# Taking the dragon by the horns: Towards a comprehensive study of learning in non-avian reptiles

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## Abstract

The field of comparative cognition has recently advanced towards a wider taxonomic approach evidenced by an increase in non-avian reptile learning studies. As a diverse group of animals, non-avian reptiles include squamates (lizards, snakes and amphisbaena), turtles, tuatara and crocodilians which vary greatly in their habitat, mating systems, feeding ecology, social structure, reproductive tactics and behaviour. Consequently, they provide new opportunities to study cognitive processes such as learning in novel contexts. Furthermore, their brain exhibits several prototypic features and neural architecture not found in other vertebrates. Our systematic review provides an up-to-date overview of the currently available data on learning in non-avian reptiles and ties the collected evidence together to form a comprehensive unit of knowledge. Non-avian reptiles show a diverse range of abilities from taste aversion, spatial and discrimination learning to non-symbolic quantity discrimination, behavioural flexibility, learning of novel foraging techniques and social learning. Our synthesis revealed several knowledge gaps and based on these shortcomings we want to direct attention towards seven research avenues which, we belief, will be of special interest in the near future. Taken together, research in the last 40 years has undoubtedly demonstrated non-avian reptiles’ capability for more than just instinctive reactions and basic cognition. With the appropriate methodology, this still young field of research will certainly advance greatly in the coming years.

*Keywords:* Cognition, learning processes, reptilia, systematic review, testudines

## Content

I. Introduction 5

II. A recap: 40 years of studying learning in reptiles 8

1. Avoiding aversive stimuli 8

2. Spatial cognition 10

3. Learning during foraging 14

4. Quality and quantity discrimination 15

5. Reacting to change 16

6. Solving novel problems 18

7. Social learning 19

8. Memory 22

III. Future directions 22

1. “Invader” smart reptiles 23

2. Spatial cognition in the context of sexual selection 23

3. Executive function 24

4. Innovative problem solving 24

5. Social learning in social reptiles 25

6. Cognition in ecologically relevant contexts 25

7. The reptile brain and cognition 26

IV. Conclusions 27

V. Acknowledgements 28

VI. Supporting information 28

VII. References 28

VIII. Appendix 42

## Introduction

Cognition, the process by which animals collect, store, manipulate and use information, plays a pivotal role in their everyday life when, for example, searching for food and shelter or avoiding predators. Hence, cognition is an important determinant of fitness (Shettleworth, 2009; Wright et al., 2010) and crucial when responding to change, promoting invasion success and for ecological niche expansion (Wright et al. 2010; Leal & Powell, 2012).

Contemporary animal cognition is moving towards a comprehensive comparative approach utilising a broader range of vertebrate and invertebrate species to test the generality of cognitive processes. Thus the number of learning studies testing non-avian reptiles, from here on called reptiles (including turtles, crocodilians, tuatara and squamates - lizards, snakes and caecilians), have increased within the last decade (Figure 1). A first account of reptile learning ability was compiled by Gordon Burghardt (1978) in his book section “Learning processes in Reptiles” describing the methods used and insights gained. Since the start of the 21st century, the field of reptile cognition has become more structured reflected in recent reviews by Wilkinson and Huber (2012) and Whiting and Noble (2018). A systematic review addressing the development since Burghardt (1978), is, however, missing as of yet.

Modern reptiles are the third most species rich group of vertebrates inhabiting a wide range of different habitats, showing diversity in mating systems (monogamy to polygynandry), feeding ecology, social structure (solitary to groups of many individuals), reproductive tactics (parthenogenesis, oviparity or viviparity) and differ substantially in behaviour (Whiting & While, 2017). For example, many reptiles exhibit oviparity without parental care representing a unique opportunity to study developmental effects on cognition not answerable using mammals or birds (Matsubara et al., 2017). Furthermore, most reptiles are precocial and the juvenile brain is much more developmentally advanced at birth compared to altricial species which should affect cognitive ability at an early age (Charvet & Striedter, 2011; Grand, 1992). Moreover, reptiles diverged from mammals about 280 million years ago (Macphail, 1982) and their brain exhibits several prototypic features (Nomura et al., 2013). Extant reptiles have, however, also experienced similar selective pressures as modern mammals since the split (Wilkinson & Huber, 2012). Expanding the taxonomic approach might give insight into a more prototypic vertebrate cognitive ability but can also help understand convergent evolution.

Our systematic literature search identified over 80 studies on reptile learning (Figure 1) not included in Burghardt (1978) testing abilities diverse as taste aversion, discrimination and learning flexibility, number competencies, spatial orientation and social information use. Although some of these studies have been included in previous work (e.g. Whiting & Noble, 2018; Wilkinson & Huber, 2012), they are important contributions and included here to give a full overview of the current knowledge. Our aim is to first, give a comprehensive overview of the research conducted over the last 40 years. Second, to link the gathered results and highlight methodological innovations and shortcomings and sections are therefore organised to link results from different species (some studies fall under more than one subheading). Lastly, we want to emphasise the importance of the ecological relevance in cognitive studies and give some directions for future research.

## A recap: 40 years of studying learning in reptiles

### Avoiding aversive stimuli

Animals need to know what to eat, when to hide and which threats to avoid. Importantly, avoiding toxic food with a noxious effect aids survival. Reptiles, like other animals, show taste aversion learning (e.g. Bernstein, 1999). Male green anoles (*Anolis carolinensis*), for example, can distinguish between neutral, bitter (coated in quinine hydrochloride) and sweet (coated in Equal®) tasting crickets (a coloured dot improved discriminability). Lizards rejected bitter prey but failed when the vomeronasal organ was blocked highlighting their reliance on olfactory cues (Stanger-Hall et al., 2001). Similarly, hatchling oriental garden lizards (*Calotes versicolor*) associated dish colour with prey taste. Independent cohorts of hatchlings received the same experience: non-painted dish – neutral taste, orange dish – sweet taste from sucrose and green dish – bitter taste from chloroquine phosphate. When confronted with the same combinations they avoided dishes in the colour previously containing bitter prey but attacked the same prey during a transposition to novel colour-taste combinations (Shanbhag et al., 2010). Furthermore, *Basiliskus vittatus*, B. *basiliscus*, *Eumeces schneideri* and *Eutropis multifasciata* avoided a novel food one week after lithium chloride (LiCl) injection (inducing sickness). A second novel control food, however, was accepted one week after a saline injection (Paradis & Cabanac, 2004). Likewise, Australian blue-tongue lizards (*Tiliqua scincoides scincoides* and *T. s. intermedia*) avoided cane toad sausages (*Rhinella marina*, a toxic invader) paired with a LiCl injection or mixed with LiCl seven weeks later. A control group treated with saline showed little to no aversion and both groups accepted sausages of reptile feed nine weeks after illness (Price-Rees et al., 2011). These studies highlight how bitter tastes or illness are quickly avoided after only a few encounters, which was also demonstrated in the wild. Bonaire island whiptail lizards (*Cnemidophorus murinus)* distinguished palatable (soaked in tomato juice) from unpalatable (soaked in quinine hydrochloride) sponges placed along their natural habitat based on visual (green - toxic versus red - sweet) and spatial (ground versus vegetation) cues (Schall, 2000). Furthermore, conditioned taste aversion can teach animals to avoid novel or invasive unpalatable pray. Hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*), for example, avoided freshly metamorphosed cane toads after training and were more likely to reject toads compared to naïve individuals (Somaweera et al., 2011). Contrary, populations of juvenile eastern fence lizards (*Sceloporus undulates*), either invaded by toxic fire ants or uninvaded, did not learn to avoid this toxic prey when given a choice between unpalatable fire ants and crickets but instead increased ant consumption over time (Robbins et al., 2013). Taken together, some species might be more apt to learn to avoid unpalatable or toxic prey; differences in methodology might account for some mixed results.

Undoubtedly, avoiding harmful food is important, escaping predators is, however, no less crucial for survival. In their natural habitat, curly-tailed lizards (*Leiocephalus schreibersii*) rapidly learnt to avoid capture. Females did so faster than males and after only one capture event (Marcellini & Jenssen, 1991). In male eastern fence lizardsescape behaviour was linked to corticosterone: compared to control animals, that showed increased flight initiation distance (FID) and decreased hiding time, males receiving a corticosterone blocker showed no change in these behaviours and no retention 24h later (Thaker et al., 2010). Moreover, little brown skinks (*Scincella lateralis*) used horizontal and vertical stripes to find a safe refuge but performed better when presented with vertical compared to horizontal lines, presumably because of the nature of sheltering sites which are at the base of trees (Paulissen, 2014). Lizards don’t just use pattern to choose a ‘safe’ refuge, they are similarly skilled using colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, escaped a simulated predator attack into a ‘safe’ refuge using location or colour (Chung et al., 2017). More lizards learnt when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang et al., 2018). Besides population effects, developmental conditions can also alter escape behaviour. Hatchling White’s skins (*Liopholis whitii*) whose mothers received a low resource treatment were more likely to escape into a ‘safe’ refuge compared to hatchlings from mothers receiving a high resource treatment (Munch et al., 2018a).

Similarly significant for survival is to avoid potentially harmful environmental conditions such as excessive heat or shock (Shettleworth, 2009). A group of brown anoles (*Anolis sagrei*), for example, learnt to lift their tail to avoid shock while a second group receiving a shock whenever group one was shocked did not. After cycloheximide injection (inhibiting protein synthesis) into the basal forebrain, however, lizards failed to show shock avoidance (Punzo, 1985). Furthermore, two out of three *Anolis grahami* avoided being pushed of their perch by leaving the perch after hearing a tone (Rothblum, Watkins, & Jenssen, 1979).

These examples provide evidence of the cues reptiles are able to learn to avoid toxic foods, dangerous predators or adverse conditions. Although some mechanisms were identified, much is still unexplained. Especially, why some species quickly avoid noxious food while others don’t is largely unexplored. Furthermore, investigations into how species differ when successfully inhabiting urban environments might advance measures to protect vulnerable species within cities. Both present a potentially fruitful avenue for future research.

### Spatial cognition

Navigating the environment is essential when searching or returning for food, shelter or mating partners. Resources and conspecifics are rarely found in the same location and efficiently navigating as opposed to randomly moving through space is accomplished through mechanisms like remembering landmarks, path integration or cognitive maps (Shettleworth, 2009). Mazes are primarily used to test animals spatial abilities. They are easily constructed, modified and applied to many different species. Examples are the radial arm maze, made of eight arms, or plus- or X-shaped mazes with four arms. Red footed tortoise (*Chelonoidis carbonaria*), for instance, learnt to avoid previously food depleted arms in the radial arm maze adopting a response-based strategy dependant on different spatial cues (Wilkinson et al., 2007; Wilkinson et al., 2009). Similarly, male jewelled lizards (*Timon lepidus*) successfully navigated the same maze preferentially entering arms next to the last visited arm (Mueller-Paul et al., 2012). Pond sliders (*Trachemys scripta*), were able to either use distal, extra-maze cues to find a goal in a plus-shaped maze or a single intra maze cue even when starting from a new location (Lopez et al., 2000). After lesions to the medial cortex, however, only cue trained turtles (using a single intra maze cue) learnt during a spatial reversal while turtles using a map like strategy (based on distal cues) were unable to stop responding to the previously correct location implicating the medial cortex in map representation and inhibition (Lopez et al., 2003a). Furthermore, during spatial learning in an X-maze, lesions to the dorsal cortex and basal forebrain of painted turtles (*Chrysemys picta*) impaired memory when relearning to navigate the same maze (Petrillo et al., 1994).

