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ABSTRACT.—Procedural memory allows animals to solve previously encountered tasks over weeks, months, or years efficiently. Although thoroughly documented in vertebrate clades such as mammals and birds, studies of procedural memory in squamate reptiles are lacking. Filling the gap in knowledge regarding procedural memory in squamates is important to understanding the degree to which procedural memory is unique to birds and mammals, as it is related to their unique cognitive abilities. We tested for memory of a problem-solving task in two species of monitor lizard (*Varanus* spp.) and a beaded lizard (*Heloderma* sp.) after a 20-mo hiatus in exposure, representing approximately 25% of their ages at the time of testing. All the monitor lizards had lower initial latencies to solve the task upon re-exposure posthiatus than they had as naïve individuals during the prehiatus trials and reached minimum latencies in fewer trials than when previously tested. Our results indicate procedural memory of puzzle-solving behaviors on the time scales of years. Our results add to an emerging literature suggesting that squamate and other nonavian reptiles share a number of cognitive traits with birds and mammals, suggesting that such traits are far more widespread across taxa than previously recognized. We also discuss a framework for studying cognition in squamates that would allow tests of cognition across a great diversity of body forms and ecologies.

Although reptiles have quite elaborate patterns of instinctive behaviour, no one could claim that they are good at adapting to unfamiliar situations, or have much ability to learn from experience.

—Angus Bellairs (1970:339)

Cognition is best understood within the context of ecological and evolutionary processes; the evolutionary backdrop shaping the framework for cognitive abilities in an organism is both preceded by, and shaped by, the ecological obstacles an organism encounters (Adams-Hunt and Jacobs, 2007). The intimate relationship between cognition and ecological and evolutionary processes underpins the importance of comparative studies when evaluating behavioral cognition. Historically, work in cognition has focused largely on mammals (Wilkinson and Huber, 2012). But substantial work on birds has shown clearly that, despite having a very different brain morphology (Striedter, 2015), they perform comparably with mammals on many tests of cognition. In contrast, fewer studies have included other clades such as the nonavian reptiles (Wilkinson and Huber, 2012; Burghardt, 2013), resulting in an incomplete phylogenetic perspective on the origins and evolution of cognitive traits in tetrapods. The lack of inclusion of nonavian reptiles in studies of cognition may be, in part, due to a persistent problem in the relevant literature regarding the inconsistent use of the taxonomic term "reptile." Some studies and reviews (e.g., Striedter, 2015) embrace the fact that birds are, in fact, reptiles, whereas others (e.g., Wilkinson and Huber, 2012; Roth et al., 2019) discuss results comparing birds to the nonmonophyletic assemblage of nonavian reptiles. In any case, there have been relatively few behavioral studies on cognition in squamate reptiles, relative to birds and mammals (e.g., Day et

al., 1999; Manrod et al., 2008; LaDage et al., 2012, 2017; Cooper et al., 2019). The taxonomic imbalance in the number of studies of mammals and birds versus nonavian reptiles is problematic because, as brain anatomy underlies brain function (Rodriguez et al., 2002; Striedter, 2015; Tosches et al., 2018), the knowledge of homologous regions in the brain among organisms underlies our abilities to recognize homologous behaviors (Greene, 1994), or homologous abilities in cognition (e.g., Finn, 2017; Murray et al., 2018). An appropriately comparative approach (Harvey and Pagel, 1991) to evaluate homology or convergence of behaviors or cognitive abilities among species will require phylogenetically diverse exemplars.

