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

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## Abstract

## Introduction

Cognition, the process by which human and non-human animals collect, store, manipulate and use information acquired from the environment, plays a pivotal role in animals everyday life when searching for food, navigating the environment or avoiding predators and is therefore a fundamentally important determinant of fitness (Shettleworth, 2009; Wright, Eberhard, Hobson, Avery, & Russello, 2010). Furthermore, cognitive processes are crucial when responding to changing environments, promoting invasion success and allowing populations to expand or change their ecological niche (Wright et al. 2010; Leal & Powell, 2012).

Contemporary animal cognition is slowly moving towards a comparative approach utilising a broader range of species from all vertebrate and invertebrate taxa. With this interest in more unusual model species the number of studies using non-avian reptiles (from here on called reptiles) to study learning has surged within the last 10 years (Figure 1). A first comprehensive description of reptile learning ability was written by Gordon Burghardt (1978) in his book section “Learning processes in Reptiles”. He gave a detailed account of the methods used and what insights were gained from these studies. Since the start of the 21st century, the field of reptile cognition is slowly advancing towards a more structured approach reflected in some recent reviews by Wilkinson and Huber (2012) or Whiting and Noble (2018), a comprehensive review addressing the development over the last 40 years, similar to Burghardt (1978), is, however, missing as of yet.



**Figure 1.** Number of studies from before 1960 to 2017 (in 10 year steps) split between the four main orders of Reptilia: Corocodilia, Rhynchocephalia, Squamata and Testudines. Superimposed as a line is the cumulative number of studies.

Modern reptiles, including turtles, crocodilians, tuatara and squamates (lizards, snakes and caecilians), are the third most species rich group of vertebrates. Many, in other vertebrates well established learning concepts such as sex differences in spatial learning or executive function, have yet to be tested in non-avian reptiles. Reptiles inhabit a wide range of different habitats, show a range of mating systems (monogamy to polygynandry), feeding ecology (herbivorous, insectivorous or omnivorous), social structure (solitary to groups of over 20 individuals) and differ substantially in their reproductive tactics (parthenogenesis, oviparity or viviparity) and behaviour (Whiting & While, 2017). For example, many reptiles exhibit oviparity without parental care representing a unique opportunity to study questions relating to developmental effects on cognition which cannot be answered using mammal or bird species (Matsubara, Deeming, & Wilkinson, 2017). Furthermore, reptiles diverged from lineages leading to mammals about 280 million years ago (Macphail, 1982). Their brain exhibits several features with prototypic phenotypes (Nomura, Kawaguchi, Ono, & Murakami, 2013), reptiles have, however, also experienced similar selective pressures as extant mammals since the split (Wilkinson & Huber, 2012). Investigating learning in these vertebrates might give insight into a more prototypic vertebrate cognitive ability as well as reveal convergent evolution based on similar selective pressures.

We conducted a systematic online literature search and identified over 80 studies investigating learning in reptiles not included in Burghardt (1978). Although a small number of these studies has been included in previous work (Whiting & Noble, 2018; Wilkinson & Huber, 2012), they are important contributions to understanding the full extent of the current knowledge and are therefore included here. The aim of our systematic review 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. The following sections are therefore organised to be able to link results between species (some studies fall under more than one subheading). Lastly, we feel that it is of great importance for the field to move forward by paying closer attention to the ecological background of model reptilian species. After reviewing the current knowledge we want to shortly summarise best practise and give some directions to improve future research design to test learning in a more ecologically relevant context.

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

### Avoiding aversive stimuli

Animals need to know what to eat, when and where to hide and which conspecifics to avoid. Avoiding potentially harmful stimuli encountered in the environment aids survival (Shettleworth, 2009). Groups of brown anoles (*Anolis sagreis*), for example, were tested on their shock avoidance learning. Group one received a shock whenever their tail touched a grid and group two received a shock whenever group one was shocked. Animals in the first group learnt to avoid shock by lifting their tails and retained this behaviour for six hours after training; animals in group two did not. After cycloheximide injection in the basal forebrain, however, lizards failed to show any shock avoidance (Punzo, 1985). This outdated practice using shock, however, provides only evidence of basic ability with no relevant link to ecological needs.