The (Morris) water maze; a water filled pool containing a hidden goal platform, is another common spatial task. In a modified version with visible feeders, pond sliders used either a single local cue to guide them to the goal or a map based strategy based on distal, extra-maze cues (Lopez et al., 2001). Lesions to the medial cortex selectively impaired turtles using a map strategy affecting memory of the cognitive map when relearning to find the hidden food and when distal cues were partly concealed (Lopez et al., 2003b). Furthermore, male Italian wall lizards (*Podarcis sicula*) located a hidden goal platform in a water maze using a sun compass; covering the parietal eye (a photoreceptive third eye found on the head) revealed that it was essential for successful navigation (Foa et al., 2009).

Some studies use an open arena to test animals on their spatial learning ability. Sleepy lizards (*Tiliqua rugose*), for instance, preferred the location of familiar refuge sites within their enclosure. When brightness or shape were associated with the refuge, lizards preferred the familiar signal no matter its’ location (Zuri & Bull, 2000). For little brown skinks, 48h of experience with an arena was crucial to escaped under a randomly chosen correct refuge, without experience, they did not learn within the two days of testing (Paulissen, 2008). Furthermore, male Australian water skinks (*Eulamprus quoyii*) learnt to escape into a ‘safe’ refuge avoiding an ‘unsafe’ hide based on spatial location (Noble et al., 2014) and male *Acanthodactylus boskianus* and A. *scutellatus*, differing in foraging strategies, both learnt to find a heated goal rock in a round arena. Unexpectedly, no difference in latency or spatial learning strategy were found between these species. When tested with a single local cue, however, the active forager, A. *boskianus*, took longer to learn pointing towards subtle species specific differences in spatial orientation (Day et al., 1999). In a related study, malewhiptail lizards (*Cnemidophorus inornatus*) navigated the same arena using no apparent spatial strategy. Lesions to the dorsal cortex slowed learning while damage to the medial cortex greatly impaired search efficiency by increasing time moving along the edge of the maze (Day et al., 2001).

A special case of a circular arena is the Barnes maze, a round open space with 10 holes equidistant along the edge. Male side-blotched lizards (*Uta stansburiana*) used extra-maze spatial cues to find the goal hole even after 180° rotation (LaDage et al., 2012). Likewise, a group of juvenile corn snakes (*Pantherophis guttatus*) successfully navigated the Barnes maze decreasing distance travelled and errors below chance on all trials (Holtzman et al., 1999). Whereas only half of a group of juvenile pythons (*Antaresia maculosa*) learnt to find the goal hole in the same task. Pythons did not decrease latency and no specific learning strategy could be identified. While corn snakes are terrestrial, pythons are usually arboreal. Habitat preference might explain these different findings (Stone et al., 2000).

Two studies investigated spatial learning in a naturalistic setting. Using radiotracking, only residential wild painted turtles (with knowledge of the habitat) used specific routes to find water, translocated animals (with no knowledge of the habitat) failed this task. Experience especially during the first few years of life proved crucial for these turtles to navigate successfully and find a water body. Follow-up experiments highlighted the importance of UV vision during navigation, while olfaction was not important (Roth & Krochmal, 2015). Furthermore, male eastern water skinks located a ‘safe’ refuge out of three possible hides within a semi-natural outdoor enclosure (Noble et al., 2012) which spatial strategy lizards’ used, however, was not assessed.

Conditions experienced during development can also affect spatial learning, potentially influencing brain development. For example, hatchling velvet geckos (*Amalosia lesueurii*) incubated at ‘cold’ temperatures were faster spatial learners compared to ‘hot’ incubated geckos. Furthermore, after release at their mothers capture site, hatchlings with higher learning scores survived longer indicating a lasting effect on survival (Dayananda & Webb, 2017). Contrary, hatchling three lined skinks (*Bassiana duperreyi*) incubated under ‘hot’ conditions earned higher learning scores compared to ‘cold’ incubated lizards (Amiel & Shine, 2012). Furthermore, hypoxic conditions during incubation decreased hatchling *Eremias argus* probability to located a save refuge compared to both normoxic and hyperoxic animals (Sun et al., 2014). Finally, no effect of rearing environment (social or non-social) after birth was found in juvenile tree skinks solving a vertical maze (Riley et al., 2016). Little is known about how incubation treatments or rearing environment alters the reptilian brain. The examples above do, however, demonstrate these treatments prolonged influence on behaviour and survival.

Reptiles possess a range of spatial abilities using response based strategies to avoid depleted food patches, map like representations of the environment to find either food or shelter, they can use landmarks or beacons (single local cues) to guide them and use the sun to navigate. Evidence indicates that previous experience with a habitat can be crucial for successful navigation and that species might show nuanced differences in their use of spatial information. Importantly, research in snakes demonstrated the importance of ecology in task design. Furthermore, in turtles the basal forebrain, the dorsal and medial cortex store spatial information; in lizards, the involvement of the dorsal and medial cortex is less clear. Finally, incubation environment affects spatial learning although differently in different species. Together, we still know little about spatial learning in reptiles. Especially how sex, spatial ecology or foraging strategy affect navigation could be an interesting and productive research focus in the future.

### Learning during foraging

While foraging it is important to discriminate food sources or patches providing food from those already depleted. To save time and energy when searching, animals need to recognise cues associated with food availability (optimal foraging theory, Pyke, 1984). During discrimination learning, animals are confronted with at least two stimulus choices (such as two colours, patterns or light frequencies), one rewarded and the other not. Florida red-bellied cooters (*Pseudemys nelsoni*), for instance, successfully discriminated between two bottles based on a visible food pellet or bottle-brightness (black and white). Pond sliders too, learnt the same black and white discrimination (Davis & Burghardt, 2007; 2012). Using coloured paddles, common box turtles (*Terrapene carolina*) successfully learnt and transferred a rule (lighter or darker) to novel stimuli of different colours (blue and green; Leighty et al., 2013), and similarly, rough-necked monitors (*Varanus rudicollis*) and a Comodo dragon (*Varanus komodoensis*) used paddle brightness (black and white) to obtain a food reward (Gaalema, 2007; 2011). Finally, male eastern water skinks relied on colour to solve a three-choice discrimination; no correlation was found between successful learning in the colour discrimination and a previously tested spatial learning task.

Reptiles can also be trained to use light stimuli such as coloured light bulbs to find food. Wild crested anoles (*Anolis cristatellus*) first received food whenever a yellow or green bulb was raised and later preferred the trained colour during a simultaneous two-choice test (Shafir, 1995). Tuataras were able to discriminate between a trained and three different flicker frequencies in a simultaneous two-choice test (Woo et al., 2009) and painted turtles learnt to rely on illuminated response keys to receive a reward. Turtles showed impaired performance during negative patterning (testing for configural association learning of compound stimuli) after blocking of nitric oxide and acetylcholine in the dorsal cortex. While blocking nitric oxide affected responses towards single elements, blocking acetylcholine affected responses towards the non-reinforced compound stimulus but discrimination learning was not affected (Powers et al., 2009; Yeh & Powers, 2005). Hence, reptiles can use many visual stimuli to find food while avoiding cues indicating no food, however, not all experiments were successful. Invasive delicate skinks and non-invasive common garden skinks (*L. guachenoti)* failed to learn which arm in a Y-maze setup (one arm painted solid orange or blue, the other in orange or blue stripes) provided a reward; common garden skinks, however, reached the maze end faster (Bezzina et al., 2014).

Using these simple cues, reptiles can be trained to discriminate visual stimuli using a range of methods. With some exceptions, research in reptile discrimination learning only test one or two sequential discrimination stages, however, some more sophisticated tests (e.g. negative patterning and rule transfer) demonstrated that reptiles possess abilities previously unattributed to this group of animals. Furthermore, we still know little about how different cognitive abilities are processed in the reptile brain; most research was done in turtles. The reptile brain possesses prototypic features and is missing a sophisticated cerebral cortex. Gaining insight into how cognition is mapped onto the reptilian brain might lead to a better understanding of the mechanisms underlying brain evolution (Nomura et al., 2013).

### Quality and quantity discrimination

Judging non-symbolic quality and quantity are important capabilities during foraging, mate choice or when making decisions joining a group (e.g. shoal choice in fish). Previously, a number of species demonstrated numerical abilities (e.g. Agrillo & Bisazza, 2018; Benson-Amram et al., 2018; Shettleworth, 2009) and reptiles are no exception. For example, after associating a stimulus with a specific reward quality or quantity, red footed tortoises showed a preference for preferred foods and larger quantities during the simultaneous presentation of two stimuli differing in value (Soldati et al., 2017). The speed with which Chinese pond turtles (*Mauremys reevesii*) moved down a runway was also contingent on the magnitude of reward provided at the end. Turtles receiving 24 pellets each trial moved faster than turtles receiving only two pellets. During extinction trials, with no food present, animals previously receiving large quantities took longer to extinguish responding than animals previously trained with less reward (Papini & Ishida, 1994). Furthermore, Italian wall lizards discriminate between 1 versus 4 (N = 6/10) and 2 versus 4 (N = 1/6) but not between 2 versus 3 yellow disks and none were able to discriminate between two differently sized disks (ration of 0.25; Petrazzini et al., 2018). According to Weber’s Law a 0.25 ration between stimuli might have been too small for the lizards to discriminate (Agrillo & Bisazza, 2014; Ferrigno & Cantlon, 2017). These studies demonstrate that reptiles have a sense of reward quality, size and quantity. Artificial or naturalistic stimuli might be used to test for numerosity, both, however, pose some benefits and limitations (for further reading see Agrillo & Bisazza, 2014). The pool of evidence on numerical abilities in reptiles is still small and we want to encourage research in the future to mitigate this paucity.

### Reacting to change

Flexibly responding to environmental stimuli and adapting to change quickly is important for survival especially in unpredictable environments (Tello-Ramos et al., 2018). Behavioural flexibility, the ability to adjust to environmental variation by adapting attention and behaviour or using existing skills to solve novel problems, can be measured through different tests. One test is reversal learning, when a previously established stimulus-reward relationship changes (Brown & Tait, 2015). Another is attentional set-formation and shift, during which an animal is first trained to recognise an attentional set (a rewarded stimulus set) that is later shifted (to a stimulus in a different set, e.g. a second, formerly irrelevant dimension; Brown & Tait, 2015). Furthermore, innovation frequency or problem solving skill might also represent behavioural (or cognitive) flexibility (Auersperg et al., 2014).

