2015

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Repository Citation

Robinson, C. D., Patton, M.S., Andre, B. M., & Johnson, M. A. (2015). Convergent evolution of brain morphology and communication modalities in lizards. *Current Zoology, 61*(2), 281-291. https://doi.org/10.1093/czoolo/61.2.281

Current Zoology 61 (2): 281–291, 2015

Convergent evolution of brain morphology and communication modalities in lizards

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Abstract Animals communicate information within their environments via visual, chemical, auditory, and/or tactile modalities. The use of each modalityis generally linked to particular brain regions, but it is not yet known whether the cellular morphology of neurons in these regions has evolved in association with the relative use of a modality.We investigated relationships between the behavioral use of communication modalities and neural morphologies in six lizard species. Two of these species (*Anolis carolinensis* and *Leiocephalus carinatus*) primarily use visual signals to communicate with conspecifics and detect potential prey, and two (*Aspidoscelis gularis* and *Scincella lateralis*) communicate and forage primarily using chemical signals. Two other species (*Hemidactylus turcicus* and *Sceloporus olivaceus*) use both visual and chemical signals. For each species, we performed behavioral observations and quantified rates of visual and chemical behaviors. We then cryosectioned brain tissues from 9–10 males of each species and measured the soma size and density of neurons in two brain regions associated with visual behaviors (the lateral geniculate nucleus and the nucleus rotundus) and one region associated with chemical behaviors (the nucleus sphericus). With analyses conducted in a phylogenetic context, we found that species that performed higher rates of visual displays had a denser lateral geniculate nucleus, and species that used a higher proportion of chemical displays had larger somas in the nucleus sphericus. These relationships suggest that neural morphologies in the brain have evolved convergently in species with similar communication behaviors [*Current Zoology* 61 (2): 281–291, 2015].

Keywords Brain, Communication modality, Lizards, Pheromones, Social behavior, Vision

Animals send and receive messages about their social and ecological environments via one or more of several sensory modalities, including visual, chemical, auditory, and tactile means of communication (Dangles et al., 2009). Specialized structures are often needed to detect messages communicated using a particular modality – for example, species that use visual signals must have light-sensitive photoreceptor cells, such as those in an eye (Chow and Lang, 2001), and tetrapods that communicate with chemical signals detect molecules such as pheromones using an accessory organ called the vomeronasal organ (VNO; Stoddart, 1980; Keverne, 1999). Further, messages received via different modalities are initially processed in different areas of the brain.The well-supported hypothesis of mosaic evolution (proposed by Barton and Harvey, 2000) asserts that natural selection may differentially act on the relative volumes of brain regions associated with different behaviors, but less work has investigated whether the neuroanatomy within different regions of the brain varies in association with behavior. In this study, we examined whether the cellular morphologies of sensory-associated brain regions differ among lizard species that primarily use different modes of communication, and if communication behaviors evolved in association with the neuroanatomy of these regions.

Lizards are an excellent system for studying the evolutionary associations between communication modalities and brain morphology. First, lizard communication behaviors (particularly in adult males) are readily observed in the lab and field, and lizards employ a diversity of signaling behaviors using multiple modalities (reviewed in Fox et al., 2003). Further, several lizard brain atlases are available (e.g., Cruce, 1974; Northcutt and Butler, 1974; Greenberg, 1982), and the phylogenetic relationships among the major taxonomic groups are well established (e.g., Wiens et al., 2012). Here, we examined relationships between brain and behavior in a group of six lizard species (Fig. 1) that exhibit variation in visual and chemical behaviors. We focused on these two modalities because they are the most commonly used among lizard taxa (e.g. Simon, 1983; Hall, 2008);

Received Nov. 2, 2014; accepted Feb. 23, 2015.

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behaviors associated with these modalities are critical in interactions with conspecifics, prey, and potential predators (e.g., Martín and López, 2015); and these behaviors are easily observed and quantified.

Clear associations between particular brain regions in reptiles and their communication modalities have been determined through studies utilizing methods such as tract-tracing and experimental brain lesions, and most of these brain regions have direct homologues across vertebrate taxa (reviewed in Bruce, 2009). In the reptilian visual system, signals received by the retina project to the telencephalon via the lateral geniculate nucleus (LGN; also called the dorsal thalamus) and the optic tectum, which further projects to the LGN and the nucleus rotundus (NR; Bruce and Butler, 1984; Kenigfest et al., 1997). The LGN plays multiple roles in processing color and spatial information (De Valois et al., 1965; Casagrande et al., 2005), and the NR is involved in the perception of motion, color, and illumination (Wang et al., 1993). The chemosensory system in reptiles consists of the main olfactory organ, which detects small, airborne chemicals and projects to the main olfactory bulb, and the VNO, which detects heavy molecules such as pheromones and projects to the accessory olfactory bulb (Bruce and Neary, 1995; Johnson and Leon, 2000). The accessory olfactory bulb then projects to the nucleus sphericus (NS) of the amygdala (Lohman and Smeets, 1993), and reptilian species with well-developed olfactory systems have more pronounced NS (reviewed in Lanuza and Halpern, 1998).

In this study, we used two species that communicate predominantly using visual behaviors, two that use predominantly chemical behaviors, and two that use both visual and chemical behaviors. The two visual species were the green anole (*Anolis carolinensis*; Family: Dactyloidae) and the northern curly tail lizard (*Leiocephalus carinatus*; Family: Leiocephalidae). Both of these species exhibit head-bob and push-up displays, while anoles also frequently extend a throat fan (i.e., dewlap; Fig.1A; Jenssen, 1977), and curly tails, as their name suggests, often curl their tails in display (Fig. 1B; Evans, 1953). These species are also both sit-and-wait predators, identifying potential prey by visual inspection of their surroundings. The two chemical species were the spotted whiptail (*Aspidoscelis gularis*; Family: Teiidae) and the little brown skink (*Scincella lateralis*; Family: Scincidae). These species communicate primarily using pheromones spread through femoral pore secretions (whiptails; Alberts et al., 1992) or feces (skinks; Duvall et al., 1980), and both sample their chemical environments to detect conspecific signals, potential prey, and predators by licking the air or substrate to bring molecules into contact with their VNO (Cooper and Hartdegen, 1999; Punzo, 2007). Finally, the two species that

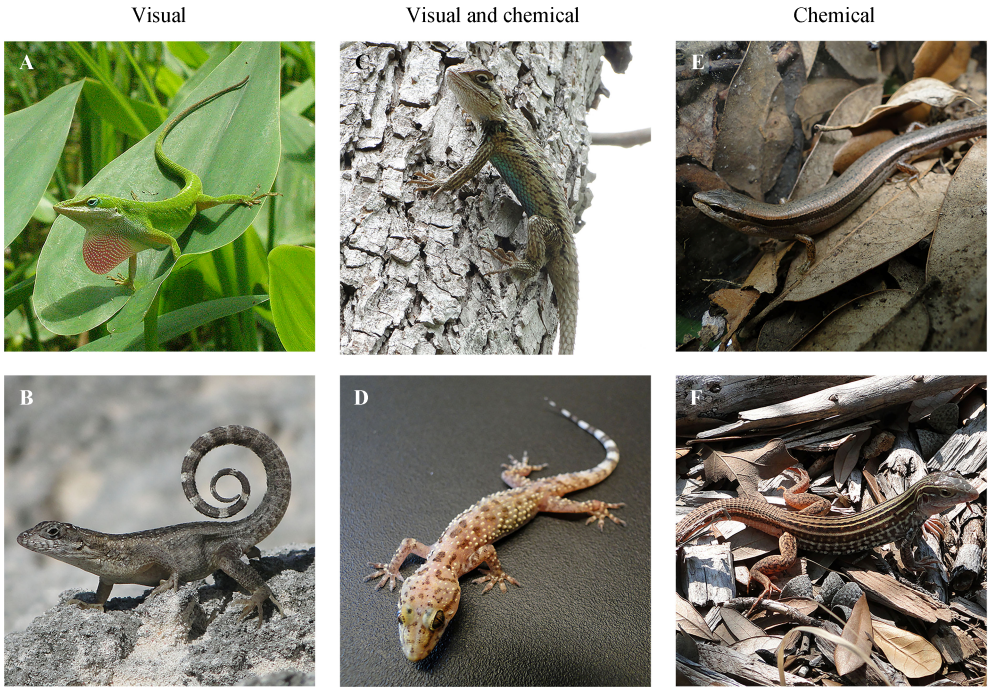

Fig. 1 Six lizard species in this study

A. Green anole *Anolis carolinensis*. **B**. Northern curly tail *Leiocephalus carinatus*. **C**. Texas spiny lizard *Sceloporus olivaceus*. **D.** Mediterranean house gecko *Hemidactylus turcicus*. **E.** Little brown skink *Scincella lateralis*. **F**. Spotted whiptail *Aspidoscelis gularis*. All photographs by Michele A. Johnson.