Another important skill when it comes to survival is to know which food to avoid because it might be toxic or have a noxious effect. Male green anoles (*Anolis carolinensis*) were tested on their ability to discriminate neutral, bitter and sweet tastes. Crickets were coated with either quinine hydrochloride (QHCl; bitter), Equal® (sweet) or were untreated and received a coloured dot to increase discriminability. Lizards generally rejected bitter tasting prey but were not able to do so when the vomeronasal organ was blocked (Stanger-Hall, Zelmer, Bergren, & Burns, 2001) highlighting these animals strong reliance on olfactory cues. Similarly, a few days old hatchlings of the oriental garden lizard (*Calotes versicolor*) learnt to associate dish colour with prey taste. Independent cohorts of hatchlings with the same basic learning experience (non-painted dish – neutral taste, orange dish – sweet taste from coating in sucrose and green dish – bitter taste from coating in Chloroquine phosphate) were simultaneously confronted with either the same combinations or with new colour and taste combinations. The results show that hatchlings choice of prey was affected by previously learnt associations of dish colour and prey taste (Shanbhag, Ammanna, & Saidapur, 2010). Furthermore, when a novel food was paired with an Lithium chloride (LiCl) injection (to make them sick), *Basiliskus vitattus*, B. *basiliscus* as well as *Eumeces schneideri* and *Mabuya mutifasciata* avoided the same novel food item a week later after experiencing illness. A second novel control food, however, was readily accepted one week after a saline injection (Paradis, & Cabanac, 2004). These examples highlight how especially salient stimuli such as bitter tastes lead to quickly acquired and strong learning.

Conditioned taste aversion can also be used to teach animals to avoid invasive unpalatable pray. Australian blue-tongue lizard (*Tiliqua scincoides scincoides* and *T. s. intermedia*) presented with cane toad meat in the form of a sausage (*Rhinella marina*, an invasive toxic toad) paired with a LiCl injection or meat mixed with LiCl (making them sick after ingestion) still avoided the meat seven weeks after the first encounter. A control group eating meat treated with saline, however, showed little to no aversion and all lizards readily accepted sausages of reptile cow nine weeks after illness (Price-Rees, Webb, & Shine, 2011). Similarly, hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*) rapidly learnt to avoid freshly metamorphosed cane toads. Informed crocodiles were more likely to reject toads compared to naïve individuals (Somaweera, Webb, Brown, & Shine, 2011). Both experiments indicate a possible role of learning in avoiding novel toxic prey after only a single encounter.

Two experiments used a more naturalistic approach testing taste aversion learning. Wild Bonaire island whiptail lizards (*Cnemidophorus murinus)* learnt to distinguish palatable from unpalatable artificial fruit placed along their natural habitat (sponges soaked in sweet tomato juice versus toxic quinine hydrochloride) based on visual (colour) and spatial cues (Schall, 2000). A more recent study investigated how populations of juvenile fence lizards (*Sceloporus undulates*), either invaded by toxic fire ants or uninvaded, reacted when simultaneously presented with a choice between unpalatable fire ants and an alternative prey (crickets) on two consecutive days. Juveniles from both populations did not learn to avoid this toxic prey but instead increased ant consumption over time (Robbins, Freidenfelds, & Langkilde, 2013). Taken together, these studies show that some species might be more apt to learn to avoid unpalatable or toxic prey while others show less avoidance learning; differences in methodology might account for some mixed results.