Discrimination reversals are a common test used in reptiles applicable in different contexts (e.g. foraging or escape behaviour) and with various stimuli (e.g. spatial, visual or olfactory) while attentional set-shifting has only recently be adopted for reptile cognitive studies. Chinese pond turtles, for instance, reversed a simple left/ right discrimination; animals that were overtrained on the initial discrimination for an additional 100 trials, however, reversed slower (Ishida & Papini, 1997). Eastern water skinks learnt to locate a ‘safe’ refuge to escape an attack even after a spatial reversal in the lab (Noble et al., 2014) and in semi-natural conditions (Noble et al., 2012). Furthermore, whiptail lizards’ avoided a heat lamp using features (colour, brightness or pattern) or the location of a ‘safe’ refuge in a reversal; spatial cues, however, were more salient than visual cues during acquisition but not during reversals (Day et al., 2003). Male rough-necked monitors and one Comodo dragon increased performance during a serial reversal (Gaalema, 2007; 2011) and red footed tortoises (*Chelonoidis carbonaria*) transferred knowledge about a food patch (left/ right food bowl) acquired on the touchscreen to a real life setup but did not transfer knowledge about a reversal trained on a real life set up back to the touchscreen (Mueller-Paul et al., 2014). Tree skinks (*Egernia striolata*) were the first lizard species to be tested using an attentional intra-dimensional/ extra-dimensional (ID/ED) set-shifting approach. Unexpectedly, lizards did not establish an attentional set but performed each set of two stages (discrimination and reversal of one stimulus pair) as if facing a new problem. Skinks, however, reversed four discriminations showing behavioural flexibility (Szabo et al., 2018).

Studies implicated the involvement of different brain areas during discrimination and reversal learning. The core nucleus, dorsal cortex and parts of the forebrain of the painted turtle process visual stimuli. Lesions to these regions slowed acquisition, reversals and extra-dimensional shifts from colour to pattern, whereas damage to the medial cortex had no impact (Blau & Powers, 1989; Cranney & Powers, 1983; Grisham & Powers, 1989; 1990; Reiner & Powers, 1980; 1983). Furthermore, in European legless lizards (*Pseudopus apodus*), damage to the hippocampus and DVR (dorsal ventricular ridge) affected reversal performance (distinguishing between a triangle and a circle); both lesion groups took longer to learn compared to normal lizards but hippocampal lesions affect inhibition while lesions to the DVR affect visual processing (Ivazov, 1983). Moreover, in hatchling three lined skinks, incubation treatment (‘hot’ versus ‘cold’) affected discrimination of lid colour; only ‘hot’ incubated lizards learnt the given tasks (Clark et al., 2014) indicating an effect of temperature on brain development, as to how, however, has not yet been studied.

A comparative approach testing multiple species with the same methodology can reveal subtle learning differences. A comparison between three Anole species (A. *evermanni*, A. *cristatellus* and A. *pulchellus*) revealed less behavioural flexibility in a reversal task in *A.* *cristatellus* compared to A. *evermanni* and A. *pulchellus*. Differences were attributed to neophobia but sample sizes were small (Leal & Powell, 2012; Powell, 2012). Similarly, *Acanthodactylus* *boskianus*, an active forager learnt faster during reversals applying the fork method (one spine holding the reward while the second spine providing a visual cue) compared to *A. scutellatus*, a sit-and-wait forager. Inhibition is crucial in reversal learning; active foraging might require better inhibitory skill to inspection prey before striking (Day et al., 1999).

The gathered evidence demonstrates behavioural flexibility in reptiles. In turtles, the medial cortex is involved in visual processing and in a lizard lesions to the hippocampus and DVR impaired reversal learning, albeit differently. Interestingly, incubation temperature affected hatchling learning, a promising future research avenue especially in the context of climate change. Furthermore, behavioural flexibility might only be adaptive for certain hunting strategies (Day et al., 1999) or ecological conditions (Tello-Ramos et al., 2018). A broad taxonomic approach comparing species differing in social complexity, habitat preference, diet or hunting strategy could improve our understanding of behavioural flexibility and its’ fitness consequences.

### Solving novel problems

Some species are well known to be good problem-solvers. New Caledonian crows (*Corvus moneduloides*) bending wires into hooks to reach a reward (Weir et al., 2002), or rats (*Rattus rattus*) developing a new technique to feed on pine cones when little other food is available (Zohar & Terkel, 1991) are just two examples of innovation and problem solving skill. Reptiles, as well, can learn novel foraging techniques. Painted turtles and sub-adult Burmese pythons (*Python bivittatus*), for example, both learnt to push response keys (Blau & Powers, 1989; Cranney & Powers, 1983; Emer et al., 2015; Grisham & Powers, 1989; 1990; Powers et al., 2009; Reiner & Schade Powers, 1978; Reiner & Powers, 1980; 1983; Yeh & Powers, 2005) and seven different studies trained lizards to remove lids from wells for a reward. *Anolis evermanni*, A. *pulchellus and A. cristatellus* learnt lid removing, *A. cristatellus,* however, were less successful compared to the other two species. Although *A. cristatellus* is invasive which was linked to increased flexibility (Sol et al., 2002), individuals exhibited greater neophobia, a possible explanation for low performance (Leal, & Powell, 2012; Powell, 2012). Hatchling three lined skinks also learnt lid removal, however, only ‘hot’ incubated lizards acquired this behaviour (Clark et al., 2014). Furthermore, both water skinks and tree skinks removed lids but neither age (young and old; Noble et al., 2014) nor rearing environment (social or solitary; Riley et al., 2018) affected performance, respectively. Moreover, spatial learning proficiency did not predict lid opening ability in water skinks (Qi et al., 2018) and finally, Italian wall lizards and a closely related specie *P. bocagei* learnt the same technique. Although training procedures were used, these are examples of reptiles solving a novel problem. Adding to lid opening and pressing response keys, Florida red-bellied cooters and pond sliders both exited water to climb a platform and tip bottles for food which can also be interpreted as a novel foraging technique (Davis & Burghardt, 2007; 2011, 2012). Only a single study attempted to test a reptile on a puzzle box task. Black-throated monitors (*Varanus albigularis albigularis*) opened a plastic tube to retrieve a reward within 10 minutes of the first presentation and even solved this novel task faster during the second and third trial (Manrod et al., 2008). Little is still known about reptiles capabilities in acquiring and/ or innovating novel foraging techniques. Further studying these innovative problem solvers could prove a fruitful undertaking in the context of invasion and range expansion. Moreover, a large comparative study in 39 carnivores revealed a significant relationship between relative brain size and problem solving ability on a puzzle box (Bendon-Amram et al., 2016), the relationship between brain size and cognitive ability in reptiles, however, is as of yet unexplored.

### Social learning

Social learning refers to learning from other individuals. These might be conspecifics, from the same species, or heterospecifics, from a different species (Shettleworth, 2009). Previous research focused mainly on socially aggregating animals (Wilkinson & Huber, 2012), much less is known about less social species’ social information use. We know little about reptiles’ social structure and even less about their social organisation (Whiting & While, 2017), however, recent work showed that even ‘unsocial’ reptiles can learn from their conspecifics (Doody et al., 2013).

Solitary living red footed tortoises were the first reptile species to show social learning in a detour task (Wilkinson et al., 2010). Turtles observing a demonstrator walking around a barrier learnt to detour for a reward, while a control group receiving no demonstration did not. During follow-up experiments observers generalised to novel barriers (inverted V- and U-shaped) being more successful than control turtles (Wilkinson & Huber, 2012). Furthermore, solitary bearded dragons (*Pogona vitticeps)* opened a sliding door in the same direction as a demonstrator after watching a video of a conspecifics performance. A control group watching a ghost control (door opening by itself) did not learn indicating some involvement of socially facilitated enhancement (Kis et al., 2015). Interestingly, ‘cold’ incubated hatchling bearded dragons opened the door faster than ‘hot’ incubated lizards. There was, however, no significant difference between groups in the number of door openings (Siviter et al., 2017). Moreover, Florida red-bellied cooters matched the choice of a demonstrator during a brightness discrimination demonstrating stimulus enhancement (Davis & Burghardt, 2011). Thence social group living is not a prerequisite for social learning. As a shortcut towards the acquisition of new information it is beneficial even for non-social animals by avoiding costly trial-and-error learning and saving time and energy (Galef & Laland, 2005).

The relationship between individuals and factors such as age or sex can affect the probability with which animals employ socially provided information (Galef & Laland, 2005). In water skinks, age and dominance status predicted if lizards learnt a two-choice discrimination from a conspecific. Lizards selected the correct out of two coloured lids with and without a demonstration, young males, however, learnt faster than controls while old lizards did not (Noble et al., 2014). Furthermore, dominant observers learnt faster than subordinate observers during task acquisition but not during reversals (Kar et al., 2017). Water skinks are often found in high densities around water bodies (Cogger, 2014); socially provided information is therefore readily available.

Although most reptiles are considered solitary, some Australian skinks exhibit social group living (Whiting & While, 2017). In monogamous White’s skinks, familiarity improved social information use during reversal learning but not during acquisition. Three treatment groups were tested: Individuals observing their mating partner, an unfamiliar conspecific, or a non-demonstrator. Lizards observing their mate reversed faster than controls (Munch et al., 2018b). Reversals might be more challenging and social information more valuable for this task. Contrary juvenile tree skinks, also a monogamous species, did not use information provided by an adult in a similar discrimination task. Furthermore, rearing treatment (social or solitary) did not affect discrimination or reversal learning (Riley et al., 2018). Although tree skink families stay together for at least one season (Whiting & While, 2017) and juveniles have opportunity to learn from parents, learning from any adult might be less important. Using parents as demonstrators might have led to different result.

Typically, animals are tested with conspecific demonstrators but it can also be beneficial to learn from heterospecifics. Accordingly, observer Italian wall lizards made less errors than individual learners in a colour discrimination when provided with information from a conspecific or a heterospecific species (*Podarcis bocagei*). Wall lizards are highly invasive and these results suggest a role for social learning when invading new habitats (Damas-Moreira et al., 2018).

The only non-lab study was conducted on wild *Podarcis lilfordi.* Lizards were presented with a choice between food with and without conspecifics (including static copper models). Animals preferred locations with conspecifics present showing social enhancement when feeding; social attraction was also observed with no food present. *Podarcis lilfordi* occur in high densities, are generalist foragers and conspecifics can be a reliable source of information regarding foraging opportunities (Perez-Cembranos & Perez-Mellado, 2015).

Although considered solitary animals, reptiles show a range of social groupings exhibiting simple social tolerance to family group living (Whiting & While, 2018). Studies revealed social learning ability both in solitary species (e.g. Kis et al., 2015; Wilkinson et al., 2010; Wilkinson & Huber, 2012) and social species such as in the White’s skink in which familiarity affected learning in a reversal task (Munch et al., 2018b). Future studies could reveal important new insights into the difference in social information use between species with varying degree of sociality.

### Memory

Memory can be important for survival especially if information stays relevant for extended amounts of time and a good memory is energetically cheaper compared to relearning (Shettleworth, 2009). Turtles are generally long lived and proved to be good models to study long-term memory. The Florida red-bellied cooter, red footed tortoises, common box turtles and pond sliders can remember learnt stimuli or rules for up to 36 months after initial training (Davis & Burghardt, 2007; 2011; 2012; Leighty et al., 2013; Soldati et al., 2017) but lesions to turtles basal forebrain, medial or dorsal cortex can abolish the memory of previously learnt tasks (Petrillo et al., 1994, Lopez et al., 2003a; 2003b). In lizards, studies investigating memory are rare and to the best of our knowledge only one study in Crevice spiny lizards (*Sceloporus poinsettii*) specifically tested short term memory. Lizards remembered the location of a patch previously providing food within an arena 24h later (Punzo, 2002). Some degree of retention is imperative for fitness and survival (Shettleworth, 2009). Memory, however, has been little studies in reptiles although many species life span exceeds 40 years (REF). Previous research has shown long term and short term memory in reptiles. Importantly, learning involves memory but studies targeting memory capacity and memory processing in the reptilian brain are scarce. We hope to see more research on reptilian memory in the future.