use both visual and chemical modalities to communicate, obtain prey, and avoid predators were the Texas spiny lizard (*Sceloporus olivaceus*; Family: Phrynosomatidae) and the Mediterranean house gecko (*Hemidactylus turcicus*; Family: Gekkonidae). Spiny lizards perform push-ups and dorsoventral flattening (to display the bright blue belly; Fig. 1C), and secrete pheromones from femoral pores (Bissinger and Simon, 1981; Carpenter, 1978). House geckos perform tail wags and back arches, secrete pheromones from pre-anal glands, and produce clicking sounds (although auditory communication was not included in this study; Regalado, 2003; Khannoon, 2012).

We hypothesized that the performance of visual behaviors in lizards evolved in association with the cellular morphology of brain regions associated with vision, and that the performance of chemical behaviors evolved in association with the cellular morphology of brain regions associated with the chemical sense. To test these hypotheses, we investigated three brain regions thought to play a role in lizard communication: two regions involved in vision (LGN and NR), and one involved in chemical sensing (NS). Although few studies have compared neural morphologies across multiple lizard species, in *intraspecific* studies of brain and behavior in lizards, brain regions used more frequently generally exhibit larger and/or denser neurons (reviewed in Wade, 2011). In general, larger or more numerous neurons in sensory regions may allow for the processing of larger amounts of information, potentially by receiving more neural afferent projections, or may allow individuals to process this information more efficiently or with more sensitivity. Therefore, we predict that 1) lizards that exhibit more frequent visual communication behaviors will have larger and/or denser neurons in the LGN and NR and 2) lizards that exhibit more frequent chemical communication behaviors will have larger and/or denser neurons in the NS.

1 Materials and Methods

1.1 Behavioral observations

To quantify the behavioral use of visual and chemical modalities, we performed focal behavioral observations of adult males from six lizard species in summer (May–August) 2012 and 2013. We focused on males in this study because male lizards in many species perform display behaviors at a much higher frequency than females (e.g., Martins, 1993; Nunez et al., 1997). We observed five species in south-central Texas, as follows. We observed green anoles *A. carolinensis* and Mediterranean house geckos *H. turcicus* in Palmetto State Park in Gonzales, Texas (29°35.56'N, 97°35.14'W) and on the campus of Trinity University in San Antonio, Texas (29°27.91'N, 98°29.05'W). We observed spotted whiptails *A. gularis* and Texas spiny lizards *S. olivaceus* on private properties in Bastrop, Bexar, Comal, Hays, and Travis Counties in Texas. Little brown skinks *S. lateralis* were captured by hand at Brazos Bend State Park in Needville, Texas (29°22.42'N, 95°38.49'W), and observed at Trinity University, as described below.We observed the final species, the northern curly tail *Leiocephalus carinatus*, in natural areas on Crooked Island, Bahamas (22°38.70'N, 74°00.54'W).

For males of each species except the little brown skinks, we performed 10- to 60-min focal observations of undisturbed behavior in the field, collecting 18–33 h of behavioral data for each species (Table 1). During observations, we recorded the number and type of visual and chemical communication behaviors for each individual. Visual behaviors included push-up displays, extensions of a dewlap, tail curls, and dorsoventral flattening. Chemical behaviors included spreading femoral pore or fecal secretions by rubbing the hindlimbs or cloaca on a substrate, and licking the air or substrate to detect pheromones or other chemical signals.

Because of the complex structural niche occupied by little brown skinks (they are primarily found under leaf litter on the ground), undisturbed skink behavior is extremely difficult to observe in the field. Therefore, we captured 9 male little brown skinks and transported them to our field laboratory at Trinity University to observe their behavior in captive semi-natural conditions. Prior to observation, these lizards were housed for one week in Trinity's animal care facility, following recommendations for lizard care described in Sanger et al. (2008). In brief, animals were housed in individual cages with leaf litter collected from their site of capture, and fed 2–3 crickets coated in calcium powder every other day. Cages were misted with water daily to pro-

Table 1 Summary of behavioral data collection

Species	Total Obs Time (h)	Ave. Obs./Lizard (min ±1 *SE*)	Number observed
Green anole	33.1	25.1 ± 7.0	79
Curly tail	20.3	35.8 ± 18.1	34
Spiny lizard	19.6	40.6 ± 16.9	29
Gecko	21.9	20.6 ± 9.1	63
Skink	9.0	60.0 ± 0.0	9
Whiptail	18.7	26.0 ± 13.1	43
Total	122.6	28.5	257

vide drinking water and to increase the humidity in the cage. The light cycle was set to 13 h light/11 h dark to simulate the natural summer environment.

Within one week of capture, individual skinks were placed into a shallow plastic pool (93 cm in diameter, 21 cm in depth; Summer Escapes^{TM}) with a thin, loosely packed layer of leaf litter covering the bottom 1 cm of the pool. We recorded the behavior of each skink in two 30-min trials. During the behavioral trials, the skinks were almost always visible to the observers, as they generally moved constantly throughout the leaves. In the few occasions that a skink was blocked from our view by the leaf litter, the trial was stopped until the animal moved into sight again. Because little brown skinks avoid areas where other male odors are sensed (Duvall et al., 1980), between trials we wiped the pool with 100% ethanol and replaced the leaf litter to ensure an individual's behavior was not influenced by skinks used in previous trials.

1.2 Morphological and brain measurements

After observations of each species were complete, we captured 9–10 male lizards per species by hand or by noose from the same localities where observations occurred. We measured the snout-vent length (SVL) of each lizard to the nearest 0.5 mm using a ruler, and weighed each lizard to the nearest 0.1 g using a Pesola scale. We transported the lizards to the laboratory at Trinity University, where lizards were euthanized via rapid decapitation. Brain tissues were immediately flash-frozen in cold isopentane on dry ice, and then stored at -80°C. At this time of dissection, we confirmed that each male had large, vascularized testes, indicating that all lizards were in breeding condition.

We coronally sectioned each frozen brain at 20 μm in four alternate series, and thaw-mounted the sections onto SuperFrost Plus microscope slides (Fisher Scientific; Hampton, NH). Slides were stored at -80℃ until further processing. Alternate slide series (i.e., those containing sections at 40 μm intervals) were dehydrated, cleared with xylene, and stained using thionin. A researcher blind to the species identity for each slide measured the cross-sectional area of neuron somas (hereafter, soma size) and their density in LGN, NR, and NS at 400X magnification using the software program ImageJ (Rasband, 1997–2014; Fig. 2). In each of the three brain regions for an individual, in both the right and left brain hemispheres, we measured the soma size of 30 arbitrarily chosen neurons within the rostrocaudal central third of the region, for a total of 60 measurements in 2–4 tissue sections in each region per individual. These measurements were averaged for use in subsequent statistical analyses, and ln-transformed to meet the assumptions of normality. We calculated the density of neurons in each region by counting the number of neurons in four 80 μm× 80 μm areas, using the same sections from which the soma size measurements were taken. To ensure that only neurons were counted, we included only cells with a clearly defined nucleolus and classic neuronal morphology (following Beck and Wade, 2009). Finally, as a measure of overall brain size, we used the Cavalieri method to estimate brain volume from a systematic-random series of 9–32 thionin-stained sections, measuring the area of every eighth 20 μm section for an average of 18.7 sections measured per individual (Mouton, 2002). We then multiplied the volume corresponding to the measurement of each brain section by the intersection distance to calculate the volume of the whole brain. Brain volume measures were ln-transformed to meet the assumptions of normality.