Undoubtedly, avoiding unpalatable food and adverse environmental conditions are important skills and can potentially increase fitness. Escaping predators is, however, no less important. In their natural habitat, female curly-tailed lizards (*Leiocephalus schreibersii*) rapidly learnt to avoid capture. They did so faster than males and after only one capture event (Marcellini, & Jenssen, 1991). When threatened, male eastern fence lizards (*Sceloporus undulates)* escape into hiding. Escape behaviour was linked to corticosterone: compared to control animals, who showed an increase in flight initiation distance and decreased hiding time, males treated with a corticosterone blocker showed no change in these behaviours and no retention 24h later (Thaker, Vanak, Lima, & Hews, 2010). Moreover, little brown skinks (*Scincella lateralis*) used patterns (horizontal and vertical black and white 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 are not just able to use pattern to find a ‘safe’ refuge, they are similarly skilled at using colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicate*) learnt to escape a simulated predator attack into a ‘safe’ refuge using both location and colour alone to find the safe hide (Chung et al., 2017). The same methodology was used to compare performance of male delicate skinks from urban and natural areas. A greater proportion of lizards learnt when both colour and location stimuli were available than when only colour stimuli indicated which refuge was safe. Furthermore, a greater proportion of the lizards from more naturalistic habitats were successful learners (Kang, Goulet, & Chapple, 2018). Besides population effects on escape behaviour, developmental conditions can also alter escape behaviour. Hatchling White’s skins (*Liopholis whitii*) whose mothers received less food (low resource treatment) were more likely to avoid threat and learn to locate a ‘safe’ refuge compared to hatchlings from mothers receiving more food (high resource treatment; Munch et al., 2018).

These examples provide a first glimpse into how reptiles use stimuli provided by the environment to learn to avoid harmful stimuli, potentially toxic food items and predators. Although some mechanisms were identified, much is still unexplained. Especially, why some species are able to quickly avoid noxious food items while others do not is largely unexplored. Furthermore, a more detailed investigation into how species differ when successfully inhabiting urban habitats might further our ability to implement measure to protect vulnerable species within cities. Both present a potentially fruitful avenue of research in the future.

### Discriminating between stimuli that indicate food and those that don’t

While foraging it is important to be able to discriminate between food sources or patches that provide food and those that are already depleted. Learning to recognise specific cues associated with the availability of food is important to not waste time and energy on searching for food when the source is already empty (optimal foraging theory, Pyke, 1984). During discrimination learning, animals are confronted with at least two choices of which one is rewarded (e.g. provides food or shelter) and the other is not. This might be indicated by different stimuli such as colour, brightness, pattern or light flicker frequency.

Florida red-bellied cooters (*Pseudemys nelsoni*) successfully discriminated between two bottles based on a visible food pellet or bottle-colour (black and white). Pond sliders (*Trachemys scripta*) 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) to gain a reward (Leighty et al., 2013), and similarly, rough-necked monitors (*Varanus rudicollis*) and a komodo dragon (*Varanus komodoensis*) used paddle colour (black and white) to obtain a food reward (Gaalema, 2007; 2011).

Reptiles can also be trained to use light stimuli to gain a reward. Coloured light bulbs were used to study the discriminative ability of wild crested anoles (*Anolis cristatellus*). First, lizards were trained to receive food whenever a yellow bulb was raised, later, they preferred the trained colour during a simultaneous two-choice test (Shafir, 1995). To test discrimination learning and negative patterning, painted turtles (*Chrysemys picta*) learnt to press response keys illuminated with different visual stimuli to receive a reward. Nitric oxide and Acetylcholine played an important role during negative patterning but were not involved in learning a discrimination (Powers et al., 2009; Yeh, & Powers, 2005). Moreover, tuataras were able to discriminate between a trained flicker frequency and different flicker frequencies in a simultaneous two-choice test using food rewards (Woo, Hunt, Harper, Nelson, Daugherty, & Bell, 2009).