## Future directions

In the last 40 years, studies on reptile learning undoubtedly demonstrated these animals capability for more than just instinctive reactions and basic cognition (Whiting & Noble, 2018). Due to the paucity of data, the evidence has as of yet to be strung together into a coherent story. In our review we attempted to link findings, present a comprehensive overview and clearly outline existing knowledge gabs to be filled by future investigations. We, however, want to highlight some particularly interesting topics for future research.

### “Invader” smart reptiles

Studies demonstrated how a single aversive event can prevent reptiles from consuming novel toxic invaders (e.g. Price-Rees et al., 2011; Somaweera et al., 2011) which can have detrimental effects on naïve native species. For example, numbers of northern quolls (*Dasyurus hallucatus*) have drastically declined because of invasive toxic cane toads. Some populations, however, coexist with the invader. These toad-smart quolls avoid toads and genetically pass this behaviour on to their offspring which can be utilised as a protective measure for the remaining wild population (Indigo et al., 2018; Kelly & Phillips, 2017; 2018). If behaviour is heritable in reptiles has not yet been investigated. Taste aversion could also be socially transmitted to naïve individuals. Previous work demonstrated information transmission through enhancement and facilitation (e.g. Davis & Burghardt, 2011; Perez-Cembranos & Perez-Mellado, 2015) even in wild animals (e.g. Schall, 2000). Conservation interventions might benefit from adopting a behaviour centred approach by incorporating species cognitive ability.

### Spatial cognition in the context of sexual selection

Between the sexes, differences in ecological demands and resulting selective pressures can lead to adaptive specialisation including cognitive abilities (Kimura, 1992; Alcock, 1998). For example, when spatial demands differ between males and females, promiscuous mammals differ in spatial memory ability while monogamous species do not (Gaulin & Fitzgerald, 1989; Perdue et al., 2011). Most studies on spatial learning, especially in lizards, tested males only (e.g. Day et al., 1999; 2001; Foa et al., 2009; LaDage et al., 2012; Mueller-Paul et al., 2012) and studies investigating both sexes rarely considered sex during analyses (e.g. Lopez et al., 2000; 2001; Zuri & Bull, 2000) despite known sex differences in home range sizes (Stamps, 1977). Furthermore, the sexes might use different learning strategies similar to humans. Women, for example, can memorise more landmarks while men show better mental rotation skills (Kimura, 1992). Venturing in this unexplored research field might proof to produce novel insights into spatial navigation and how sexual selection shapes spatial learning.

### Executive function

Core executive function comprise inhibitory skills, selective attention, associated memory and flexibility in cognition. These processes prevent automatic responses to make informed decisions. Tests for executive function include reversal learning, set-shifting or detour tasks (Brown & Tait, 2015; Diamond, 2013) which were successfully adopted in reptiles (e.g. Leal & Powell, 2012, Powell, 2012; Szabo et al., 2018; Wilkinson & Huber, 2012). Impairments in executive function were linked to diseases such as Alzheimer’s, Parkinson's or Schizophrenia (e.g. Royall et al., 2002). Understanding how executive function is processed in reptile brains which differ from mammals in neurological architecture (Nomura et al., 2013) might aid the development of better treatments for these diseases.

### Innovative problem solving

In lizards, sit-and-wait foragers ambush passing prey, use little olfactory cues and rely heavily on vison while active foragers typically move through the habitat while tongue flicking to detect prey odour. Concealed prey is often uncovered by removing debris, leaves or soil (Whiting & Noble, 2018). Previous examples demonstrated lizards’ capability to acquire novel foraging techniques and to solve complex problems such as puzzle boxes. It is our firm believe that lizards can invent or apply behaviour in new ways when facing novel problems. Active foragers might be especially suited, and in Australia, Varanids (considered ‘smart’ lizards) are frequently found in picnic areas habituated to humans (Whiting & Noble, 2018) representing a great opportunity to study wild lizards on different problems (Whiting & Noble, 2018).

### Social learning in social reptiles

Social learning is usually studied in group living animals (Wilkinson & Huber, 2012) because it is hypothesised that the demands of group living act as a selective pressure to improve cognition to cope with these demands (Social Intelligence Hypothesis: Byrne & Whiten, 1988; Social Brain Hypothesis: Reader & Laland, 2002). Solitary reptiles, however, demonstrated that grouping is not a prerequisite for social learning (e.g. Noble et al., 2014; Wilkinson et al., 2010). We agree that testing non-social species is an important research endeavour, but we want to encourage researchers to also test social reptiles (Whiting & While, 2018). A comparison between related species differing in social complexity might reveal which aspects of cognition are affected by sociality. Furthermore, with the available smart phone technology, video demonstrations (e.g. Siviter et al., 2017; Kis et al., 2015) could be adapted to test wild reptiles; a novel opportunity to study social information use in an ecologically relevant, naturalistic setting.

### Cognition in ecologically relevant contexts

Only a few studies covered in our review attempted to test learning in the wild (e.g. Marcellini & Jenssen, 1991; Roth & Krochmal, 2015; Schall, 2000; Shafir, 1995), in ecologically relevant contexts (e.g. Foa et al., 2009; Price-Rees et al., 2011; Robbins et al., 2013; Somaweera et al., 2011) or link findings to fitness and/ or survival (e.g. Dayananda & Webb, 2017). Furthermore, previous work showed how disregarding species ecology can affect study results. While corn snakes, a terrestrial species, successfully learned to escape a Barnes maze, pythons, an arboreal species, showed little learning in the same maze. Pythons do not retreat into refuges underground while corn snakes are often found under rocks (Holtzman et al., 1999; Stone et al., 2000). Considering species ecology and life history could enhance cognitive studies and testing cognition in the wild would make results better relatable to ecology. We are aware of the difficulties of studies in wild population (see also Whiting & Noble, 2018), some questions can only be tested within a controlled laboratory setting, but using wild caught individuals could be a suitable alternative. In certain cases a comparative approach might be recommendable to better answer how cognition relates to ecology. The field of reptile cognition is rapidly advancing, carefully considering ecology ensures high quality research output in the future.

### The reptile brain and cognition

Brain correlates of cognition have intrigued researchers for many years. What are the neural substrates of cognitive processes? What measure explains the difference between species best: Absolute or relative brain size, size of specific regions or neural complexity (Chittka & Niven, 2009; Healy & Rowe, 2007; 2013)? We still have no answer to these questions (Benson-Amram et al., 2016; Reader & Laland, 2002). Available data is taxonomically biased towards primates, selective other mammals and birds (Reader & Laland, 2002), consequently, we know little about reptile brains in general or how cognitive abilities map onto the reptilian brain. Only a few reptile learning studies looked at how learning is processed in specific brain structures (e.g. Day et al., 2001; Ivazov, 1983; Punzo, 1985) and these focused on turtles (e.g. Avigan & Powers, 1995; Blau & Powers, 1989; Cranney & Powers, 1983; Grisham & Powers, 1989; 1990; Lopez et al., 2003a; 2003b; Petrillo et al., 1994; Powers et al., 2009; Reiner & Powers, 1980; 1983; Reiner & Schade Powers, 1978; Yeh & Powers, 2005). Furthermore, reptiles provide a unique opportunity to study environmental effects on brain development during incubation which can not be tested in mammals or birds. Some previous studies have already shown how incubation temperature can affect cognitive ability in lizards (e.g. Amiel & Shine, 2012; Clark et al., 2014; Dayananda & Webb, 2017; Siviter et al., 2017). In the context of climate change, this research approach can give novel insights into how brain development in poikilotherms could be affected by future conditions and what fitness consequences might arise from these changes.

## Conclusions

1. The knowledge about reptile learning has greatly advanced especially in the last decade. Increasingly, researchers become interested in these neglected animals because of the need for a more comprehensive, wide taxonomic approach to the study of learning. Most studies included here were conducted on lizards and turtles but little is known about learning ability in snakes, tuatara and crocodilians. Our review emphasises the general paucity of learning studies in reptiles and the need for the application of a broader taxonomic range within reptiles (Figure 1).
2. Our systematic review provides an up-to-date overview of the currently available data. Although we identified a number of existing knowledge gaps to hopefully be closed in the near future, we highlight seven research avenues which might be of special interest in the near future such as invader-smart reptiles or temperature dependent developmental changes in learning affecting fitness and survival especially in the context of climate change.
3. The field has reached a point in which it will be important to carefully consider methodological design appropriate for reptiles to ensure high quality research in the future. Furthermore, a more ecologically adapted approach will produce higher quality data better interpretable in relation to fitness. We want to encourage researcher to venture into this young and promising field and to be more bold in applying complex methodologies. For further reading on methodological considerations see Matsubara et al. (2017) and Whiting & Noble (2018).

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## Supporting information

Due to the large number of studies our review focused on the main results; further details on each study are summarised in Appendix Table 1.

## References

Agrillo, C. & Bisazza, A. (2014). Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* **234**, 82-91. doi:10.1016/j.jneumeth.2014.04.027

Agrillo, C. & Bisazza, A. (2018). Understanding the origin of number sense: A review of fish studies. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20160511.

Alcock, J. (1998). *Animal behavior: an evolutionary approach.* 6th ed. Sunderland, Mass: Sinauer Associates.

Amiel, J. J., Lindström, T. & Shine, R. (2014). Egg incubation effects generate positive correlations between size, speed and learning ability in young lizards. *Animal Cognition* **17**, 337-347. doi:10.1007/s10071-013-0665-4

Amiel, J. J. & Shine, R. (2012). Hotter nests produce smarter young lizards. *Biology Letters* **8**, 372-374. <doi:papers3://publication/doi/10.1098/rsbl.2011.1161>

Auersperg, A. M. I., Gajdon, G. K. & von Bayern, A. M. P. (2014). A new approach to comparing problem solving, flexibility and innovation. *Communicative & Integrative Biology* **5**, 140-145. doi:10.4161/cib.18787

Avigan, M. R. & Powers, A. S. (1995). The effects of MK-801 injections and dorsal cortex lesions on maze-learning in turtles (*Chrysemys picta*). *Psychobiology* **23**, 63-68.

Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M. & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *PNAS* **113**, 2532-2537. doi:10.1073/pnas.1505913113

Benson-Amram, S., Gilfillan, G. & McComb, K. (2018). Numerical assessment in the wild: Insights from social carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20160508.

Bernstein, I. L. (1999). Taste aversion learning: A contemporary perspective. *Nutrition* **15**, 229-234.