1.3 Statistical analyses

For each behavioral observation, we calculated the rates of visual and chemical communication behaviors, and the total rate of visual and chemical behavior combined, with each rate defined as the number of behavioral displays per minute. Because the different lizard species displayed at dramatically different rates (see Results), for each individual we also calculated the proportion of total communication behaviors that involved visual communication, and the proportion that involved chemical communication. Proportion data were arcsine transformed to meet the assumptions of normality (Sokal and Rohlf, 1995).

To determine whether lizards with larger brains had larger neurons, and thus whether it was necessary to perform any size correction metrics with measures of soma size, we used a series of linear regression analyses in which the average ln-transformed soma size for each region was regressed against the average ln-transformed brain volume for each species.

To determine whether the six species differed in measures of brain and behavior, we used ANOVA, with significant results followed by Tukey's HSD post hoc tests. We then used a series of phylogenetically informed regression analyses to determine whether behavioral measures evolved in association with brain morphology. These analyses were performed using the squamate phylogeny in Wiens et al. (2012), pruned to include only the taxa in this study (or their closest congener; Fig.3). We conducted regressions using PGLS (phylogenetic generalized least squares), using the spe-

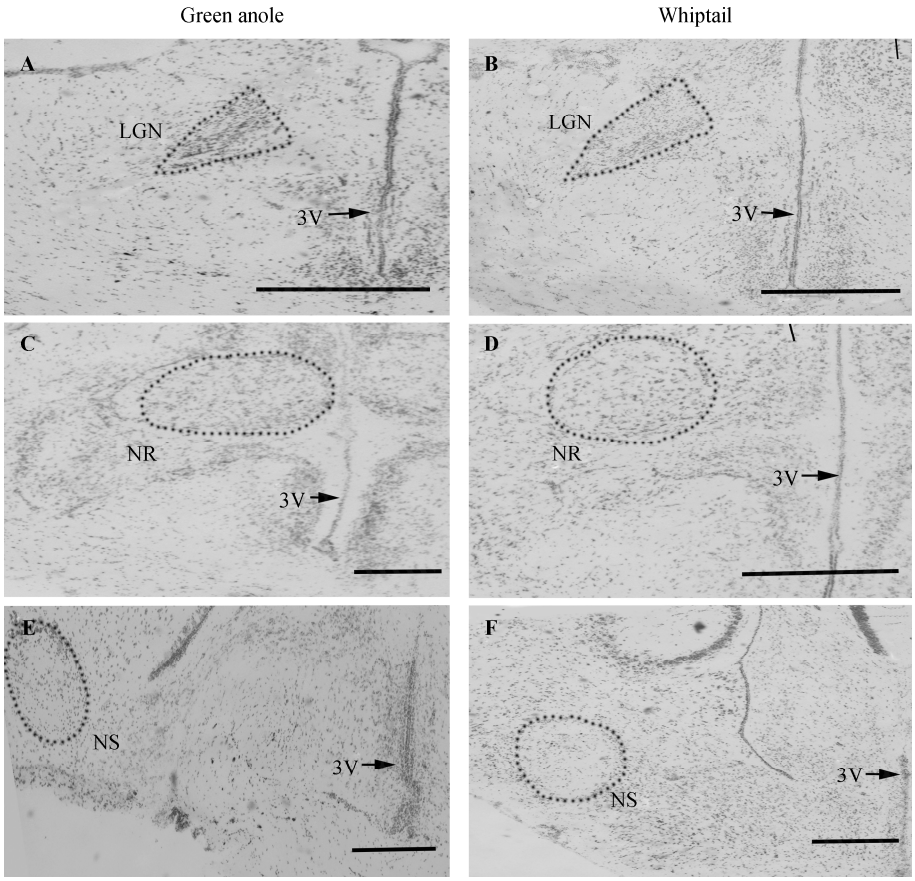

Fig. 2 Brain regions analyzed in this study

Regions in the brain of the green anole (a visually communicating species) are shown on the left, and regions in the whiptail (a chemically communicating species) are shown on the right. **A, B**) lateral geniculate nucleus (LGN); **C, D**) nucleus rotundus (NR); **E, F**) nucleus sphericus (NS). 3V indicates the third ventricle. Scale bar in each image is 500 μm.

cies averages of all behavioral and brain measures, with the *pgls* function in the *caper* package (Freckleton et al., 2002) in R (R Development Core Team, 2014). The goals of these analyses were to determine the relationships between i) visual behavior measures and soma size and density in the LGN and the NR, and ii) chemical behavior measures and NS soma size and density. Because the hypotheses tested in this study were directional in nature, all regression analyses were one-tailed.

2 Results

2.1 Relationships between brain morphology and brain size

Ln-transformed brain volume ($F_{5,54}$ = 382, P < 0.001) differed among the species in a pattern largely parallel to body size, with curly tails, spiny lizards, and whiptails exhibiting the largest brains, followed by anoles, then geckos, and finally skinks (Table 2). There were no significant relationships between brain volume and soma size in the NR ($F_{1,4}$ = 0.52, R^2 = 0.12, P = 0.51) or NS ($F_{1,4}$ = 0.02, R^2 = 0.01, P = 0.89), but the soma in the LGN were significantly larger in species with larger brains ($F_{1,4}$ = 14.5, R^2 = 0.78, P = 0.019). Thus, brain volume was retained as a covariate in subsequent analyses of this region.

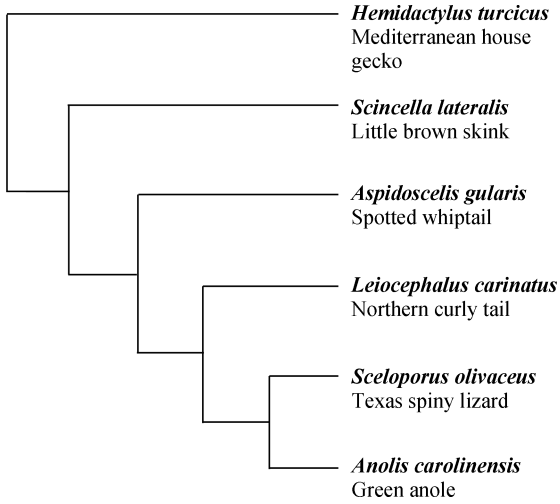

Fig. 3 Phylogenetic relationships of species included in this study, pruned from tree in Wiens et al. (2012)

