study, which may have partially mitigated certain nonhormonal reproductive differences mandated by sex, male morphs do have different hormonal profiles, which may also influence space use (DeNardo & Sinervo 1994). Furthermore, individuals may show differences in hormonal sensitivity based on morphotype (Comendant et al. 2003; Knapp et al. 2003). Because of these differences in hormone profiles, space use and other correlated responses such as survival, activity level, immune function and stress response may be affected and differ between morphs (e.g. Comendant et al. 2003; Knapp et al. 2003; Stapley & Keogh 2004). Although the mechanistic basis of the relationship between space use and the brain was beyond the scope of this study, hormonal underpinnings probably constitute a mechanism underlying the relationship between space use, dorsal cortex volume and potentially other correlated behavioural responses in

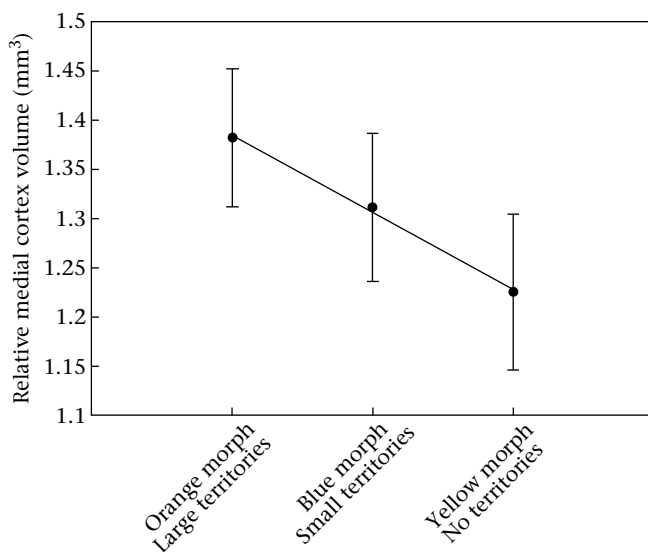


Figure 4. Relative medial cortex volume \pm SE (least squares means from the model with telencephalon volume as the covariate) across three male morph types. $N = 9$ orange males, 8 blue males and 7 yellow males.

this species. Future work should consider manipulating hormone levels among these morphs to ascertain the importance of hormone levels on the dorsal and medial cortical volumes, while concurrently controlling for space use.

Furthermore, our results suggest that differential spatial use tactics may be correlated with one of the putative reptilian homologues of the mammalian and avian hippocampus. Many previous studies have examined the effects of spatial use, spatial abilities and hippocampal attributes in birds and mammals (e.g. Krebs et al. 1989; Sherry et al. 1989, 1993; Jacobs et al. 1990; Jacobs & Spencer 1994; Healy & Krebs 1996; Pravosudov & Clayton 2002; Lucas et al. 2004; Pravosudov et al. 2006; Roth & Pravosudov 2009). Many of these studies have found a positive relationship between spatial abilities and hippocampal volume. However, only a few studies have studied whether these effects occur in different taxa, specifically in lizards (Day et al. 1999, 2001). Some studies have found that reptiles can use spatial maps to orient (Holtzman et al. 1999; Zuri & Bull 2000; López et al. 2001; but see Day et al. 2001), and both the dorsal cortex and the medial cortex have been shown to be involved in spatial tasks. In turtles, lesions of the medial cortex impair performance on spatial tasks (Rodríguez et al. 2002a, b; López et al. 2003); similarly, dorsal cortex lesions impair spatial mapping in turtles (Grisham & Powers 1990; Petrillo et al. 1994; Reiman-Avigan & Schade-Powers 1995). However, Day et al. (2001) found that medial and dorsal cortical lesions slowed locating a goal, but none of the subjects used a spatially dependent strategy to locate a goal. We have no data to date on whether differential spatial abilities exist among morphs in side-blotched lizards, but this would be the logical next step in connecting space use, spatial abilities and brain volume among morphs. Because of the limited and conflicting studies to date, future studies addressing spatial abilities in reptiles may be especially fruitful to ascertain whether these animals do in fact use spatial strategies, if natural selection has acted on these abilities in particular contexts and whether these abilities are reflected by larger hippocampal homologues. While our study did not address specific mechanisms responsible for causing the differences in brain morphology among the three morphs, it demonstrated an association between a brain region thought to be important in spatial processing and differences in spatial tactics.

Acknowledgments

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