Bezzina, C. N., Amiel, J. J. & Shine, R. (2014). Does Invasion Success Reflect Superior Cognitive Ability? A Case Study of Two Congeneric Lizard Species (*Lampropholis*, Scincidae). *PLoS One* **9**, e86271. doi:10.1371/journal.pone.0086271

Blau, A. & Powers, A. S. (1989). Discrimination-learning in turtles after lesions of the dorsal cortex or basal forebrain. *Psychobiology* **17**, 445-449.

Brown, V. J. & Tait, D. S. (2015). Behavioral flexibility: attentional shifting, rule switching and response reversal. In I. P. Stolerman & L. H. Price (Eds.), *Encyclopedia of Psychopharmacology* (pp. 264-269). Berlin, Germany: Springer-Verlag.

Burghardt, G. M. (1978). Learning Processes in Reptiles. In C. Gans & D. W. Tinkle (Eds.), *Biology of the Reptilia. Ecology and Behaviour A* (Vol. 7, pp. 555-681). London, New York: Academic Press.

Byrne, R. W. & Whiten, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Oxford University Press.

Carazo, P., Noble, D. W. A., Chandrasoma, D. & Whiting, M. J. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133275-20133275. <doi:papers3://publication/doi/10.1098/rspb.2013.3275>

Charvet, C. J. & Striedter, G. F. (2011). Developmental modes and developmental mechanisms can channel brain evolution. *Frontiers in Neuroanatomy* **5**, 1-5. doi:10.3389/fnana.2011.00004.

Chittka, L. & Niven, J. (2009). Are bigger brains better? *Current Biology* **19**, R995–R1008. doi:10.1016/j.cub.2009.08.023

Chung, M., Goulet, C. T., Michelangeli, M., Melki-Wegner, B., Wong, B. B. M. & Chapple, D. G. (2017). Does personality influence learning? A case study in an invasive lizard. *Oecologia* **185**, 641-651. doi:10.1007/s00442-017-3975-4

Clark, B. F., Amiel, J. J., Shine, R., Noble, D. W. A. & Whiting, M. J. (2014). Colour discrimination and associative learning in hatchling lizards incubated at 'hot' and 'cold' temperatures. *Behavioral Ecology and Sociobiology* **68**, 239-247. doi:10.1007/s00265-013-1639-x

Cogger, H. G. (2014). *Reptiles and Amphibians of Australia* (7th edition ed.). Victoria, USA: Csiro Publishing.

Cranney, J. & Powers, A. S. (1983). The effects of core nucleus and cortical lesions in turtles on reversal and dimensional shifting. *Physiological Psychology* **11**, 103-111. doi:10.3758/BF03326779

Damas-Moreira, I., Oliveira, D., Santos, J. L., Riley, J. L., Harris, D. J. & Whiting, M. J. (2018). Learning from others: an invasive lizard uses social information from both conspecifics and heterospecifics. *Biology Letters* **14**, 20180532. doi:10.1098/rsbl.2018.0532

Davis, K. & Burghardt, G. M. (2007). Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). *Behavioral Processes* **75**, 225-230.

Davis, K. M. & Burghardt, G. M. (2011). Turtles (*Pseudemys nelsoni*) Learn About Visual Cues Indicating Food From Experienced Turtles. *Journal of Comparative Psychology* **125**, 404-410. doi:10.1037/a0024784

Davis, K. M. & Burghardt, G. M. (2012). Long-term retention of visual tasks by two species of emydid turtles, *Pseudemys nelsoni* and *Trachemys scripta*. *Journal of Comparative Psychology* **126**, 213-223. doi:10.1037/a0027827

Day, L. B., Crews, D. & Wilczynski, W. (1999). Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour* **57**, 393-407. doi:10.1006/anbe.1998.1007

Day, L. B., Crews, D. & Wilczynski, W. (2001). Effects of medial and dorsal cortex lesions on spatial memory in lizards. *Behavioural Brain Research* **118**, 27-42.

Day, L. B., Ismail, N. & Wilczynski, W. (2003). Use of Position and Feature Cues in Discrimination Learning by the Whiptail Lizard (*Cnemidophorus inornatus*). *Journal of Comparative Psychology* **117**, 440-448. doi:10.1037/0735-7036.117.4.440

Dayananda, B. & Webb, J. K. (2017). Incubation under climate warming affects learning ability and survival in hatchling lizards. *Biology Letters* **13**, 20170002. doi:10.1098/rsbl.2017.0002

Diamond, A. (2013). Executive functions. *Annual Reviews in Psychology* **64**, 135-168. doi:10.1146/annurev-psych-113011-143750

Doody, J. S., Burghardt, G. M. & Dinets, V. (2013). Breaking the Social-Non-social Dichotomy: A Role for Reptiles in Vertebrate Social Behavior Research? *Ethology* **119**, 95-103. doi:10.1111/eth.12047

Emer, S. A., Mora, C. V., Harvey, M. T. & Grace, M. S. (2015). Predators in training: operant conditioning of novel behavior in wild Burmese pythons (*Python molurus bivitattus*). *Animal Cognition* **18**, 269-278. doi:10.1007/s10071-014-0797-1

Ferrigno, S. & Cantlon, J. F. (2017). Evolutionary constraints on the emergence of human mathematical concepts. In J. Kaas (Ed.), *Evolution of nervous systems* (pp. 511–521). Oxford, UK: Elsevier. doi:10.1016/B978-0-12-804042-3.00099-3

Foa, A., Basaglia, F., Beltrami, G., Carnacina, M., Moretto, E. & Bertolucci, C. (2009). Orientation of lizards in a Morris water-maze: roles of the sun compass and the parietal eye. *Journal of Experimental Biology* **212**, 2918-2924. doi:10.1242/jeb.032987

Gaalema, D. E. (2007). Food choice, reinforcer preference, and visual discrimination in monitor lizards (*Varanus spp.).* (MSc), Georgia Institute of Technology, Georgia.

Gaalema, D. E. (2011). Visual Discrimination and Reversal Learning in Rough-Necked Monitor Lizards (*Varanus rudicollis*). *Journal of Comparative Psychology* **125**, 246-249. doi:10.1037/a0023148

Galef, B. G. J. & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience* **55**, 489–499.

Gaulin, S. J. C. & Fitzgerald, R. W. (1989). Sexual selection for spatial-learning ability. *Animal Behaviour* **37**, 322-331.

Gavish, L. (1979). Conditioned-Response of Snakes (*Malpolon monspessulanum*) to Light (Reptilia, Serpentes, Colubridae). *Journal of Herpetology* **13**, 357-359. doi:10.2307/1563333

Grand, T. I. (1992). Altricial and precocial Mammals - A model of neural and muscular development. *Zoo Biology* **11**, 3-15.

Grisham, W. & Powers, A. S. (1989). Function of the Dorsal and Medial Cortex of Turtles in Learning. *Behavioral Neuroscience* **103**, 991-997. doi:10.1037/0735-7044.103.5.991

Grisham, W. & Powers, A. S. (1990). Effects of dorsal and medial cortex lesions on reversals in turtles. *Physiology & Behavior* **47**, 43-49. doi:10.1016/0031-9384(90)90040-b

Healy, S. D. & Rowe, C. (2013). Costs and benefits of evolving a larger brain: Doubts over the evidence that large brains lead to better cognition. *Animal Behaviour* **86**, e1–e3. doi:10.1016/j.anbehav.2013.05.017

Healy, S. D. & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society B: Biological Sciences* **274**, 453–464. doi:10.1098/rspb.2006.3748

Holtzman, D. A., Harris, T. W., Aranguren, G. & Bostock, E. (1999). Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Animal Behaviour* **57**, 51-60. doi:10.1006/anbe.1998.0971

Indigo, N., Smith, J., Webb, J. K. & Phillips, B. (2018). Not such silly sausages: Evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. *Australian Ecology* **43**, 592-601. doi:10.1111/aec.12595

Ishida, M. & Papini, M. R. (1997). Massed-trial Overtraining Effects on Extinction and Reversal Performance in Turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology* **50**, 1-16.

Ivazov, N. I. (1983). Role of the hippocampal cortex and dorsal ventricular ridge in conditioned reflex activity of the anguid lizard Scheltopusik (*Ophisaurus apodus*). *Neuroscience and Behavioral Physiology* **13**, 397-403.

Kang, F., Goulet, C. T. & Chapple, D. G. (2018). The impact of urbanization on learning ability in an invasive lizard. *Biological Journal of the Linnean Society* **123**, 55-62. doi:10.1093/biolinnean/blx131

Kar, F., Whiting, M. J. & Noble, D. W. A. (2017). Dominance and social information use in a lizard. *Animal Cognition* **20**, 805-812. doi:10.1007/s10071-017-1101-y

Kelly, E. & Phillips, B. (2017). Get smart: native mammal develops toad-smart behavior in response to a toxic invader. *Behavioral Ecology* **28**, 854-858. doi:10.1093/beheco/arx045

Kelly, E. & Phillips, B. L. (2018). Targeted gene flow and rapid adaptation in an endangered marsupial. *Conservation Biol*ogy 1-10. doi:10.1111/cobi.13149

Kimura, D. (1992). Sex Differences in the Brain. *Scientific American* **267**, 118-125.

Kirkish, P. M., Fobes, J. L. & Richardson, A. M. (1979). Spatial reversal learning in the lizard *Coleonyx variegatus*. *Bulletin of Psychonomic Science* **13**, 265-267.

Kis, A., Huber, L. & Wilkinson, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal Cognition* **18**, 325-331. doi:10.1007/s10071-014-0803-7

LaDage, L. D., Roth, T. C., Cerjanic, A. M., Sinervo, B. & Pravosudov, V. V. (2012). Spatial memory: are lizards really deficient? *Biology Letters* **8**, 939-941. doi:10.1098/rsbl.2012.0527

Leal, M. & Powell, B. J. (2012). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters* **8**, 28-30. doi:10.1098/rsbl.2011.0480

Leighty, K. A., Grand, A. P., Courte, V. L. P., Maloney, M. A. & Bettinger, T. L. (2013). Relational Responding by Eastern Box Turtles (*Terrapene carolina*) in a Series of Color Discrimination Tasks. *Journal of Comparative Psychology* **127**, 256-264. doi:10.1037/a0030942

Lopez, J. C., Gomez, Y., Rodriguez, F., Broglio, C., Varagas, J. P. & Salas, C. (2001). Spatial learning in turtles. *Animal Cognition* **4**, 49-59. doi:10.1007/s100710100091

Lopez, J. C., Gomez, Y., Vargas, J. P. & Salas, C. (2003a). Spatial reversal learning deficit after medial cortex lesion in turtles. *Neuroscience Letters* **341**, 197-200. doi:10.1016/s0304-3940(03)00186-1

Lopez, J. C., Rodriguez, F., Gomez, Y., Vargas, J. P., Broglio, C. & Salas, C. (2000). Place and cue learning in turtles. *Animal Learning & Behavior* **28**, 360-372. doi:10.3758/bf03200270

Lopez, J. C., Vargas, J. P., Gomez, Y. & Salas, C. (2003b). Spatial and non-spatial learning in turtles: the role of medial cortex. *Behavioural Brain Research* **143**, 109-120. doi:10.1016/s0166-4328(03)00030-5

Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford, England: Clarendon Press.