Table 2 Average measures (*SE*) of brain morphology for six lizard species†

Species	Brain volume (mm^3)	LGN soma size (μm^2)	LGN density‡	NR soma size (μm^2)	NR density‡	NS soma size (μm^2)	NS density‡
Green anole	26.9 (1.26)^{c}	27.1 (0.42)^{b}	56.7 (2.48)^{c}	29.6 (0.90)^{bc}	36.5 (2.68)^{ab}	30.9 (0.47)^{a}	23.0 (1.77)^{a}
Curly tail	69.2 (1.80)^{d}	34.5 (0.66)^{d}	33.1 (1.80)^{a}	32.7 (0.81)^{d}	28.5 (2.23)^{a}	33.6 (0.57)^{ab}	33.8 (1.45)^{b}
Spiny lizard	69.1 (3.17)^{d}	30.4 (0.85)^{c}	40.6 (1.66)^{ab}	25.8 (0.43)^{a}	53.8 (2.59)^{c}	38.6 (0.94)^{cd}	36.6 (2.14)^{b}
House gecko	20.4 (0.87)^{b}	29.1 (0.86)^{bc}	48.7 (2.26)^{bc}	30.9 (0.95)^{cd}	30.3 (2.54)^{a}	36.3 (0.74)^{bc}	39.7 (2.42)^{b}
Little brown skink	9.3 (0.85)^{a}	23.7 (0.49)^{a}	44.9 (3.49)^{b}	27.3 (0.58)^{ab}	45.9 (4.28)^{bc}	38.2 (0.68)^{cd}	40.2 (1.29)^{b}
Spotted whiptail	64.4 (2.83)^{d}	30.9 (0.47)^{c}	35.9 (1.57)^{a}	29.0 (0.43)^{bc}	44.9 (1.43)^{bc}	40.6 (1.27)^{d}	33.3 (1.79)^{b}

†Species with different superscripts were statistically different using Tukey's HSD post hoc tests; ‡Average neural density in 80 μm x 80 μm area.

2.2 Species differences in brain and behavior

The six species differed in the rates of visual display behaviors ($F_{5,269}$ = 32.57, P < 0.001; Fig. 4A), such that anoles had a higher rate of visual behaviors than all other species (Tukey's HSD post hoc test: P < 0.05). The species also differed in their rates of chemical behaviors ($F_{5,269}$ = 45.84, P < 0.001; Fig. 4A), such that whiptails exhibited a higher rate of these behaviors than skinks, which had a higher rate than the other four species (Tukey's HSD post hoc test: P < 0.05). In addition, the species differed in the relative proportions of visual and chemical displays ($F_{5,269}$ = 282.78, P < 0.001), with anole and curly tail lizards using a larger proportion of visual displays (and thus smaller proportion of chemical displays) than all other species, followed by spiny lizards, then house geckos, and finally whiptails and skinks (Tukey's HSD post hoc test: P < 0.05; Fig. 4B).

The neural morphologies of each of the three brain regions also differed among the six species (Table 2; Supplementary Table 1). The ln-transformed soma size of the LGN ($F_{5,53}$ = 7.5, P < 0.001; brain volume was not a significant covariate: P = 0.71) was largest in curly tails and spiny lizards, and smallest in anoles and skinks. Soma in the other region associated with visual behaviors, the NR ($F_{5,54}$ = 12.1, P < 0.001), differed such that ln-transformed NR soma were largest in curly-tails and geckos, and smallest in spiny lizards. The region associated with chemical behaviors, the NS ($F_{5,54}$ = 22.1, P < 0.001) had the largest ln-transformed soma in three of the four chemically communicating species – whiptails, spiny lizards, and skinks – with the visual species (anoles and curly tails) having the smallest soma in this region (Fig. 5A, B).

Neural densities differed in the three regions as well (Table 2; Supplementary Table 1). Neurons in the LGN of anoles and geckos were denser than those of whiptails and curly tails ($F_{5,54}$ = 15.3, P < 0.001; Fig.5C, D), and neurons in the NR of spiny lizards were significantly denser than in anoles, geckos, and curly tails ($F_{5,54}$ = 14.0, P < 0.001). In the NS ($F_{5,54}$ = 11.7, P= 0.001), anoles had less dense neurons than the other five species.

2.3 Evolutionary relationships between brain and behavior

In assessing the relationships between brain morphology and measures of visual display, we found that the density of neurons in the LGN was positively associated with the rate of visual behaviors (Table 3). No other measure of soma size or density in the LGN or NR was associated with the rate or proportion of visual display (Table 3).

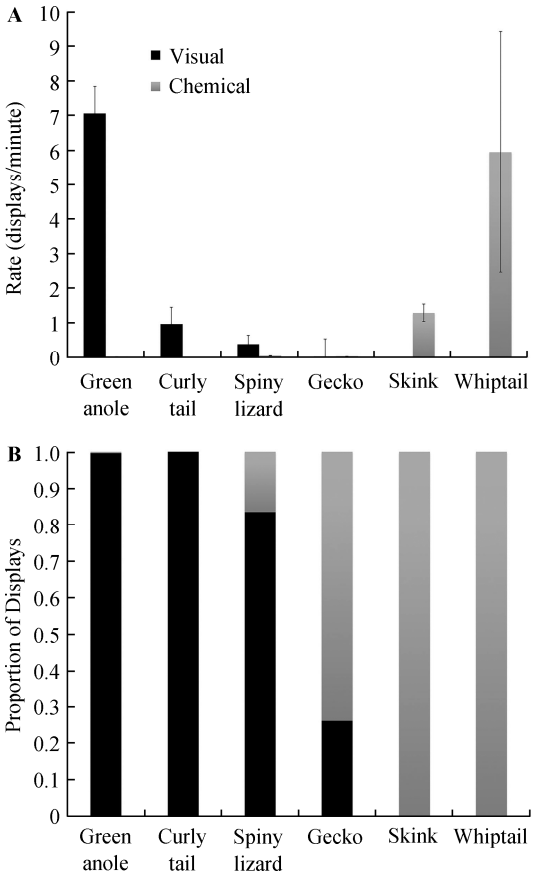

Fig. 4 Species differences in visual and chemical behaviors
A. Average rates of visual and chemical displays (± 1 *SE*) of the six lizard species. **B**. Proportion of visual vs. chemical communication behaviors in the six lizard species.

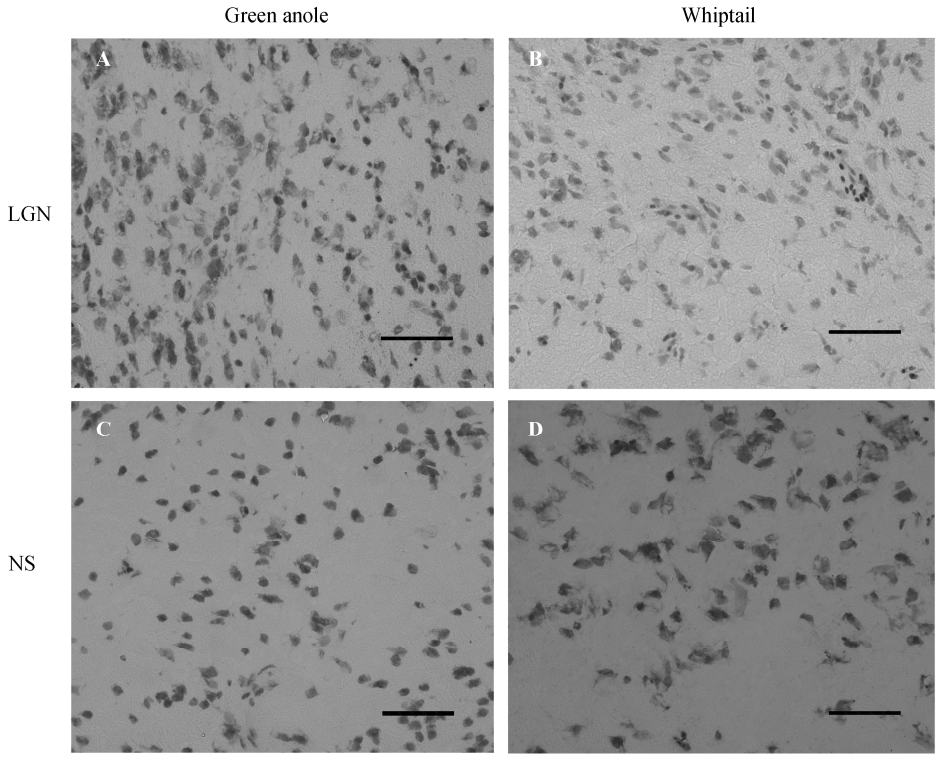

Fig. 5 Species differences in lateral geniculate nucleus (LGN) density and nucleus sphericus (NS) soma size
Regions in the brain of the green anole (a visually communicating species) are shown on the left, and regions in the whiptail (a chemically communicating species) are shown on the right. **A)** The green anole has denser neurons in the LGN than **B)** the whiptail. **C)** The green anole has smaller neurons in the NS than **D)** the whiptail. Scale bar in each image is 50 μm.