Procedural memory, or the ability to store and retrieve information on how to perform specific skills, provides advantages to individuals to solve previously encountered tasks more efficiently over weeks, months, or even years, and has not been studied extensively in squamates. Of the few studies of what could be considered long-term memory in nonavian reptiles, most have focused on chelonians (Davis and Burghardt, 2007; Wilkinson et al., 2010; Soldati et al., 2017). In this study, we tested long-term retention of a problem-solving skill in two species of monitor lizards (*Varanus* spp.) over a period of 20 mo; we also examined the performance on the same task of a species of beaded lizard (*Heloderma charlesbogerti*) as a phylogenetic outgroup. Varanids are good candidates for long-term memory given that they live a relatively long time, approximately 10–20 yr (Mendyk, 2015), and maintain large territories in complex environments, with evidence that they learn about these landscapes (Auffenberg, 1981, 1988, 1994; Sweet, 1999; Pianka et al., 2004; Sweet, 2007). Previous work has also demonstrated learning and problem-solving abilities in the clade (e.g., Burghardt et al., 2002; Manrod et al., 2008; Gaalema, 2011; Mendyk and Horn, 2011; Cooper et al., 2019). Considered together, these characteristics suggest that varanids may be capable of developing long-term memory (sensu Snell-Rood, 2013) related to a problem-solving task. We had no precon-

Fig. 1. The puzzle-feeder device. Mertens' Water Monitor (*Varanus mertensi*) investigating puzzle feeder device, in situ in its home enclosure. The dashed line marks the vertical plane of the device base. Once crossed, the latency time measures were initiated.

ceived notions regarding *Heloderma,* as the only cognitive work with those lizards of which we are aware was by Cooper et al. (2019).

Here, we report a study of long-term procedural memory in two clades of squamate reptiles and discuss the results at different levels of evolutionary generality. We used the foraging task described by Cooper et al. (2019) to test for reconsolidation of a problem-solving task. The subjects had to manipulate a puzzle device, requiring them to use their claw or snout to open the door of a clear, nonairtight box to access a food reward. We compared problem-solving latencies in the current study to the same individuals' latencies in previous work performed 20 mo prior (Cooper et al., 2019). Specifically, we sought to determine if, after the 20-mo hiatus, the subjects would show solving latencies similar to their performance when they were naïve to the puzzle, or if their latencies would reflect memory retrieval and be similar to those shown after they had learned how to solve the puzzle (i.e., after approximately 40 trials, as reported by Cooper et al., 2019). To the extent that an individual is able to access the relevant procedural memory, the initial solving latency posthiatus will be shorter than the novel exposure, and the minimum latency posthiatus will be met in fewer trials than in the previous experiment.

MATERIALS AND METHODS

We studied two Emerald Tree Monitors (*Varanus prasinus*; 1 = 13R077, adult female, age = 79 mo; 2 = 13R076, adult female, age = 67 mo), two Mertens' Water Monitors (*Varanus mertensi*; 1 = 11R071 and 2 = 11R072, adults, sex undetermined, age = 91 mo), and one Guatemalan Beaded Lizard (*Heloderma charlesbogerti*; 13R027, subadult, sex undetermined, age = 67 mo). All individuals were maintained in off-exhibit enclosures at Zoo Atlanta, Georgia, USA, and all trials occurred in the lizards' home enclosures; that is, animals were not relocated to test arenas for the trials. All procedures were approved by The Scientific Research Committee of Zoo Atlanta.

Individuals were exposed to a similar puzzle device as that used by Cooper et al. (2019). The device (Fig. 1) was a clear acrylic cylinder approximately 18.0 cm tall and 11.4 cm in diameter. A side-hinged (zip-tie hinges) door was cut into one lower side of the cylinder; the doors were flush-fitting with a notch cut into the lower nonhinged corner to allow the lizards to insert a claw or snout to open the door. Thirteen equally spaced holes were drilled through the sides of the tube. The top was capped with a rubber lid and the bottom glued onto a heavy resin platform (10.0×10.0 cm) to ensure stability and to prevent the lizards from moving the device itself. A dead mouse (the routine food item offered to these lizards) was placed in the cylinder and could only be accessed by opening the door.