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

Marcellini, D. L. & Jenssen, T. A. (1991). Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: implication for anti-predator behavior. *Journal of Herpetology* **25**, 238-241.

Matsubara, S., Deeming, D. C. & Wilkinson, A. (2017). Cold-blooded cognition - new directions in reptile cognition. *Current Opinion in Behavioural Sciences* **16**, 126-130. doi:10.1016/j.cobeha.2017.06.006

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G. & Huber, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (*Chelonoidis carbonaria*). *Behavioural Processes* **106**, 187-192. doi:10.1016/j.beproc.2014.06.003

Mueller-Paul, J., Wilkinson, A., Hall, G. & Huber, L. (2012). Response-stereotypy in the jewelled lizard (*Timon lepidus*) in a radial-arm maze. *Herpetology Notes* **5**, 243-246.

Munch, K. L., Noble, D. W. A., Botterill-James, T., Koolhof, I. S., Halliwell, B., Wapstra, E. & While, G. M. (2018a). Maternal effects impact decision-making in a viviparous lizard. *Biology Letters* **14**. doi:10.1098/rsbl.2017.0556

Munch, K. L., Noble, D. W. A., Wapstra, E. & While, G. M. (2018b). Mate familiarity and social learning in a monogamous lizard. *Oecologia* **188**, 1-10. doi:10.1007/s00442-018-4153-z

Noble, D. W. A., Byrne, R. W. & Whiting, M. J. (2014). Age-dependent social learning in a lizard. *Biology Letters* **10**, 20140430. doi:10.1098/rsbl.2014.0430

Noble, D. W. A., Carazo, P. & Whiting, M. J. (2012). Learning outdoors: Male lizards show flexible spatial learning under semi-natural conditions. *Biology Letters* **8**, 946-948. doi:10.1098/rsbl.2012.0813

Nomura, T., Kawaguchi, M., Ono, K. & Murakami, Y. (2013). Reptiles: A New Model for Brain Evo-Devo Research. *Journal of Experimental Zoology Part B - Molecular and Developmental Evolution* **320B**, 57-73. doi:10.1002/jez.b.22484

Papini, M. R. & Ishida, M. (1994). Role of magnitude of reinforcement in spaced-trial instrumental learning in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology Section B - Comparative and Physiological Psychology* **47**, 1-13.

Paradis, S. & Cabanac, M. (2004). Flavour aversion learning induced by lithium chloride in reptiles but not in amphibians. *Behavioural Processes* **67**, 11-18. doi:10.1016/j.beproc.2004.01.014

Paulissen, M. A. (2008). Spatial learning in the little brown skink, *Scincella lateralis*: the importance of experience. *Animal Behaviour* **76**, 135-141. doi:10.1016/j.anbehav.2007.12.017

Paulissen, M. A. (2014). The role of visual cues in learning escape behaviour in the little brown skink (*Scincella lateralis*). *Behaviour* **151**, 2015-2028. doi:10.1163/1568539x-00003228

Perdue, B. M., Snyder, R. J., Zhihe, Z., Marr, M. J. & Maple, T. L. (2011). Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora. *Biology Letters* **7**, 380-383. doi:10.1098/rsbl.2010.1116

Perez-Cembranos, A. & Perez-Mellado, V. (2015). Local enhancement and social foraging in a non-social insular lizard. *Animal Cognition* **18**, 629-637. doi:10.1007/s10071-014-0831-3

Petrazzini, M. E. M., Bertolucci, C. & Foa, A. (2018). Quantity Discrimination in Trained Lizards (*Podarcis sicula*). *Frontiers in Psychology* **9**, 1-6. doi:10.3389/fpsyg.2018.00274

Petrillo, M., Ritter, C. A. & Powers, A. S. (1994). A role for Acetylchlorine in spatial memory in turtles. *Physiology & Behavior* **56**, 135-141. doi:10.1016/0031-9384(94)90271-2

Pyke, G. H. (1984). Optimal foraging Theory: A critical Review. *Annual Review of Ecology and Systematics* **15**, 523-575.

Powell, B. J. (2012). A Comparative Study of Habitat Complexity, Neuroanatomy, and Cognitive Behavior in Anolis Lizards. (PhD), Duke University.

Powers, A. S., Hogue, P., Lynch, C., Gattuso, B., Lissek, S. & Nayal, C. (2009). Role of Acetylcholine in Negative Patterning in Turtles (*Chrysemys picta*). *Behavioral Neuroscience* **123**, 804-809. doi:10.1037/a0016320

Price-Rees, S. J., Webb, J. K. & Shine, R. (2011). School for Skinks: Can Conditioned Taste Aversion Enable Bluetongue Lizards (*Tiliqua scincoides*) to Avoid Toxic Cane Toads (Rhinella marina) as Prey? *Ethology* **117**, 749-757. doi:10.1111/j.1439-0310.2011.01935.x

Punzo, F. (1985). Neurochemical correlates of learning and role of the basal forebrain in the brown anole, *Anolis sagrei* (Lacertilia: *Iguanidae*). *Copeia* **1985**, 409-414.

Punzo, F. (2002). Spatial associative learning in the crevice spiny lizard, *Sceloporus poinsettii* (Sauria: *Iguanidae*). *Texas Journal of Science* **54**, 45-50.

Reader, S. M. & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *PNAS* **99**, 4436-4441. doi:10.1073/pnas.062041299

Reiner, A. & Powers, A. S. (1980). The effects of extensive fore brain lesions of visual discriminative performance in turtles *Chrysemys picta picta*. *Brain Research* **192**, 327-338. doi:10.1016/0006-8993(80)90887-2

Reiner, A. & Powers, A. S. (1983). The effects of lesions of telencephalic visual structures on visual discriminative performance in turtles (*Chrysemys picta picta*). *Journal of Comparative Neurology* **218**, 1-24. doi:10.1002/cne.902180102

Reiner, A. J. & Schade Powers, A. (1978). Intensity and pattern discrimination in turtles after lesions of nucleus rotundus. *Journal of Comparative and Physiological Psychology* **92**, 1156-1168.

Riley, J. L., Küchler, A., Damasio, T., Noble, D. W. A., Byrne, R. W. & Whiting, M. J. (2018). Learning ability is unaffected by isolation rearing in a family-living lizard. *Behavioral Ecology and Sociobiology* **72**. doi:10.1007/s00265-017-2435-9

Riley, J. L., Noble, D. W., Byrne, R. W. & Whiting, M. J. (2016). Does social environment influence learning ability in a family-living lizard? *Animal Cognition* **20**, 449–458. doi:10.1007/s10071-016-1068-0

Robbins, T. R., Freidenfelds, N. A. & Langkilde, T. (2013). Native predator eats invasive toxic prey: evidence for increased incidence of consumption rather than aversion-learning. *Biological Invasions* **15**, 407-415. doi:10.1007/s10530-012-0295-9

Roth, T. C., II & Krochmal, A. R. (2015). The Role of Age-Specific Learning and Experience for Turtles Navigating a Changing Landscape. *Current Biology* **25**, 333-337. doi:10.1016/j.cub.2014.11.048

Rothblum, L. M., Watkins, J. W. & Jenssen, T. A. (1979). A learning paradigm and the behavioural demonstration of audition for the lizard *Anolis graham*. *Copeia* **1979**, 490-494.

Royall, D. R., Lauterbach, E. C., Cummings, J. L., Reeve, A., Rummans, T. A., Kaufer, D. I., LaFrance, W. C. & Coffey, C. E. (2002). Executive control functions: A review of its promise and challenges for clinical research. *Journal of Neuropsychology and Clinical Neuroscience* **44**, 377-405.

Schall, J. J. (2000). Learning in free-ranging populations of the whiptail lizard *Cnemidophorus murinus*. *Herpetologica* **56**, 38-45.

Shafir, S. (1995). Learning, memory, and optimal foraging in Anolis lizards. *Stanford University*.

Shanbhag, B. A., Ammanna, V. H. F. & Saidapur, S. K. (2010). Associative learning in hatchlings of the lizard *Calotes versicolor*: taste and colour discrimination. *Amphibia-Reptilia* **31**, 475-481. doi:10.1163/017353710x518432

Shettleworth, S. J. (2009). *Cognition, Evolution and Behavior*. USA: Oxford University Press.

Siviter, H., Deeming, D. C., van Giezen, M. F. T. & Wilkinson, A. (2017). Incubation environment impacts the social cognition of adult lizards. *Royal Society Open Science* **4**, 9. doi:10.1098/rsos.170742

Sol, D., Timmermans, S. & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**, 495-502. doi:10.1006/anbe.2001.1953

Soldati, F., Burman, O. H., John, E. A., Pike, T. W. & Wilkinson, A. (2017). Long-term memory of relative reward values. *Biology Letters* **13**, 20160853. doi:10.1098/rsbl.2016.0853

Somaweera, R., Webb, J. K., Brown, G. P. & Shine, R. (2011). Hatchling Australian freshwater crocodiles rapidly learn to avoid toxic invasive cane toads. *Behaviour* **148**, 501-517. doi:10.1163/000579511x565763

Stamps, J. A. (1977). Social behaviour and spacing patterns in lizards. In C. Gans & D. W. Tinkle (Eds.), *Biology of the Reptilia. Ecology and Behavior A* (Vol. 7, pp. 149-171). New York: Academic Press.

Stanger-Hall, K. F., Zelmer, D. A., Bergren, C. & Burns, S. A. (2001). Taste discrimination in a lizard (*Anolis carolinensis*, Polychrotidae). *Copeia* **2001**, 490-498. doi:10.1643/0045-8511(2001)001[0490:tdiala]2.0.co;2

Stone, A., Ford, N. B. & Holtzman, D. A. (2000). Spatial learning and shelter selection by juvenile spotted pythons, *Anteresia maculosus*. *Journal of Herpetology* **34**, 575-587.

Sun, B.-J., Wang, T.-T., Pike, D. A., Liang, L. & Du, W.-G. (2014). Embryonic oxygen enhances learning ability in hatchling lizards. *Frontiers in Zoology* **11**, 21-29. <doi:papers3://publication/doi/10.1186/1742-9994-11-21>

Szabo, B., Noble, D. W. A., Byrne, R. W., Tait, D. S. & Whiting, M. J. (2018). Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility? *Animal Behaviour* **144**, 17-26. doi:10.1016/j.anbehav.2018.07.018

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M. & Pravosudov, V. V. (2018). Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Animal Behaviour*. doi:10.1016/j.anbehav.2018.02.019

Thaker, M., Vanak, A. T., Lima, S. L. & Hews, D. K. (2010). Stress and Aversive Learning in a Wild Vertebrate: The Role of Corticosterone in Mediating Escape from a Novel Stressor. *American Naturalist* **175**, 50-60. doi:10.1086/648558

Weir, A. A. S., Chappell, J. & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science* **297**, 981. doi:10.1126/science.1073433

Whiting, M. J. & Noble, D. W. A. (2018). Lizards - Measuring Cognition: Practical Challenges and the Influence of Ecology and Social Behaviour. In N. Bueno-Guerra & F. Amici (Eds.), *Field and Laboratory Methods in Animal Cognition* (pp. 266-285). Cambridge, UK: Cambridge University Press.