Table 3 PGLS regression analyses between visual and chemical behaviors, and measures of brain morphology

Behavior measure	Brain morphology	Covariate	β	*df*	*t*	R^2	*P*
Visual rate	LGN soma size	Brain volume	-0.005	2,3	-0.39	0.83†	0.364
	LGN density		2.42	1,4	2.10	0.53	0.051
	NR soma size		0.02	1,4	0.27	0.02	0.400
	NR density		-0.80	1,4	-0.42	0.04	0.350
Visual proportion	LGN soma size	Brain volume	0.02	2,3	0.24	0.83†	0.414
	LGN density		-0.39	1,4	-0.05	<0.01	0.483
	NR soma size		-0.24	1,4	-0.54	0.07	0.308
	NR density		-5.62	1,4	-0.57	0.08	0.299
Chemical rate	NS soma size		0.026	1,4	1.51	0.36	0.103
	NS density		-0.080	1,4	-0.06	<0.01	0.479
Chemical proportion	NS soma size		0.139	1,4	2.15	0.54	0.046
	NS density		7.93	1,4	1.64	0.40	0.088

† In analyses of LGN soma size, including brain volume as a covariate, R^2 value represents the full model with both variables.

The proportion of chemical display was positively correlated with the soma size of the NS (Table 3), such that species with larger soma sizes in the NS used a higher proportion of chemical communication than those with smaller soma. However, NS soma size was not associated with the rate of chemical display, and NS density was not associated with the rate or proportion of chemical display (Table 3).

3 Discussion

The comparative method has long been a central approach in the field of evolutionary neuroscience (reviewed in Kaas, 2009). One general finding from this rich literature is that the size of a brain region is frequently associated with the behavioral functions it supports, i.e., Jerison's (1973) principle of proper mass. A

well-known example of this relationship is the association across birds between the relative volumes of brain regions involved in song production and the complexity of the species' song (e.g., DeVoogd et al., 1993; Brenowitz, 1997). Further, selection can act on the relative sizes of different regions of the brain independently of overall brain size (i.e., mosaic evolution) in taxa as diverse as mammals, birds, and fish (e.g., Barton and Harvey, 2000; Iwaniuk et al., 2004; Pollen et al., 2007; Smaers and Soligo, 2013; Gutiérrez-Ibáñez et al., 2014). The influence of natural selection on brain morphology is particularly relevant in the evolution of the sensory systems that allow an animal to interact with its environment. For example, in primates and insectivorous mammals, nocturnal species have larger brain regions associated with olfaction than diurnal species, and diurnal primates have larger visual cortexes than their nocturnal counterparts (Barton et al., 1995). Further, the size and cell number of regions in the visual system of primates, and the sizes of their olfactory bulbs, have evolved in association with ecological factors such as diet, activity period, and social structure (Barton, 1998; Barton, 2006). Likewise, in cartilaginous fishes, the size of the optic tectum is also associated with ecology, as this region is smallest in fish living in ocean depths where vision is highly constrained (Yopak and Lisney, 2012); yet, in these dark habitats, the volume of the olfactory bulb is enhanced, supporting chemical communication behaviors (Yopak et al., 2014). Similarly, in the present study, the two lizard species that rely on chemical communication (skinks and whiptails) primarily occur in a complex habitat (i.e., leaf litter) where visual signals may be less effective than chemical signals. Overall, we found support among six lizard species for the hypothesis that the behavioral use of a communication modality has convergently evolved with the neuroanatomy of brain regions associated with that modality. Our results provide evidence for evolutionary associations between visual communication behaviors and neuron density in the LGN, and chemical communication behaviors and neuron size in the NS.

The LGN directly receives input from the retina, the source of visual information, and it sends further projections to other regions of the brain in the telencephalon (Aboitiz and Montiel, 2007). Due to the LGN's central role in processing visual signals, species that have an increased number of neurons in the LGN could potentially process larger amounts of visual information, or could process visual information more efficiently. Indeed, across primate species, the number of neurons in the LGN increases as the number of neurons in the primary visual cortex increases, and visual resolution increases in association with these neural densities (Stevens, 2002). In lizards, subtle changes in visual displays can communicate complex information. For example, in *Sceloporus* and *Anolis* lizard displays, the shape, number, or speed of push-ups in a display, and the body posture from which push-ups are performed, can communicate information about the status or identity of an animal (Martins, 1993; Ord and Martins, 2006). Thus, an increase in the neural density of the LGN could allow visually oriented lizard species to process subtle but important information about its social environment.

Because the NS is a secondary projection of the VNO (Halpern, 1987), species that communicate primarily using chemical signals likely rely on information processed by the NS more frequently than other species. In support of this hypothesis, previous work has determined that squamate species with highly developed olfactory systems have larger NS (Lanuza and Halpern, 1998), and the present study suggests that this may result from larger soma in the NS in chemically communicating species (Fig. 5 and Table 3). Larger neurons in the NS could allow the NS to receive a larger number of axonal connections from the VNO, which could then allow the NS to process more chemosensory information. Additionally, because action potentials require energy (Attwell and Laughlin, 2001), neurons that fire more frequently may require more energy-producing mitochondria to meet their energy needs (Kann and Kovács, 2007). An increased number of mitochondria would take up a larger amount of space in the cell, leading to the need for a larger cell body.

In contrast to our predictions, we found no relationships between the neural morphology of the NR and visual behaviors. Thus, the diversity of cellular morphology in the NR (Table 2) could be related to many fundamentally important behaviors in addition to the visual displays examined here, including navigation through a habitat, capturing mobile prey, and identifying territorial boundaries. Further, in pigeons *Columba livia*, the NR is associated with the detection of looming, such as occurs when a flying predator grows larger in one's field of view as it approaches (Wang et al., 1993; Sun and Frost, 1998). As one of the most common and threatening predators of all of the lizards in this study is birds, the functional use of the NR in an ecological context may be quite similar across these species. Thus, the reliance of all six of the lizard species in this study on visual cues could suggest why neither soma size nor

density in this region served as a predictor for the visual communication behaviors quantified here.

The visual and chemical systems in lizards may further evolve in response to constraints resulting from the investment made in the primary sensory system. For example, trade-offs in the relative volume of brain regions involved in the auditory and visual systems have been shown in bats (Baron et al., 1996) and owls (Gutiérrez-Ibáñez et al., 2013), and trade-offs in neural density in the primary visual cortex and hippocampus have been found in carnivores and primates (Lewitus et al., 2012). Although there was no negative correlation between neuron size or density in visual *vs*. chemical regions in this study (results not shown; all $P > 0.3$), this may be due to the small number of species included in this study. We urge continued study of reptilian neuroanatomy to address the hypothesis of evolutionary constraint in sensory investment in this group.

In sum, visual and chemical modalities provide the primary means by which many animals interact with their social and physical environments, and the neuroanatomy of the brain regions that process information from visual and chemical signals is thus critical to a species' habitat use, social interactions, prey capture, and predator evasion. Although we found evidence for the convergent evolution of neural morphologies associated with visual and chemical modalities across a distantly related group of lizard species, our results also revealed the diversity of patterns of neural size and density in this group. By examining the structure of brain regions associated with behaviors that rely on sensory perception, we gain a more nuanced understanding of the cellular traits that underlie the fundamental mechanisms of animal ecology.