The initial trials of Cooper et al. (2019) were concluded on 28 May 2017 and were followed by the present trials conducted approximately twice weekly between 30 January and 23 February 2019 between 1100 and 1300 h. Because trials replaced the subjects' normal feeding regimen, zoo staff ensured that trial days and times coincided with the normal daily feeding schedule of each individual, and the mice offered were consistent in size with the animals' normal diet. Eight trials were conducted with each lizard using the same procedures described by Cooper et al. (2019). A baited device was placed into the lizard's home enclosure, situated approximately at one body-length distance, with the device's door oriented towards the lizard. The animals were not touched or moved. Trials were digitally recorded by stationary human observers approximately 2 ft away from the enclosure. The time elapsed between a lizard's initial contact with the device and successfully gaining entry and grasping the food item with its mouth was recorded as its measure of latency. Initial contact was defined as the anterior portion of the lizard's body crossing the vertical plane of the base of the device (Fig. 1); tongue flicks crossing this plane were not considered to represent contact with the device. If a lizard failed to open the device and seize the food within 30 min, the trial was stopped, the device was removed, and the food item was offered to the lizard. Video of a successful trial is available (https://youtu.be/ukayoMTScXw), and full raw data are posted on Dryad (doi:10.5061/dryad.gm286rk).

To test the impact of the 20-mo hiatus, we compared posthiatus latency data from each individual to previously published data from Cooper et al. (2019). Both the pre- and posthiatus data were scored by TLC. We analyzed both the posthiatus data set and the combined pre- and posthiatus data sets using Bayesian multilevel modeling in a repeated-measures censored generalized linear model and specified a lognormal distribution for the latencies. The latency data conformed to a lognormal distribution with a long upper tail, thus requiring the use of a generalized linear model (Gustavsson et al., 2014). Bayesian modeling allowed us to include unsuccessful trials (i.e., trials in which the problem was not solved within 30 min) into the data set in the form of censored data (Young and Crumer, 2018; see also Cooper et al., 2019). The censored data points in our analyses were modeled as if each latency was at least 30 min, even though the actual time is unknowable. For each lizard, we estimated its initial solving latency (intercept) and the decrease in latency as trials progressed (slope). Statistical analyses were conducted using R software (R Core Team, 2019); the code used is available (https://www.copeiajournal.org/ch-18-119).