Simple mazes with two arms have proven useful in two choice discrimination tasks. Both *Lampropholis delicate*, an invasive species, and L. *guachenoti*, non-invasive, tested in a Y-maze setup (one arm painted solid orange or blue, the other in orange or blue stripes) failed to learn which of the two arms provided a reward; *L. guichenoti*, however, reached the end of a maze arm faster (Bezzina, Amiel, & Shine, 2014).

Using these simple cues, reptiles can be trained to discriminate visual stimuli using different methods. With some exceptions, most discrimination experiments applied in reptile learning only test one or two sequential discriminations. The examples above, however, also include some more sophisticated tests investigating negative patterning and rule transfer showing that reptiles possess sophisticated abilities previously unattributed to this group of animals. The upcoming sections will give further evidence to strengthen this view.

### Quality and quantity discrimination

To understand if and how animals count can help better understand if our own mathematical abilities are a unique result of our ability to use language or if there is a conserved neural basis present in all vertebrates. Many species were able to discriminate between different reward quantities and qualities (e.g. Agrillo & Bisazza, 2018; Benson-Amram, Gilfillan, & McComb, 2018; Shettleworth, 2009), reptiles are no exception. Red footed tortoises (*Chelonoidis carbonaria*), for example, were first trained to associate a given stimulus with a specific reward quality or quantity, after which they were given preference tests by simultaneously presenting two stimuli with different values. Tortoises discriminated between preferred and less preferred foods as well as large and small quantities of food and retained this knowledge for 18 months (Soldati, Burman, John, Pike, & Wilkinson, 2017). The speed with which Chinese pond turtles (*Geoclemys reevesii*) moved down a runway was contingent on the amount of reward provided at the end. Turtles in the large reward group, receiving 24 pellets each trial, moved faster than turtles receiving only two pellets. During extinction trials, with no food present, similar results were obtained (Papini, & Ishida, 1994); animals receiving large quantities during training took longer to extinguish responding than animals previously receiving less reward. In lizards, ruin lizards (*Podarcis sicula*) were tested on a trained numerosity and size discrimination. Numerosity was tested using artificial stimuli depicting 1 versus 4, 2 versus 4 and then 2 versus 3 yellow disks. Size discrimination was tested with similar stimuli; yellow disks differing in sizes. Lizards were able to discriminate between 1 versus 4 and 2 versus 4 but not between 2 versus 3. None of the lizards, however, were able to discriminate between two different sizes of stimuli (ration 0.25; Petrazzini, Bertolucci, & Foa, 2018). Taken together, these studies demonstrate that reptiles have a sense of reward quality, size and quantity. Artificial and naturalistic stimuli might be used to test for numerosity in animals, 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. A wider taxonomic approach might help unravel the evolutionary origin of human mathematical abilities.

### Reacting to change

Being flexible when responding to environmental stimuli and adapting to change quickly is important for survival especially in unpredictable environments (Tello-Ramos, Branch, Kozlovsky, Pitera, & Pravosudov, 2018). Behavioural flexibility, the ability to adjust to environmental variation by adapting attention and behaviour or using existing skills to solve novel problems (Brown & Tait, 2015), can be measured through different tests. One simple way is reversal learning, when a previously established stimulus-reward relationship changes. Another way is to test attentional set-formation and shift, during which an animal is first trained to recognise an attentional set (a stimulus set based on which a reward can be obtained) that is later shifted (to a stimulus in a different set such as a second, formerly irrelevant dimension; Brown & Tait, 2015). Furthermore, it has been proposed that innovation frequency or problem solving skill might also be a measure for behavioural (or cognitive) flexibility (Auersperg, Gajdon, & von Bayern, 2014). In reptiles, both reversal learning and attentional set-shifting have revealed behavioural flexibility in different contexts.