Acknowledgements We thank the members of the Johnson Lab at Trinity University for assistance in the field and laboratory – particularly Bonnie Kircher, Alisa Dill, Michelle Oberndorf, Adam Silva, Taren Blackmon, Jordan Bush, McKenzie Quinn, Ellee Cook, Grayam Sailor-Tynes, and Collin Shinkle. We also thank David Ribble, Troy Murphy, Jimmy Roberts, Kevin McIntyre, and three reviewers for comments on an earlier version of this work, and Kevin McIntyre and Kimberly Phillips for statistical advice. This work was funded by a Sigma Xi GIAR (to C.D.R.), a Trinity University Mind Science Foundation grant (to C.D.R.), Trinity University's HHMI and Biology Summer Undergraduate Research Fellowships (to C.D.R.), Texas Ecolab, and the National Science Foundation (IOS 1257021 to M.A.J.). All procedures were approved by Trinity University's Animal Research Committee (protocol # 050213_MAJ2).

References

Alberts AC, Pratt NC, Phillips JA, 1992. Seasonal productivity of lizard femoral glands: Relationship to social dominance and androgen levels. Physiol. Behav. 51: 729–733.

Aboitiz F, Montiel J, 2007. Origin and Evolution of the Vertebrate Telencephalon, with Special Reference to the Mammalian Neocortex: Advances in Anatomy, Embryology, and Cell Biology, Vol 193. Berlin: Springer.

Attwell D, Laughlin SB, 2001. An energy budget for signaling in the grey matter of the brain. J. Cereb. Blood Flow Metab. 21: 1133–1145.

Baron G, Stephan H, Frahm HD, 1996. Comparative Neurobiology in Chiroptera. Basel: Birkhäuser Verlag.

Barton RA, 1998. Visual specialisation and brain evolution in primates. Proc. Roy. Soc. B 265: 1933–1937.

Barton RA, 2006. Olfactory evolution and behavioral ecology in primates. Am. J. Primatol. 68: 545–558.

Barton RA, Harvey PH, 2000. Mosaic evolution of brain structure in mammals. Nature 405: 1055–1058.

Barton RA, Purvis A, Harvey PH, 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. Philos. T. Roy. Soc. B 348: 381–392.

Beck LA, Wade J, 2009. Morphology and estrogen receptor α mRNA expression in the developing green anole forebrain. J. Exp. Zool. 311A: 162–171.

Bissinger BE, Simon CA, 1981. The chemical detection of conspecifics by juvenile Yarrow's spiny lizard *Sceloporus jarrovi*. J. Herpetol. 15: 77–81.

Brenowitz EA, 1997. Comparative approaches to the avian song system. J. Neurobiol. 33: 517–531.

Bruce LL, 2009. Evolution of the nervous system in reptiles. In: Kaas JH ed. Evolutionary Neuroscience. Amsterdam: Academic Press, Elsevier, 233–264.

Bruce LL, Butler AB, 1984. Telencephalic connections in lizards. I: Projections to cortex. J. Comp. Neurol. 229: 585–601.

Bruce LL, Neary TJ, 1995. The limbic system of tetrapods: A comparative analysis of cortical and amygdalar populations. Brain Behav. Evol. 46: 224–234.

Carpenter CC, 1978. Comparative display behavior in the genus *Sceloporus* (Iguanidae). Contrib. Biol. Geol. Milwakee Pub. Mus. 18: 1–71.

Casagrande VA, Sary G, Royal D, Ruiz O, 2005. On the impact of attention and motor planning on the lateral geniculate nucleus. Prog. Brain Res. 149: 11–29.

Chow RL, Lang RA, 2001. Early eye development in vertebrates. Ann. Rev. Cell Dev. Biol. 17: 255–296.

Cooper WE, Hartdegen R, 1999. Discriminative response to animal, but not plant, chemicals by an insectivorous, actively foraging lizard *Scincella lateralis* and differential response to surface and internal prey cues. J. Chem. Ecol. 25: 1531–1541.

Cruce JAF, 1974. A cyroarchitectonic study of the diencephalon of the tegu lizard *Tupinambis nigropunctatus*. J. Comp. Neurol. 153: 215–238.

Dangles O, Irschick D, Chittka L, Casas J, 2009. Variability in sensory ecology: Expanding the bridge between physiology and evolutionary biology. Q. Rev. Biol. 84: 51–74.

De Valois RL, Abramov I, Jacobs GH, 1965. Analysis of response patterns of LGN cells. J. Opt. Soc. Am. 56: 966–977.

DeVoogd TJ, Krebs JR, Healy SD, Purvis A, 1993. Relations between song repertoire size and the volume of brain nuclei related to song: Comparative evolutionary analyses amongst oscine birds. Proc. R. Soc. Lond. B 254: 75–82.

Duvall D, Herskowitz R, Trupiano-Duvall J, 1980. Responses of five-lined skinks *Eumeces fasciatus* and ground skinks *Scincella lateralis* to conspecific and interspecific chemical cues. J. Herpetol. 14: 121–127.

Evans LT, 1953. Tail display in an iguanid lizard *Liocephalus carinatus coryi*. Copeia 1953: 50–54.

Fox SF, McCoy JK, Baird TA, 2003. Lizard Social Behavior. Baltimore: The Johns Hopkins University Press.

Freckleton RP, Harvey PH, Pagel M, 2002. Phylogenetic analysis and comparative data: A test and review of evidence. Am. Nat. 160: 712–726.

Greenberg N, 1982. A forebrain atlas and stereotaxic technique for the lizard *Anolis carolinensis*. J. Morphol. 174: 217–236.

Gutiérrez-Ibáñez C, Iwaniuk AN, Lisney TJ, Wylie DR, 2013. Comparative studies of visual pathways in owls (Aves: Strigiformes). Brain Behav. Evol. 81: 27–39.

Gutiérrez-Ibáñez C, Iwaniuk AN, Moore BA, Fernández-Juricic E, Corfield JR et al., 2014. Mosaic and concerted evolution in the visual system of birds. PLoS ONE 9: e90102.

Hall MI, 2008. Comparative analysis of the size and shape of the lizard eye. Zoology 111: 62–75.

Halpern M, 1987. The organization and function of the vomeronasal system. Ann. Rev. Neuro. 10: 325–362.

Iwaniuk AN, Dean KM, Nelson JE, 2004. A mosaic pattern characterizes the evolution of the avian brain. Proc. Roy. Soc. B 271: S148–S151.

Jenssen TA, 1977. Evolution of anoline display behavior. Am. Zool. 17: 203–215.

Jerison HJ, 1973. Evolution of the Brain and Intelligence. New York: Academic Press.

Johnson BA, Leon M, 2000. Odorant molecule length: One aspect of the olfactory code. J. Comp. Neurol. 426: 330–338.

Kann O, Kovács R, 2007. Mitochondria and neuronal activity. Am. J. Physiol. Cell Physiol. 292: C641–C657.

Kaas JH, 2009. Evolutionary Neuroscience. Amsterdamn: Academic Press.

Kenigfest N, Martínez-Marcos A, Belekhova M, Font C, Lanuza E et al., 1997. A lacertilian dorsal retinorecipient thalamus: A re-investigation in the Old-World lizard *Podarcis hispanica*. Brain Behav. Evol. 50: 313–334.

Keverne EB, 1999. The vomeronasal organ. Science 286: 716–720.

Khannoon ERR, 2012. Secretion of pre-anal glands of house-dwelling geckos (Family: Gekkonidae) contain monoglycerides and 1,3-alkanediol: A comparative chemical ecology study. Biochem. Syst. Ecol. 44: 341–346.

Lanuza E, Halpern M, 1998. Afferent and efferent connections of the nucleus sphericus in the snake *Thamnophis sirtalis:* Convergence of olfactory and vomeronasal information in the lateral cortex and the amygdala. J. Comp. Neurol. 385: 627–640.