RESULTS

All four varanid lizards solved the puzzle device in almost all of the eight trials; *V. mertensi*–2 had one unsuccessful attempt (Trial 1) and *V. prasinus*–1 did not initiate an attempt in one trial (Trial 5). Latencies observed were comparable to latencies recorded in the final trials of the previous data set concluded nearly 2 yr prior (Cooper et al., 2019; Fig. 2). The individual *Heloderma charlesbogerti* retested in this study did not successfully complete any trials, a result also consistent with the
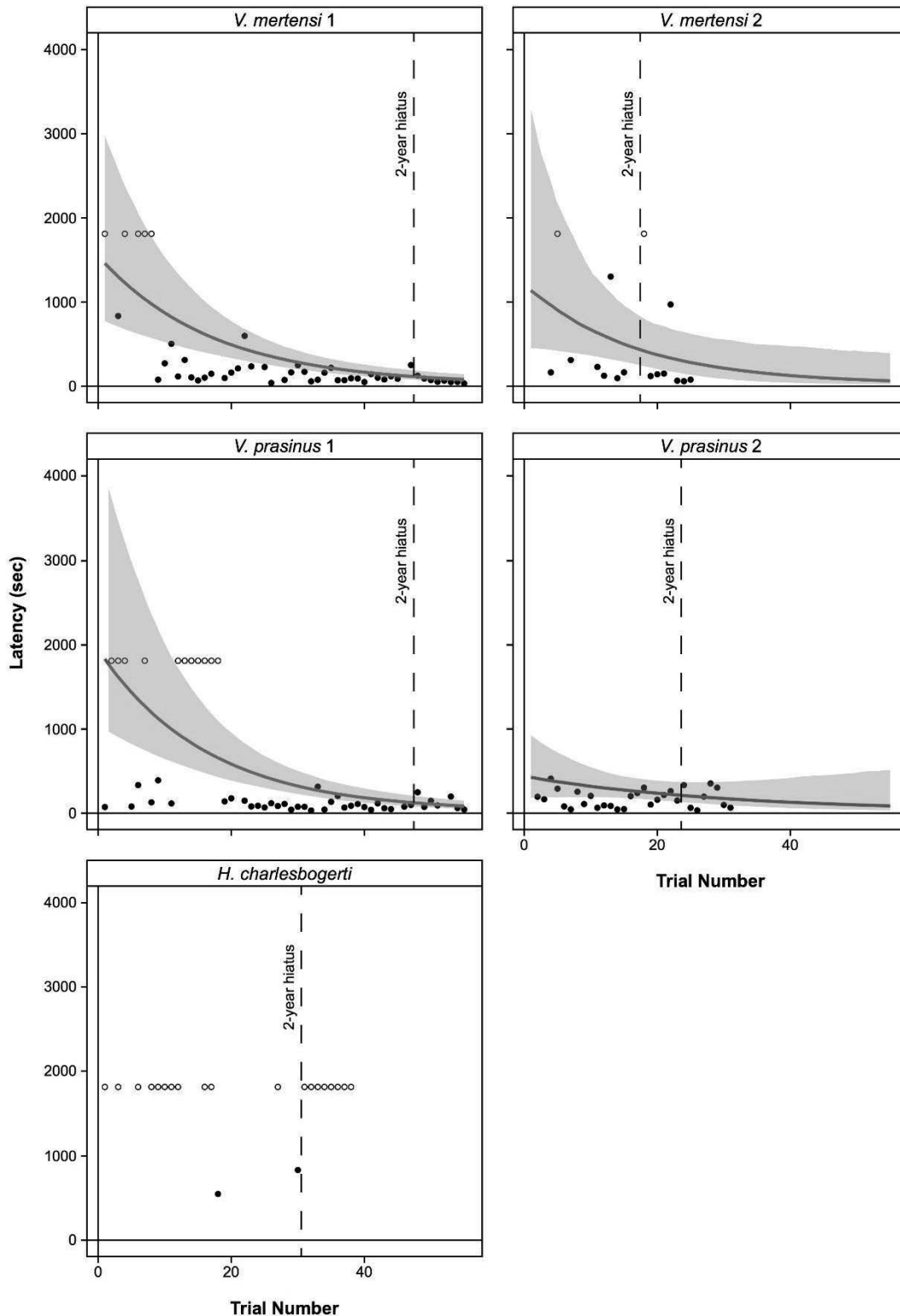
FIG. 2. Latency to solve the foraging puzzle for each lizard. Each plot displays the individual's combined latency results from both the previous (Cooper et al. 2019) and present experiment with dotted vertical lines marking the 20-mo hiatus. Solid circles = solved trials, open circles = censored data where the individual did not solve the foraging puzzle within the 30-min trial period, and the solid lines = the Bayesian model fit with 95% credible intervals (shaded regions). The y intercepts estimate the initial latencies of each lizard's naïve attempt to solve the puzzle in 2017, and the slope is the decrease in latency as trials progressed. The model fit for *H. charlesbogerti* is not shown because it is outside the plotted area.

previous data. For each varanid lizard, the combined data set from both the original and posthiatus trials were well described by the Bayesian model (Fig. 2). The analysis revealed that there was strong evidence of learning (negative slopes) for the

varanid lizards, but not for the beaded lizard. For all lizards, the most likely slope value was negative, although there were varying degrees of uncertainty in the slope estimates. Overall, the estimated slope was −0.10 with a 95% credible interval of

TABLE 1. Lognormal transformed regression equations for each lizard (*Varanus, Heloderma*) from both the previous and current experiment. A Bayesian approach for multilevel modeling over repeated measures with censoring was used to calculate the regression equations from this experiment.