Chinese pond turtles (*Mauremys reevesii)* reversed a simple left/ right discrimination; animals that were overtrained on the initial discrimination for an additional 100 trials, however, showed impaired reversal learning (Ishida, & Papini, 1997). The Australian water skink (*Eulamprus quoyii*) learnt the location of a ‘safe’ refuge and to escape a simulated predator attack even after a spatial reversal in the lab (Noble, Byrne, & Whiting, 2014) and in semi-natural conditions (Noble, Carazo, & Whiting, 2012). Furthermore, whiptail lizards’ (*Cnemidophorus inornatus*) avoided a heat lamp using features (colour, brightness or pattern) or the location of a ‘safe’ refuge and showed flexibility in their response behaviour during a reversal. Lizards trained on spatial cues, however, outperformed lizards trained on visual cues making less errors during acquisition but both groups performed at similar levels during reversals (Day, Ismail, & Wilczynski, 2003). Male rough-necked monitors (*Varanus rudicollis*) and one komodo dragon (*Varanus komodoensis*) successfully reversed a black/ white discrimination twice showing an increase in performance during the second reversal back to the initially rewarded stimulus (Gaalema, 2007; 2011). Moreover, red footed tortoises (*Chelonoidis carbonaria*) were even able to transfer knowledge about the location of food (left/ right food bowl) acquired during touchscreen training to a real life setup. After training on a real life spatial reversal, however, tortoises failed to transfer the new knowledge back to the touchscreen (Mueller-Paul et al., 2014).

Studies in the painted turtle (*Chrysemys picta*) revealed that the core nucleus, dorsal cortex and parts of the forebrain are involved in processing visual stimuli. As previously described, turtles were trained to push response keys illuminated to show different visual stimuli to gain a reward. Lesions to these brain regions negatively affected acquisition and reversal learning and selectively impaired 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; Grisham, & Powers, 1990; Reiner & Powers, 1980; Reiner & Powers, 1983). Furthermore, in the European legless lizard (*Ophisaurus apodus*), damage to the hippocampus affected reversal performance (distinguishing between a triangle and a circle; Ivazov, 1983). Moreover, in hatchling three lined skinks (*Bassiana duperreyi*), incubation treatment (‘hot’ versus ‘cold’) did effect learning using lid covered food wells; only hot incubated lizards learned throughout the experiment including the reversal (Clark, Amiel, Shine, Noble, & Whiting, 2014) indicating that incubation temperature affects brain development, as to how, however, has not been studies yet.

Using a comparative approach, three species of Anoles (A. *evermanni*, A. *cristatellus* and A. *pulchellus*) were tested on their behavioural flexibility in an associative learning and reversal task discriminating between differently coloured lids. *A.* *cristatellus* took the longest to learn a reversal compared to A. *evermanni* and A. *pulchellus* but individuals of all tested species were able to learn during at least one reversal. Differences between the species could be attributed to differences in neophobia, sample sizes were, however, small (Leal, & Powell, 2012; Powell, 2012). Similarly, when comparing *Acanthodactylus* *boskianus*, an active forager, and *A. scutellatus*, a sit-and-wait forager, in a simple two-choice discrimination reversal applying the fork method, the active forager (*A.* *boskianus*) learnt faster during reversals compared to the sit-and-wait forager (*A. scutellatus*). Inhibition plays an important role when learning a reversal. Sit-and-wait foragers might need to strike at any potential prey item while active forager might encounter a great variety of possible prey in need of some inspection before striking (Day, Crews, & Wilczynski, 1999).

Only one study, so far, looked at behavioural flexibility using a set-shifting approach. The tree skink (*Egernia striolata*) were first trained to establish an attentional set through six stages of discriminations followed by reversals between either two shape or colour stimuli in two dimensions. Afterwards, they were tested on their shift performance to the previously unreinforced dimension followed by another reversal. The results showed that 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 were, however, able to reverse four discriminations showing behavioural flexibility (Szabo, Noble, Byrne, Tait, & Whiting, 2018).

Taken together, the above summarised research provides ample evidence that reptiles possess at least some basic level of behavioural flexibility using different visual cues including colour, shape, pattern and location. The following section will provide examples on behavioural flexibility shown though problem solving skill.