Lewitus E, Hof PR, Sherwood CC, 2012. Phylogenetic comparison of neuron and glia densities in the primary visual cortex and hippocampus of carnivores and primates. Evolution 66: 2551–2563.

Lohman AHM, Smeets WJAJ, 1993. Overview of the main and accessory olfactory bulb projections in reptiles. Brain Behav. Evol. 41: 147–155.

Martín J, López P, 2015. Condition-dependent chemosignals in reproductive behavior of lizards. Horm. Behav. 68: 14–24.

Martins EP, 1993. A comparative study of the evolution of *Sceloporus* push-up displays. Am. Nat. 142: 994–1018.

Mouton PR, 2002. Principles and Practices of Unbiased Stereology. Baltimore: The Johns Hopkins Univ. Press.

Northcutt RG, Butler AB, 1974. Evolution of reptilian visual systems: Retinal projections in a nocturnal lizard *Gekko gecko* (Linnaeus). J. Comp. Neurol. 157: 453–465.

Nunez SC, Jenssen TA, Ersland K, 1997. Female activity profile of a polygynous lizard *Anolis carolinensis*: Evidence of intersexual asymmetry. Behaviour 134: 205–223.

Ord TJ, Martins EP, 2006. Tracing the origins of signal diversity in anole lizards: Phylogenetic approaches to inferring the evolution of complex behavior. Anim. Behav. 71: 1411–1429.

Pollen AA, Dobberfuhl AP, Scace J, Igulu MM, Renn SCP et al., 2007. Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain Behav. Evol. 70: 21–39.

Punzo F, 2007. Chemosensory recognition of the marbled whiptail lizard *Aspidoscelis marmorata* (Squamata: Teiidae) to odors of sympatric lizards (*Crotophytus collaris*, *Coleonyx brevis*, *Eumeces obsoletus* and *Uta stansburiana*) that represent different predation risks. J. Env. Biol. 29: 57–61.

R Development Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Regalado R, 2003. Roles of visual, acoustic, and chemical signals in social interactions of the tropical house gecko *Hemidactylus mabouia*. Caribb. J. Sci. 39: 307–320.

Rasband WS, 1997–2014. ImageJ. Bethesda, Maryland: U. S. National Institutes of Health. http://imagej.nih.gov/ij/.

Sanger TJ, Hime PJ, Johnson MA, Diani J, Losos JB, 2008. Laboratory protocols for husbandry and embryo collection of *Anolis* lizards. Herpetol. Rev. 39: 58–63.

Simon CA, 1983. A review of lizard chemoreception. In: Huey RB, Pianka ER, Schoener TW ed. Lizard Ecology: Studies of a Model Organism. Cambridge: Harvard University Press, 119–133.

Smaers JB, Soligo C, 2013. Brain reorganization, not relative brain size, primarily characterizes anthropoid brain evolution. Proc. Roy. Soc. B 280: 20130269.

Sokal RR, Rohlf FJ, 1995. Biometry: The Principals and Practice of Statistics in Biological Research. New York: WH Freeman and Company: 419–422.

Stevens CF, 2002. Predicting functional properties of visual cortex from an evolutionary scaling law. Neuron 36: 139–142.

Stoddart DM, 1980. The olfactory system of vertebrates. In: The Ecology of Vertebrate Olfaction. London: Chapman and Hall, 1–33.

Sun H, Frost BJ, 1998. Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. Nature Neurosci. 1: 296–303.

Wade J, 2011. Relationships among hormones, brain, and motivated behavior in lizards. Horm. Behav. 59: 637–644.

Wang Y, Jiang S, Frost BJ, 1993. Visual processing in pigeon nucleus rotundus: Luminance, color, motion, and looming subdivisions. Visual Neurosci. 10: 21–30.

Wiens JJ, Hutter CR, Mulcahy DG, Noonan BP, Townsend TM et al., 2012.Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. Biol. Lett.

8: 1043–1046.
Yopak KE, Lisney TJ, 2012. Allometric scaling of the optic tectum in cartilaginous fishes. Brain Behav. Evol. 80: 108–126.
Yopak KE, Lisney TJ, Collin SP, 2014. Not all sharks are "swimming noses": Variation in olfactory bulb size in cartilaginous fishes. Brain Struct. Funct. DOI: 10.1007/s00429−014−0705−0

Supplementary Table 1 Summary of brain morphology measues [average (*SE*)] for individual lizards in six species