Year	Lizard	Intercept	95% credible interval	Slope	95% credible interval
2017	All lizards combined	6.74	[4.84, 8.84]	0.061	[−0.130, −0.002]
	V. prasinus–1	7.14	[6.45, 7.89]	0.080	[−0.106, −0.055]
	V. prasinus–2	5.12	[4.08, 6.07]	0.028	[−0.091, 0.047]
	V. mertensi–1	6.66	[5.96, 7.39]	0.063	[−0.089, −0.038]
	V. mertensi–2	6.41	[5.20, 7.80]	0.074	[−0.191, 0.023]
	H. charlesbogerti	9.51	[7.89, 11.78]	0.069	[−0.178, 0.015]
2019	All lizards combined	6.30	[4.76, 8.14]	−0.10	[−0.32, 0.20]
	V. prasinus–1	5.31	[4.07, 6.50]	−0.20	[−0.44, 0.036]
	V. prasinus–2	5.17	[3.86, 6.40]	−0.11	[−0.34, 0.15]
	V. mertensi–1	4.84	[3.60, 6.10]	−0.24	[−0.50, −0.0091]
	V. mertensi–2	6.22	[4.98, 7.63]	−0.26	[−0.54, −0.033]
	H. charlesbogerti	9.53	[5.58, 15.15]	0.28	[−0.40, 2.00]

−0.32 to 0.20; the intercept was 6.30 (Table 1). Excluding the beaded lizard that failed to engage with the device in the posthiatus trials produced essentially the same results, with an estimated slope of −0.14 with a 95% credible interval of −0.32 to 0.10; the intercept was 5.51.

DISCUSSION

After learning a task, the memory of a learned behavior may be consolidated into long-term memory, but over time becomes susceptible to destruction (Sweatt, 2010; Sandrini et al., 2015). Our study demonstrates that the memory to solve a foraging puzzle device remained intact in the included varanid lizards after a 20-mo hiatus in exposures. In long-term memory, upon re-exposure, an individual can retrieve the consolidated memory and re-establish the learned behavior (Finn, 2017). Our results suggest that procedural memory was evident in the varanid lizards, as their initial re-exposure latencies were lower than their original naïve latencies and showed continued decline toward a minimum latency in fewer trials than before the hiatus (Fig. 2).

The time frame of our study represents 22–30% of the lives of these individual lizards at the time of the study; we consider this to indicate long-term memory. For comparison, Atlantic Bottlenose Dolphins (*Tursiops truncatus*) have exhibited social recognition of individual whistle communications for at least 20 yr, encompassing approximately at least 75% and possibly an entire lifetime (Bruck, 2013; Jaakkola and Willis, 2019). Garden Warblers (*Sylvia borin*) returned to the "correct" experimental room, which contained a food source during initial exposure, after up to 1 yr after testing (Mettke-Hoffmann and Gwinner, 2003), or about 15% of their life span (Payevsky and Shapoval, 2000).

The failure by the phylogenetic outgroup species, *H. charlesbogerti*, to learn to solve the device in both pre- and posthiatus trials supports the suggestions by Burghardt (2013) and others that monitor lizards may have derived improved cognitive abilities relative to other squamates. Based on reviews of studies that addressed varanid cognition and learning across different species and methods, Burghardt (2013) opined that "these animals seem to be in a different psychological place than other lizards" (p. 292). However, we do not suggest that our results indicate absence of the ability to form procedural memories in beaded lizards, as this is a single task and other experimental approaches may well find such abilities in these lizards.