### Solving novel problems

Many animals are well known to be good problem-solvers. New Caledonian crows (*Corvus moneduloides*) bending wires into hooks to reach a reward (Weir, Chappell, & Kacelnik, 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. Only a few study, so far, looked at reptiles ability to learn a novel foraging technique. Painted turtles (*Chrysemys picta picta*) as well as sub-adult Burmese pythons (*Python molurus bivittatus*) could be trained to push response keys to gain access to a reward (Blau & Powers, 1989; Cranney & Powers, 1983; Emer, Mora, Harvey, & Grace, 2015; Grisham & Powers, 1989; 1990; Powers et al., 2009; Reiner & Schade Powers, 1978; Reiner & Powers, 1980; 1983; Yeh & Powers, 2005) and six different studies successfully trained lizards to open lids covering food wells to access a reward. Anolis evermanni, A. *pulchellus and A. cristatellus* all removed lids to gain access to a reward, *A. cristatellus,* however, were less successful compared to the other two species (Leal, & Powell, 2012; Powell, 2012). Hatchling three lined skink (*Bassiana duperreyi*) also learnt to remove lids from food wells, however, incubation treatment affected this ability. Only lizards incubated at ‘hot’ temperatures were able to learn this behaviour (Clark, Amiel, Shine, Noble, & Whiting, 2014). Furthermore, both water skinks (*Eulamprus quoyii*) and tree skinks (*Egernia striolata*) were able to learn how to remove a lid from a food well. Neither age (young and old; Noble, Byrne, & Whiting, 2014) nor rearing environment (social or solitary; Riley et a;., 2018) affected performance in these two species, respectively. Finally, and Italian wall lizards (*Podarcis sicula*). Although these studies used training procedures, they provide impressive examples of how reptiles can acquiring a novel behaviour to solve a problem. Not all species, however, were able to learn lid opening. Training White’s skinks (*Liopholis whitii*), another Australian skink species, on this task has, so far, proven unsuccessful (personal conversation). Apart from lid opening and pressing response keys, climbing onto a platform to tip bottles can also be interpreted as a novel foraging technique. Florida red-bellied cooters and pond sliders both could be trained to exit water and climb on a platform to tip a bottle and reach a reward (Davis, & Burghardt, 2007; 2011, 2012). Why some reptile species are able to learn novel behaviours and others are not and what techniques these species use to solve these novel problems should be investigated in more detail in the future.

Only a single study has attempted to test a reptile in a more complex task using a puzzle box. Presented with an artificial fruit type task, black-throated monitors (*Varanus albigularis albigularis*) were able to open a plastic tube to retrieve a reward within 10 minutes of the first presentation showing their problem solving ability. They even decreased their time to solve this novel task during the second and third trial (Manrod, Hartdegen, & Burghardt, 2008). Varanids are considered as ‘smart’ lizards and in Australia, monitor lizards can be frequently found in picnic areas (Whiting & Noble, 2018); a great opportunity to study Varanids on similar puzzle boxes or more complex arrangements in the wild.

### Spatial cognition

Navigating through the environment is essential for animals when in search of or returning for food, shelter or mating partners. Resources and conspecifics are spread out and rarely found together in the same location. Efficiently navigating as opposed to randomly moving through space can be accomplished through different mechanisms such as 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. One such maze is the radial arm maze, usually made out of eight arms originating in a common centre. Red footed tortoise (*Chelonoidis carbonaria*), for example, were able to learn to avoid already visited and therefore food depleted locations within a radial arm maze while adopting a response-based strategy depending on the availability of different spatial cues (Wilkinson, Chan, & Hall, 2007; Wilkinson, Coward, & Hall, 2009). Similarly, jewelled lizards (*Timon lepidus*) successfully navigated a radial arm maze using a response based strategy preferentially entering arms next to the last visited arm (Mueller-Paul et al., 2012).