Whiting, M. J. & While, G. M. (2017). Sociality in Lizards. In D. R. Rubenstein & P. Abbot (Eds.), *Comparative Social Evolution* (pp. 390-426). Cambridge, UK: Cambridge University Press.

Wilkinson, A., Chan, H.-M. & Hall, G. (2007). Spatial learning and memory in the tortoise (*Geochelone carbonaria*). *Journal of Comparative Psychology* **121**, 412-418. doi:10.1037/0735-7036.121.4.412

Wilkinson, A., Coward, S. & Hall, G. (2009). Visual and response-based navigation in the tortoise (*Geochelone carbonaria*). *Animal Cognition* **12**, 779-787. doi:10.1007/s10071-009-0237-9

Wilkinson, A. & Huber, L. (2012). Cold-blooded cognition: reptilian cognitive abilities. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology* (pp. 129-141). New York: Oxford.

Wilkinson, A., Kuenstner, K., Mueller, J. & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters* **6**, 614-616. doi:10.1098/rsbl.2010.0092

Wilkinson, A., Mueller-Paul, J. & Huber, L. (2013). Picture-object recognition in the tortoise *Chelonoidis carbonaria*. *Animal Cognition* **16**, 99-107. doi:10.1007/s10071-012-0555-1

Woo, K. L., Hunt, M., Harper, D., Nelson, N. J., Daugherty, C. H. & Bell, B. D. (2009). Discrimination of flicker frequency rates in the reptile tuatara (*Sphenodon*). *Naturwissenschaften* **96**, 415-419. doi:10.1007/s00114-008-0491-8

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L. & Russello, M. A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution* **22**, 393-404. doi:10.1080/03949370.2010.505580

Yeh, C. I. & Powers, A. S. (2005). Effects of blocking nitric oxide on learning in turtles (*Chrysemys picta*). *Behavioral Neuroscience* **119**, 1656-1661. doi:10.1037/0735-7044.119.6.1656

Yori, J. G. (1978). Active one-way avoidance to a heat aversive stimulus in tegu lizards (*Tupinambus teguixen*). *Behavioral Biology* **23**, 100-106. doi:10.1016/S0091-6773(78)91228-2

Zohar, O. & Terkel, J. (1991). Acquisition of Pine Cone Stripping Behaviour in Black Rats (*Rattus rattus*). *International Journal of Comparative Psychology* **5**, 1-6.

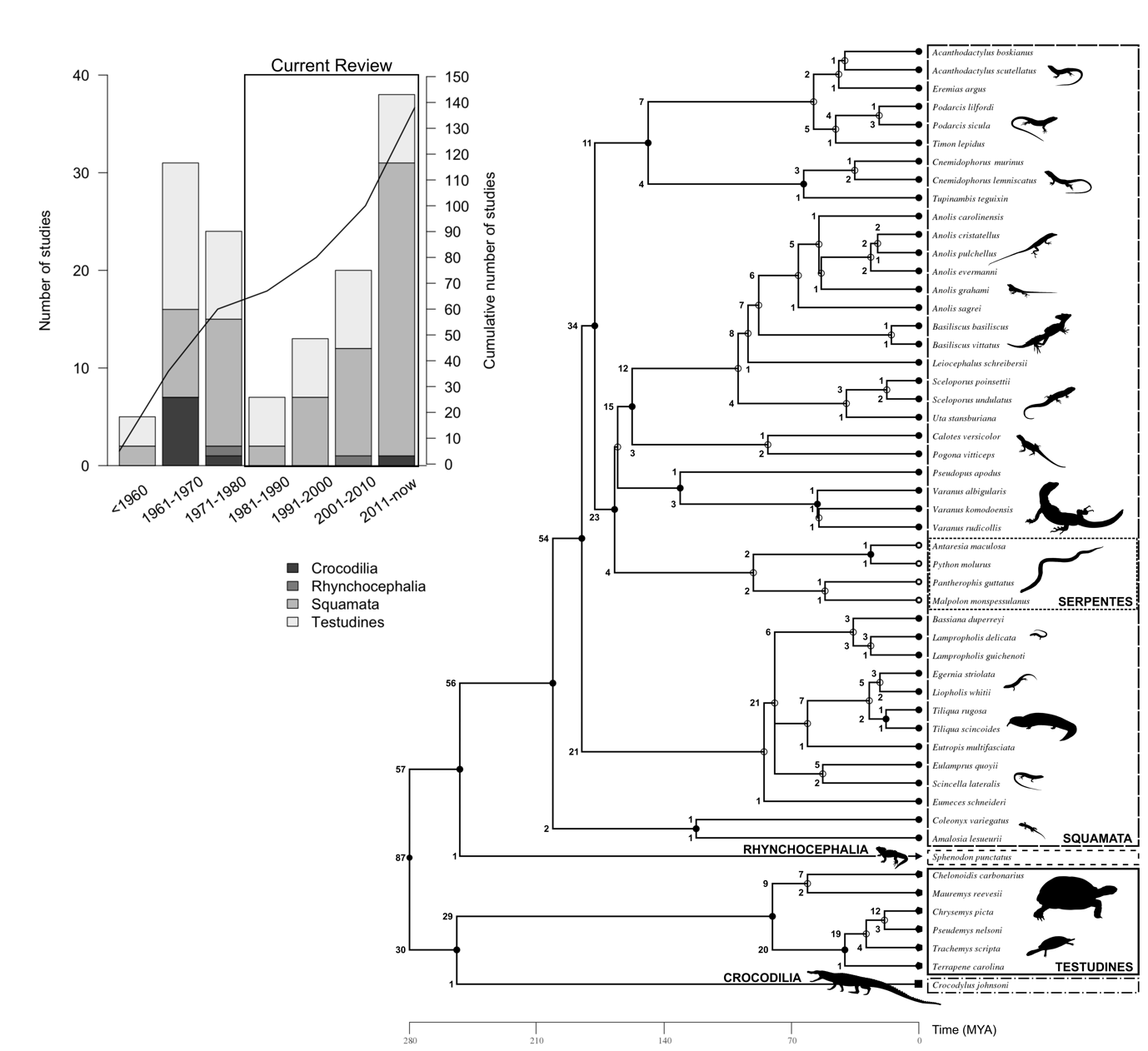
Zuri, I. & Bull, C. M. (2000). The use of visual cues for spatial orientation in the sleepy lizard (*Tiliqua rugosa*). *Canadian Journal of Zoology* **78**, 515-520.