As these results make clear, a broader exploration of cognition in varanid lizards and other squamates will expand our understanding of the evolution of behavioral plasticity and cognition within the megadiverse squamate clade that has been largely neglected in cognitive studies (Wilkinson and Huber, 2012; Burghardt, 2013). Part of the reason for this dearth of studies is undoubtedly practical; most cognitive studies require controlled experiments, which typically require captive conditions. Many of these species are rarely maintained in captivity or are, as in our case, available in small sample sizes. However, as work in other species in captivity (e.g., primates, cetaceans, elephants) has shown, small sample sizes can be informative simply to help us to understand the extent of a species' abilities (Matsuzawa, 1985a,b; Reiss and Marino, 2001; Plotnik et al., 2006).

The results of Cooper et al. (2019) and the present study document procedural memory at two different time scales in monitor lizards. In consideration of the small body of cognitive work that has been done with these lizards, we posit that the varanid clade can represent model organisms around which to develop a research program on comparative cognition. For example, the group would seem ideal to study the extents of other forms of memory (e.g., working memory or episodic memory). The sheer diversity of Squamata is at once both the source of interesting comparative questions and a formidable diversity of challenges, but all contained in a conceptually clear monophyletic framework. With body forms as distinct as snakes or chameleons, and with sensory abilities distributed along continua that include organisms who are blind (e.g., amphisbaenians), possess infrared vision (e.g., pitvipers), are heavily olfactorily-oriented (e.g., beaded lizards), or are heavily reliant on both scent and vision (e.g., monitor lizards), one can study the evolution of behavior, cognition, and sensory modalities in a monophyletic group with widely diverse ecological, behavioral, and anatomical realities. By comparison, all birds are predominantly visually oriented, active foragers. All mammals are active foragers, with important differences in sensory modalities.

As an example, our work did not necessarily demonstrate lack of procedural memory in our outgroup, *Heloderma*, but may suggest that the different ecologies and sensory modalities of helodermatids need to be better considered in order to assess their memory and cognition. Roth et al. (2019) emphasized the challenge of finding ecologically relevant means of measuring and comparing cognition across diverse animals, as well as caution in the interpretation of negative results. Roth et al.

(2019) reviewed the benefits and ongoing challenges—such as unclear homology of portions of the brain (Striedter, 2015)—of such an approach at a broader phylogenetic level. With respect to the nonmonophyletic approach of Roth et al. (2019), we emphasize the conceptual strength of employing monophyletic groups, as was nicely done by Krochmal et al. (2018) in a study of learning within a monophyletic group of snakes.

It is our hope that the growing body of evidence regarding the cognitive abilities of monitor lizards will encourage the development of a framework for comparative studies within Squamata. The group provides an opportunity to study evolution of cognition across extreme levels of diversity in form, function, physiology, and behavior, and a solid base of cognitive information from this clade will better allow careful comparisons to other vertebrate clades.

Literature Cited

Adams-Hunt, M. M., and L. F. Jacobs. 2007 Cognition for foraging. Pp. 105–138 in D. W. Stephens, J. S. Brown, and R. C. Ydenberg (Eds.), Foraging: Behavior and Ecology. University of Chicago Press, USA.

Auffenberg, W. 1981. Behavioral Ecology of the Komodo Monitor. University Press of Florida, USA.

———. 1988. Gray's Monitor Lizard. University Press of Florida, USA.

———. 1994. The Bengal Monitor. University Press of Florida, USA.

Bellairs, A. 1970. The Life of Reptiles, Vol. II. Universe Books, USA.

Bruck, J. N. 2013. Decades-long social memory in bottlenose dolphins. Proceedings of the Royal Society B 280:20131726, doi:https://doi.org/10.1098/rspb.2013.1726.

Burghardt, G. M. 2013. Environmental enrichment and cognitive complexity in reptiles and amphibians: concepts, review, and implications for captive populations. Applied Animal Behavioral Science 147:286–298, doi:http://dx.doi.org/10.1016/j.applanim.2013.04.013.