Species	Brain volume (mm^3)	LGN soma size (μm^2)	LGN density	NR soma size (μm^2)	NR density	NS soma size (μm^2)	NS density
Anolis carolinensis	17.6	27.9 (1.21)	64.8 (4.52)	28.2 (0.90)	46.5 (5.78)	32.8 (0.86)	18.3 (1.98)
Anolis carolinensis	26.7	25.6 (0.80)	70.8 (3.07)	32.1 (0.82)	31.5 (2.66)	30.4 (0.91)	34.0 (1.97)
Anolis carolinensis	27.0	26.5 (0.96)	56.0 (3.03)	28.0 (0.76)	44.5 (3.59)	30.0 (1.45)	22.5 (2.50)
Anolis carolinensis	32.8	25.7 (1.18)	51.0 (5.35)	29.3 (0.87)	48.5 (1.71)	28.5 (1.27)	14.8 (2.98)
Anolis carolinensis	30.0	27.2 (0.90)	50.5 (5.30)	35.3 (0.93)	26.0 (3.27)	31.2 (1.44)	24.0 (1.37)
Anolis carolinensis	28.8	28.7 (1.11)	47.5 (6.65)	28.8 (0.89)	36.0 (5.62)	32.8 (2.07)	19.0 (1.25)
Anolis carolinensis	28.6	28.5 (1.18)	51.3 (1.11)	31.9 (0.85)	30.0 (2.55)	30.2 (1.28)	29.0 (1.26)
Anolis carolinensis	24.7	28.6 (1.33)	56.8 (2.85)	31.5 (0.77)	42.3 (6.99)	30.8 (1.17)	25.8 (3.41)
Anolis carolinensis	26.2	27.5 (1.25)	52.5 (4.09)	25.7 (0.71)	34.3 (2.25)	29.7 (0.97)	23.3 (2.95)
Anolis carolinensis	25.9	25.2 (0.92)	66.0 (1.78)	25.3 (0.82)	25.5 (1.33)	32.7 (1.09)	19.8 (3.94)
Leiocephalus carinatus	75.6	35.4 (1.38)	35.3 (1.03)	28.2 (0.94)	26.3 (1.93)	36.9 (0.97)	31.0 (4.99)
Leiocephalus carinatus	77.1	34.8 (2.06)	26.8 (11.0)	32.0 (1.37)	20.3 (1.25)	33.7 (1.02)	45.0 (6.65)
Leiocephalus carinatus	67.2	34.7 (1.53)	29.5 (2.06)	33.0 (3.13)	19.0 (0.70)	34.6 (1.06)	30.5 (2.50)
Leiocephalus carinatus	60.9	33.7 (1.02)	39.5 (2.25)	37.6 (2.37)	22.5 (3.50)	35.3 (0.99)	32.5 (0.83)
Leiocephalus carinatus	77.6	32.2 (1.05)	37.3 (2.93)	32.6 (1.11)	25.0 (2.35)	32.5 (0.95)	32.5 (5.82)
Leiocephalus carinatus	63.7	31.7 (1.18)	31.3 (3.35)	32.6 (1.12)	31.5 (2.63)	34.6 (0.98)	33.5 (0.83)
Leiocephalus carinatus	65.9	36.1 (1.21)	28.8 (2.17)	30.5 (1.07)	36.0 (2.86)	32.9 (1.17)	29.0 (6.24)
Leiocephalus carinatus	66.3	31.9 (1.09)	41.0 (3.22)	35.7 (1.42)	39.5 (2.50)	30.8 (0.86)	35.5 (9.15)
Leiocephalus carinatus	69.1	36.2 (1.58)	37.0 (6.98)	32.2 (1.52)	30.0 (4.65)	32.2 (1.14)	37.0 (6.66)
Leiocephalus carinatus	68.8	37.9 (1.00)	24.5 (3.69)	33.0 (1.29)	35.3 (3.68)	32.0 (1.06)	31.5 (2.50)
Sceloporus olivaceus	87.1	30.9 (1.09)	48.8 (3.15)	23.2 (0.87)	51.3 (5.44)	35.5 (1.51)	30.5 (9.50)
Sceloporus olivaceus	58.1	31.4 (1.09)	48.3 (2.02)	27.2 (1.07)	40.3 (5.85)	40.3 (1.39)	30.5 (2.50)
Sceloporus olivaceus	74.4	34.1 (1.41)	43.0 (3.81)	27.3 (0.80)	70.0 (9.17)	42.7 (1.32)	32.5 (0.05)
Sceloporus olivaceus	73.8	32.8 (1.27)	36.0 (4.64)	25.9 (0.79)	52.5 (4.44)	40.4 (1.30)	40.3 (3.92)
Sceloporus olivaceus	63.7	25.4 (1.17)	35.5 (0.57)	25.8 (0.69)	48.8 (2.50)	42.2 (1.30)	48.5 (4.18)
Sceloporus olivaceus	61.3	32.0 (1.31)	36.0 (1.10)	27.6 (1.17)	52.8 (2.50)	35.4 (1.39)	29.8 (3.19)
Sceloporus olivaceus	82.3	27.8 (1.25)	44.8 (1.49)	26.0 (0.92)	55.5 (5.17)	39.5 (1.22)	30.0 (1.00)
Sceloporus olivaceus	65.9	28.8 (1.06)	37.3 (1.55)	25.0 (0.70)	63.5 (4.97)	33.9 (1.28)	47.0 (3.22)
Sceloporus olivaceus	58.0	29.8 (1.39)	36.0 (3.34)	24.8 (0.84)	54.3 (4.77)	37.5 (1.65)	34.5 (0.50)
Sceloporus olivaceus	66.0	30.9 (1.03)	40.3 (1.98)	25.1 (0.87)	48.8 (5.99)	38.0 (1.62)	34.8 (1.49)
Hemidactylus turcicus	18.5	31.2 (1.46)	49.0 (3.03)	27.6 (0.70)	25.0 (2.08	37.5 (1.31)	51.0 (1.55)
Hemidactylus turcicus	22.6	26.1 (1.06)	44.8 (3.47)	29.7 (1.74)	25.5 (1.71)	35.3 (1.03)	38.0 (2.17)
Hemidactylus turcicus	22.2	26.0 (1.00)	54.0 (3.56)	28.7 (0.99)	27.5 (1.19)	38.5 (1.11)	37.5 (4.88)
Hemidactylus turcicus	24.1	26.4 (0.96)	52.8 (8.37)	28.3 (0.73)	46.0 (4.56)	34.7 (1.32)	30.0 (2.17)
Hemidactylus turcicus	20.5	30.5 (1.24)	49.8 (4.44)	28.8 (0.91)	36.8 (7.62)	41.0 (1.27)	34.0 (6.50)
Hemidactylus turcicus	19.9	32.3 (1.55)	46.3 (5.44)	36.0 (1.75)	26.0 (1.22)	37.3 (1.56)	39.0 (2.99)
Hemidactylus turcicus	15.4	27.4 (1.01)	54.5 (2.50)	34.0 (1.51)	37.5 (3.38)	34.5 (1.14)	40.5 (1.63)
Hemidactylus turcicus	22.1	27.7 (1.07)	56.0 (4.99)	30.3 (1.04)	34.8 (2.29)	33.9 (1.22)	54.5 (0.54)
Hemidactylus turcicus	21.8	33.3 (1.76)	49.0 (1.27)	30.9 (1.26)	22.5 (0.50)	33.6 (1.09)	33.0 (4.34)
Hemidactylus turcicus	16.9	29.7 (1.35)	31.3 (1.70)	35.0 (1.21)	21.3 (0.63)	36.2 (1.24)	39.5 (8.13)
Scincella lateralis	9.2	21.1 (0.82)	51.0 (4.24)	24.5 (0.97)	65.8 (11.6)	40.5 (1.24)	41.0 (4.76)
Scincella lateralis	9.1	23.5 (1.02)	44.3 (4.80)	26.0 (1.07)	48.0 (6.98)	37.7 (1.07)	47.5 (3.33)
Scincella lateralis	8.0	23.7 (0.77)	46.3 (5.92)	26.6 (0.89)	51.8 (5.22)	41.3 (2.41)	38.0 (2.66)
Scincella lateralis	10.3	24.9 (0.95)	52.0 (8.46)	27.6 (0.99)	42.3 (4.91)	37.8 (1.38)	34.5 (3.33)
Scincella lateralis	10.5	24.8 (0.90)	55.3 (7.11)	27.7 (1.09)	39.0 (8.62)	36.6 (1.20)	44.5 (1.78)
Scincella lateralis	8.5	23.4 (0.70)	54.0 (7.55)	29.0 (1.12)	21.5 (2.33)	38.2 (1.31)	38.5 (4.29)
Scincella lateralis	8.2	24.5 (1.14)	21.5 (2.98)	30.4 (0.76)	57.8 (9.24)	39.8 (1.60)	38.0 (2.86)
Scincella lateralis	9.7	25.6 (1.46)	39.3 (3.98)	28.0 (1.00)	50.0 (6.17)	36.0 (1.40)	41.3 (3.60)
Scincella lateralis	10.4	22.0 (1.10)	41.0 (5.86)	26.2 (0.92)	37.3 (9.40)	35.4 (1.30)	38.8 (1.98)
Aspidoscelis gularis	70.6	28.9 (1.18)	34.8 (3.20)	28.7 (0.90)	46.5 (5.81)	38.9 (1.73)	31.5 (0.50)
Aspidoscelis gularis	68.6	32.0 (1.40)	31.3 (3.47)	31.0 (1.40)	36.0 (3.14)	40.2 (2.67)	34.8 (2.98)
Aspidoscelis gularis	59.0	32.7 (1.28)	33.3 (4.77)	27.8 (1.00)	45.3 (1.55)	38.7 (1.28)	36.5 (3.50)
Aspidoscelis gularis	69.3	31.3 (1.75)	33.3 (3.35)	28.5 (0.73)	40.0 (1.22)	38.5 (1.29)	39.5 (1.99)
Aspidoscelis gularis	74.8	29.8 (1.39)	32.0 (2.12)	29.4 (0.82)	44.5 (2.63)	46.1 (1.63)	40.9 (1.72)
Aspidoscelis gularis	66.8	30.5 (1.35)	33.0 (1.47)	30.3 (1.17)	43.0 (6.20)	39.6 (1.58)	31.5 (2.54)
Aspidoscelis gularis	67.9	31.4 (1.50)	38.5 (4.17)	27.1 (0.85)	45.0 (4.02)	40.9 (1.72)	37.0 (3.00)
Aspidoscelis gularis	54.7	28.3 (1.46)	38.8 (2.98)	27.1 (0.92)	47.8 (3.71)	38.8 (2.14)	21.5 (3.42)
Aspidoscelis gularis	44.9	31.0 (1.40)	48.0 (3.32)	30.2 (0.84)	52.3 (3.90)	49.0 (2.70)	34.5 (4.50)
Aspidoscelis gularis	67.1	32.6 (1.65)	36.0 (1.95)	29.7 (0.98)	48.5 (2.98)	35.1 (1.80)	39.3 (2.33)