## Appendix

**Table 1.** Summary table presenting additional information not included in the main text. # - study number, Learning task – details of the tested task (e.g. Spatial learning task with eight choices in an arena), stimuli and reward used and what learning criterion was applied. The table also includes the species tested, age-class of animals, their origin and the source (reference) of the data. Data is sorted by order, alphabetically by species name and date of publication. \* in front of the species name indicates membership of Serpentes. Studies are highlighted alternating grey and white; rows indicate number of tests applied.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| SQUAMATA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 1 | Spatial | 8-choice | Arena | Distal Cues | Heat | No criterion,  latency measured | *Acanthodactylus boskianus* | Adult | Wild | Day et al., 1999 |
| Local Cue |
| Light |
| Discrimination | 2-choice | Fork | Multiple | Food | 10/12 |
| Spatial | 8-choice | Arena | Distal Cues | Heat | No criterion,  latency measured | *Acanthodactylus scutellatus* |
| Local Cue |
| Light |
| Discrimination | 2-choice | Fork | Multiple | Food | 10/12 |
| 2 | Spatial | 2-choice | Arena | Location | Shelter | No criterion | *Amalosia*  *lesueurii* | Hatchling | Captive | Dayananda & Webb, 2017 |
| 3 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  eaten or not | *Anolis*  *carolinensis* | Adult | Captive | Stanger-Hall et al., 2001 |
| 4 | Conditioning | 1-choice | Runway | Colour | Food | No criterion,  proportion correct | *Anolis*  *cristatellus* | Adult/  Subadult | Wild | Shafir, 1995 |
| Discrimination | 2-choice | T-Maze |
| 5 | Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *cristatellus* | Adult | Wild | Powell, 2012 |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *evermanni* |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *pulchellus* |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| 6 | Discrimination | 2-choice | Wells | Colour | Food | 6/6 | *Anolis*  *evermanni* | Adult | Wild | Leal & Powell, 2012 |
| Reversal | 2-choice | Wells |
| 7 | Conditioning | 1-choice | Arena | Sound | Escape | No criterion,  80 trials | *Anolis*  *grahami* | Adult | Not Given | Rothblum et al., 1979 |
| 8 | Avoidance | 1-choice | Box | Shock | Relieve | No criterion,  number of shocks | *Anolis*  *sagrei* | Adult | Captive | Punzo, 1985 |
| 9 | Spatial | 8-choice | Arena | Multiple | Shelter | 8/10 | *\* Antaresia*  *Maculosa* | Juvenile | Captive | Stone et al., 2000 |
| 10 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  remaining food  weighed | *Basiliscus*  *vittatus* | Subadult | Not Given | Paradis & Cabanac,  2004 |
| *Basiliscus*  *basiliscus* |
| *Eumeces*  *schneideri* |
| *Eutropis*  *multifasciata* |
| 11 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  16 trials | *Bassiana*  *duperreyi* | Hatchling | Captive | Amiel & Shine, 2012 |
| 12 | Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion,  15 trials | *Bassiana*  *duperreyi* | Hatchling | Captive | Amiel et al., 2014 |
| 13 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Bassiana*  *duperreyi* | Hatchling | Captive | Clark et al., 2014 |
| Discrimination | 3-choice | Wells |
| Discrimination | 3-choice | Wells | Colour |
| Reversal | 3-choice | Wells |
| 14 | Discrimination | 2-choice | Arena | Colour | Food | No criterion,  number consumes | *Calotes*  *versicolor* | Hatchling | Captive | Shanbhag et al., 2010 |
| 15 | Spatial | 4-choice | Arena | Local Cues | Heat | No criterion,  latency measured | *Cnemidophorus inornatus* | Adult | Wild | Day et al., 2001 |
| 16 | Spatial | 2-choice | Arena | Multiple | Shelter | 2x6/8 | *Cnemidophorus inornatus* | Adult | Wild | Day et al., 2003 |
| 17 | Discrimination | n-choice | Natural Habitat | Colour | Food | No criterion,  volume and  damage recorded | *Cnemidophorus murinus* | Adult | Wild | Schall, 2000 |
| Location |
| 18 | Reversal | 2-choice | Y-Maze | Position | Food | 16/20 | *Coleonyx*  *variegatus* | Adult | Not Given | Kirkish et al., 1979 |
| Spatial | 2-choice | Y-Maze |
| 19 | Spatial | 3-choice | Vertical Maze | Multiple | Food | 5/6 | *Egernia*  *striolata* | Juvenile | Captive | Riley et al., 2016 |
| 20 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Egernia*  *striolata* | Juvenile | Captive | Riley et al., 2018 |
| Social | Discrimination | Wells | Multiple | Food | 7/8 |
| Social | Reversal | Wells |
| 21 | Discrimination | 2-choice | Wells | Multiple | Food | 6/6 or 7/8 | *Egernia*  *striolata* | Adult | Wild | Szabo et al., 2018 |
| Reversal | 2-choice | Wells |
| 22 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  16 trials | *Eremias*  *argus* | Hatchling | Captive | Sun et al., 2014 |
| 23 | Reversal | 3-choice | Arena | Location | Shelter | 5/5 | *Eulamprus*  *quoyii* | Adult | Wild | Noble et al., 2012 |
| Spatial | 3-choice | Arena |
| 24 | Spatial | 2-choice | Arena | Location | Shelter | Significant  performance | *Eulamprus*  *quoyii* | Adult | Wild | Carazo et al., 2014 |
| 25 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Mixed | Wild | Noble et al., 2014 |
| Discrimination | 2-choice | Wells |
| Social | 2-choice | Wells |
| 26 | Social | Discrimination | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Kar et al., 2017 |
| Social | Reversal | Wells |
| 27 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Qi et al., 2018 |
| Discrimination | 3-choice | Wells | Multiple |
| Discrimination | 3-choice | Wells | Colour |
| 28 | Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion, 15 trials | *Lampropholis*  *delicata* | Adult | Wild | Bezzina et al., 2014 |
| Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion, 15 trials | *Lampropholis guichenoti* |
| 29 | Spatial | 2-choice | Arena | Location | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Chung et al., 2017 |
| 30 | Discrimination | 2-choice | Y-Maze | Multiple | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Kang et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Colour |
| 31 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | Defence reaction | *Leiocephalus schreibersii* | Adult | Wild | Marcellini & Jenssen, 1991 |
| 32 | Social | Discrimination | Wells | Multiple | Food | 7/8 | *Liopholis*  *whitii* | Adult | Wild | Munch et al., 2018 |
| Social | Reversal | Wells |
| 33 | Discrimination | 2-choice | Wells | Multiple | Food | No criterion,  20 trials | *Liopholis*  *whitii* | Juvenile | Captive | Munch et al., 2018 |
| Spatial | 2-choice | Arena | Location | Shelter |
| 34 | Conditioning | 1-choice | Key | Light | Food | No criterion,  20 trials | *\* Malpolon monspessulanus* | Not Given | Not Given | Gavish, 1979 |
| 35 | Spatial | 8-choice | Arena | Location | Shelter | No criterion,  latency measured | *\* Pantherophis*  *guttatus* | Juvenile | Captive | Holtzman et al., 1999 |
| 36 | Social | Enhancement | Arena | Multiple | Food | No criterion,  number of  individuals | *Podarcis*  *lilfordi* | Adult | Wild | Perez-Cembranos &  Perez-Mellado, 2015 |
| Social | Enhancement | Arena | Multiple | Conspecifics |
| Social | Enhancement | Arena | Multiple | Models |
| 37 | Spatial | 1-choice | Water Maze | Location | Escape | >6 for two  sessions | *Podarcis*  *sicula* | Adult | Wild | Foa et al., 2009 |
| 38 | Discrimination | 2-choice | Y-Maze | Quantity | Food | 75% correct 2  days, >chance  120 trials | *Podarcis*  *sicula* | Adult | Wild | Petrazzini et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Size |
| 39 | Motor Task | 1-choice | Wells | Multiple | Food | 7/7 or 7/8 | *Podarcis*  *sicula* | Adult | Wild | Damas-Moreira et al., 2018 |
| Discrimination | 3-choice | Wells | Colour |
| Social | 3-choice | Wells |
| 40 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Kis et al., 2015 |
| 41 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Siviter et al., 2017 |
| 42 | Discrimination | 2-choice | Arena | Shape | Food | Minimum 5/6 | *Pseudopus*  *apodus* | Adult | Wild | Ivazov, 1983 |
| 43 | Conditioning | 1-choice | Key | Light | Food | No criterion,  latency measured | *\* Python*  *molurus* | Mixed | Mixed | Emer et al., 2015 |
| 44 | Spatial | 4-choice | Arena | Location | Food | No criterion | *Sceloporus*  *poinsettii* | Adult | Captive | Punzo, 2002 |
| 45 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | No criterion, hiding time and FID | *Sceloporus*  *undulatus* | Adult | Wild | Thaker et al., 2010 |
| 46 | Taste Aversion | 2-choice | Arena | Taste | Food | No criterion | *Sceloporus*  *undulatus* | Juvenile | Wild | Robbins et al., 2013 |
| 47 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  latency measured | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2008 |
| Spatial | 2-choice | Arena | Location +  Experience |
| 48 | Discrimination | 2-choice | Arena | Pattern | Shelter | 5/5 | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2014 |
| 49 | Discrimination | 2-choice | Arena | Multiple | Shelter | No criterion,  time at location | *Tiliqua*  *rugosa* | Adult | Wild | Zuri & Bull, 2000 |
| 50 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  remaining food | *Tiliqua*  *scincoides* | Adult/  Subadult | Mixed | Price-Rees et al., 2011 |
|
| 51 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | 40 trial 6/18 correct  in last 20 trials | *Timon*  *lepidus* | Adult/  Subadult | Captive | Mueller-Paul et al., 2012 |
| 52 | Avoidance | 1-choice | Shuttle Box | Light | Relieve | Mean %  avoidance | *Tupinambis*  *teguixin* | Juvenile | Not Given | Yori, 1978 |
| 53 | Spatial | 10-choices | Barnes Maze | Location | Shelter | 3/3 | *Uta*  *stansburiana* | Subadult | Captive | LaDage et al., 2012 |
| 54 | Problem Solving | 1-choice | Puzzle  Box | Visual | Food | No criterion,  3 trials | *Varanus*  *albigularis* | Juvenile | Captive | Manrod et al., 2008 |
| 55 | Discrimination | 2-choice | Target | Brightness | Food | 2x8/10 | *Varanus komodoensis* | Adult | Captive | Gaalema, 2007 |
| Reversal | 2-choice | Target |
| Reversal | 2-choice | Target |
| 56 | Discrimination | 2-choice | Target | Brightness | Food | 2x8/10 | *Varanus*  *rudicollis* | Adult | Not Given | Gaalema, 2011 |
| Reversal | 2-choice | Target |
| Reversal | 2-choice | Target |
| RHYNCHOCEPHALIA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 57 | Discrimination | 2-choice | Arena | Frequency | Food | No criterion | *Sphenodon*  *punctatus* | Juvenile | Captive | Woo et al., 2009 |
| TESTUDINES | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 58 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2007 |
| 59 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2009 |
| 60 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson et al., 2010 |
| 61 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson & Huber, 2012 |
| 62 | Discrimination | 2-choice | Arena | Visual | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Subadult | Captive | Wilkinson et al., 2013 |
|
| 63 | Discrimination | 2-choice | Touch Screen | Position | Food | Last 3 blocks  above chance | *Chelonoidis carbonaria* | Juvenile | Captive | Mueller-Paul et al., 2014 |
| Discrimination | 2-choice | Arena | Position | Food | No criterion,  20 trials |
| Reversal | 2-choice | Touch Screen | Position | Food | Last 3 blocks  above chance |
| Reversal | 2-choice | Arena | Position | Food | No criterion,  20 trials |
| 64 | Discrimination | 2-choice | Arena | Quantity | Food | no criterion | *Chelonoidis carbonaria* | Subadult | Captive | Soldati et al., 2017 |
| 65 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Reiner &  Schade Powers, 1978 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 66 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Not Given | Not Given | Reiner & Powers, 1980 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 67 | Discrimination | 2-choice | Keys | Multiple | Food | 17/20 | *Chrysemys*  *picta* | Adult | Not Given | Cranney & Powers,  1983 |
| Reversal | 2-choice | Keys |
| ED Shifts | 2-choice | Keys |
| 68 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Reiner & Powers, 1983 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 69 | Discrimination | 2-choice | Keys | Pattern | Food | Mean latency  difference of  48s for 4 days | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1989 |
| 70 | Discrimination | 2-choice | Keys | Pattern | Food | 17/20 | *Chrysemys*  *picta* | Adult | Not Given | Blau & Powers, 1989 |
| 71 | Discrimination | 2-choice | Keys | Position | Food | 2x17/20 | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1990 |
| Reversal | 2-choice | Keys |
| 72 | Spatial | 3-choice | X-Maze | Location | Water | 67% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Petrillo et al., 1994 |
|
| 73 | Discrimination | 2-choice | T-Maze | Position | Food | 2/3 for 2 days | *Chrysemys*  *picta* | Adult | Not Given | Avigan & Powers, 1995 |
| 74 | Discrimination | 3-choice | Keys | Multiple | Food | Probability  of response | *Chrysemys*  *picta* | Adult | Not Given | Yeh & Powers, 2005 |
| 75 | Discrimination | 2-choice | Keys | Multiple | Food | No criterion, responses  per day | *Chrysemys*  *picta* | Subadult | Not Given | Powers et a., 2009 |
| Negative Patterning | 3-choice | Keys |
| 76 | Spatial | n-choice | Natural Habitat | Multiple | None | No criterion | *Chrysemys*  *picta* | Adults/  Juveniles | Mixed | Roth & Krochmal, 2015 |
| Discrimination | 2-choice | Y-Maze | UV | None | No criterion, proportion correct |
| Odour |
| 77 | Conditioning | 1-choice | Runway | Quantity | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Papini & Ishida, 1994 |
| 78 | Conditioning | 1-choice | Runway | Location | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Ishida & Papini, 1997 |
| 79 | Discrimination | 2-choice | Bottles | Visual | Food | No criterion,  latency measured | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2007 |
| 80 | Social | Discrimination | Bottles | Brightness | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2011 |
| 81 | Discrimination | 2-choice | Bottles | Food Pellet | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2012 |
| 82 | Discrimination | 2-choice | Target | Brightness | Food | 9/10 for 5  sessions | *Terrapene*  *carolina* | Adult | Captive | Leighty et al., 2013 |
| Discrimination | 2-choice | Target | Brightness | Food | 11/12 for 5 sessions |
| Discrimination | 2-choice | Target | Brightness | Food | No criterion |
| Discrimination | 2-choice | Target | Brightness | Food | 9/10 for  5 sessions |
| 83 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2000 |
| Local Cue |
| 84 | Spatial | 4-choice | Water Maze | Distal Cues | Food | 9/18 | *Trachemys*  *scripta* | Subadult | Not Given | Lopez et al., 2001 |
| Local Cue |
| 85 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2003a |
| Local Cue |
| 86 | Spatial | 4-choice | Water Maze | Distal Cues | Food | 9/18 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2003b |
| CROCODILIA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 87 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  eaten or not | *Crocodylus*  *johnstoni* | Juvenile | Wild | Somaweera et al., 2011 |

**Figures**



**Figure 1.** Phylogenetic relationship of species included in our review split into Squamata (including Serpentes), Rhynchocephalia, Testudines and Cocodilia. Numbers at forks represent the number of studies (some studies include multiple species). Bar chart: Number of studies from before 1960 to 2017 (in 10 year steps) split between the four main orders of Reptiles. Superimposed as a line is the cumulative number of studies. Only studies conducted after 1977 are included in the review. Picture copyright: turtle & caiman - Scott Hartman; tortoise - Andrew A. Farke; anole - Sarah Werning; <https://creativecommons.org/licenses/by-nc-sa/3.0/>