Burghardt, G., D. Chiszar, J. Murphy, J. Romano, T. Walsh, and J. Manrod. 2002. Behavioral complexity, behavioral development, and play. Pp. 78–117 in J. Murphy, C. Ciofi, C. De La Panouse, and T. Walsh (eds.), Komodo Dragons: Biology and Conservation, Smithsonian Press, USA.

Cooper, T. L., A. Liew, G. Andrle, E. Cafritz, H. Dallas, T. Niesen, E. Slater, J. Stockert, T. Vold, M. Young, and J. R. Mendelson, III. 2019. Latency in problem solving as evidence for learning in varanid and helodermatid lizards, with comments on foraging techniques. Copeia 107:78–84, doi:https://doi.org/10.1643/CH-18-119.

Davis, K. M., and G. M. Burghardt. 2007. Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). Behavioral Processes 75:225–230, doi:https://doi.org/10.1016/j.beproc.2007.02.021.

Day, L. B, D. Crew, and W. Wilczynski. 1999. Spatial and reversal learning in congeneric lizards with different foraging strategies. Animal Behavior 57:393–407, doi:https://doi.org/10.1006/anbe.1998.1007.

Finn, B. 2017. A framework of episodic updating: an account of memory updating after retrieval. Pp. 173–211 in B. Ross (ed.), Psychology of Learning and Motivation. Elsevier, USA.

Gaalema, D. 2011 Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). Journal of Comparative Psychology 125:246–249, doi:10.1037/a0023148.

Greene, H. W. 1994. Homology and behavioral repertoires. Pp. 369–391 in B. K. Hall (Ed.), Homology: The Hierarchical Basis of Comparative Biology. Academic Press, USA.

Gustavsson, S., B. Fagerberg, G. Sallsten, and E. M. Andersson. 2014. Regression models for log-normal data: comparing different methods for quantifying the association between abdominal adiposity and biomarkers of inflammation and insulin resistance. International Journal of Environmental Research and Public Health 11:3521–3539.

Harvey, P. H., and M. D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, United Kingdom.

Jaakkola, K., and K. Willis. 2019. How long do dolphins live? Survival rates and life expectancies for bottlenose dolphins in zoological facilities vs. wild populations. Marine Mammal Science 000:1–20, doi:https://doi.org/10.1111/mms.12601.

Krochmal, A. R., A. J. Place, T. J. LaDuc, and T. C. Roth. 2018. Phylogenetic patterns in learning and decision making in pit vipers (Viperidae: Crotalinae). Animal Behavior 145:117–123.

LaDage, L. D., T. C. Roth, A. M. Cerjanic, B. Sinervo, and V. V. Pravosudov. 2012. Spatial memory: are lizards really deficient? Biology Letters 8:939–941, doi:https://doi.org/10.1098/rsbl.2012.0527.

LaDage, L. D., T. E. Cobb Irvin, and V. A. Gould. 2017. Assessing spatial learning and memory in small squamate reptiles. Journal of Visualized Experiments 119:55103, doi:https://doi.org/10.3791/55103.

Manrod, J. D., R. Hartdegen, and G. M. Burghardt. 2008. Rapid solving of a problem apparatus by juvenile black-throated monitor lizards (*Varanus albigularis albigularis*). Animal Cognition 11:267–273, doi:https://doi.org/10.1007/s10071-007-0109-0.

Matsuzawa, T. 1985a. Color naming and classification in a chimpanzee (*Pan troglodytes*). Journal of Human Evolution 14:283–291.

———. 1985b. Use of numbers by a chimpanzee. Nature 315:57–59.

Mendyk, R. W. 2015. Life expectancy and longevity of varanid lizards (Reptilia: Squamata: Varanidae) in North American zoos. Zoo Biology 34:139–152, doi: https://doi.org/10.1002/zoo.21195.

Mendyk, R. W., and H. G. Horn. 2011. Skilled forelimb movements and extractive foraging in the arboreal monitor lizard *Varanus beccarii* (Doria, 1874). Herpetological Review 42:343–349.

Mettke-Hoffmann, C., and E. Gwinner. 2003. Long-term memory for a life on the move. Proceedings of the National Academy of Sciences 100:5863–5866, doi:www.pnas.orgcgidoi10.1073pnas.1037505100.

Murray, E. A., S. P. Wise, and K. S. Graham. 2018. Representational specializations of the hippocampus in phylogenetic perspective. Neuroscience Letters 680:4–12.

Payevsky, V. A., and A. P. Shapoval. 2000. Age structure of passerine populations according to ringing results. Avian Ecology and Behavior 4:55–66.

Pianka, E., D. King, and R. A. King. 2004. Varanoid Lizards of the World. Indiana University Press, USA.

Plotnik, J. M., F. B. M. de Waal, and D. Reiss. 2006. Self-recognition in an Asian elephant. Proceedings of the National Academy of Sciences 103:17053–17057, doi:https://doi.org/10.1073/pnas.0608062103.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria. https://www.R-project.org/.

Reiss, D., and L. Marino. 2001. Self-recognition in the bottlenose dolphin: A case of cognitive convergence. Proceedings of the National Academy of Sciences 98:5937–5942.

Rodriguez, F., J. C. López, J. P. Vargas, C. Broglio, Y. Gómez, and C. Salas. 2002. Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. Brain Research Bulletin 57:499–503.

Roth, T. C., A. R. Krochmal, and L. D. LaDage. 2019. Reptilian cognition: a more complex picture via integration of neurological mechanisms, behavioral constraints, and evolutionary context. BioEssays 41:1900033, doi: https://doi.org/10.1002/bies.201900033.

Sandrini, M., L. Cohen, and N. Censor. 2015. Modulating reconsolidation: a link to causal systems-level dynamics of human memories. Trends in Cognitive Sciences 19:475–482, doi:https://doi.org/10.1016/j.tics.2015.06.002.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behavior 85, 1004–1011, doi:http://dx.doi.org/10.1016/j.anbehav.2012.12.031.

Soldati, F., O. H. Burman, E. A. John, T. W. Pike, and A. Wilkinson. 2017. Long-term memory of relative reward values. Biology Letters 13: 20160853.

Striedter, G. F. 2015. Evolution of the hippocampus in reptiles and birds. Journal of Comparative Neurology 524:496–517.

SWEATT, J. D. 2010. Rodent behavioral learning and memory models. Pp. 77–103 in J. D. Sweatt (ed.), Mechanisms of Memory, 2nd ed. Elsevier, UK.

SWEET, S. S. 1999. Spatial ecology of *Varanus glauerti* and *V. glebopalma* in northern Australia. Mertensiella 11:317–366.

———. 2007. Comparative spatial ecology of two small arboreal monitors in northern Australia. Mertensiella 16:378–402.

TOSCHES, M. A., T. M. YAMAWAKI, R. K. NAUMANN, A. A. JACOBI, G. TUSHEV, AND G. LAURENT. 2018. Evolution of pallium, hippocampus, and cortical cell types revealed by single-cell transcriptomics in reptiles. Science 360:881–888.

WILKINSON, A., AND L. HUBER. 2012. Cold-blooded cognition: reptilian cognitive abilities. Pp. 129–143 in T. K. Shackelford and J. Vonk (eds.), The Oxford Handbook of Comparative Evolutionary Psychology. Oxford University Press, UK.

WILKINSON A, K. KUENSTNER, J. MUELLER, AND L. HUBER. 2010. Social learning in a non-social reptile (*Geochelone carbonaria*). Biology Letters 6:614–616, doi:10.1098/rsbl.2010.0092.

YOUNG, M. E., AND A. CRUMER. 2018. Reaction times. Pp. 1–10 in J. Vonk and T. Shackelford, (eds.), Encyclopedia of Animal Cognition and Behavior. Springer Press, Switzerland.