Similar to the radial arm maze but with less possible entry points are plus- or X-shaped mazes. In the painted turtle the dorsal cortex and especially Acetylcholine play an important role during spatial learning in a X-maze; treatment turtles were impaired when relearning to navigate the maze after surgery which was attributed to an impairment in memory (Petrillo, Ritter, & Powers, 1994). In the pond slider, turtles trained to use distal, extra-maze cues were unable to find the goal in a plus-shaped maze when these cues were removed while turtles trained on a single intra maze cue showed impaired performance only when the single intra maze cue was removed. Furthermore, both groups were able to find the goal when starting from a new location (Lopez et al., 2000). After lesions to the medial cortex, however, only turtles using a map like strategy (based on distal cues) were still able to learn the new goal location during a spatial reversal (Lopez, Gomez, Vargas, & Salas, 2003).

Another popular maze is the (Morris) water maze. A pool filled with water in which a goal platform is hidden. Pond sliders (*Trachemys scripta*) trained with intra-maze cues used a single local cue to guide them to the goal, whereas animals trained with distal, extra-maze cues used a map based strategy to escape the water (Lopez et al., 2001). After lesions to the medial cortex, turtles using the map strategy were impaired in finding the goal when distal cues were partly concealed while a control group was unimpaired (Lopez, Vargas, Gomez, & Salas, 2003). Furthermore, male ruin lizards (*Podarcis sicula*) use a sun compass to locate a hidden goal platform in the Morris water maze; the parietal eye (a photoreceptive third eye found on the head) is essential for successful navigation in the maze (Foa et al., 2009).

Instead of a maze, some studies use an open arena to test animals on their spatial learning ability. Sleepy lizards (*Tiliqua rugose*), for instance, preferred familiar sites within their enclosure when no visual cues were available. When trained on a brightness or shape discrimination, lizards preferred the familiar signal even after they were moved to a different location (Zuri & Bull, 2000). For little brown skinks (*Scincella lateralis*) previous experience with an arena was crucial for learning. Skinks needed 48h of experience to learn to escaped under a randomly chosen correct carboard box refuge, without experience, they did not learn within two days of testing (Paulissen, 2008). Male *Acanthodactylus boskianus* and A. *scutellatus*, two closely related species with different foraging strategies, both learnt to navigate a round arena to find a heated goal rock but did not differ in their latency and spatial learning strategy. When tested with a single local visual cue, the active forager, A. *boskianus*, took longer to learn (Day, Crews, & Wilczynski, 1999). In a related study, male *Cnemidophorus inornatus* readily learnt to navigate the same arena but did not use spatial strategies to reach the goal. Lesions to the dorsal cortex impaired learning and only mildly interfered with navigation. Damage to the medial cortex, however, slowed learning and strongly interfered with navigation (Day, Crews, & Wilczynski, 2001).

A special case of a circular arena is the Barnes maze, a round open space with 10 holes equidistant along the edge. Side-blotched lizards (*Uta stansburiana*) learnt to navigate a Barnes maze based on extra-maze spatial cues and found the goal hole even after the maze was rotated 180° (LaDage et al., 2012). Likewise, juvenile corn snakes (*Elaphe guttata guttata*) successfully navigated the Barnes maze to find the exit. During trials, snakes decreased the latency to find the goal as well as distance travelled and made less errors than expected by chance on all trials (Holtzman et al., 1999). While all corn snakes learn to exit the maze, only half of a group of juvenile pythons (*Antaresia maculosa*) tested on the same task learnt to find the goal hole. Pythons did not decrease latency and no specific learning strategy could be identified (Stone, Ford, & Holtzman, 2000). While corn snakes are terrestrial and mostly found on the ground, Pythons are usually found in trees. This difference in habitat preference might explain why only half of the pythons successfully navigated the Barns maze (Stone et al, 2000).

Only one study investigated a reptiles spatial learning ability in a natural setting. Using radiotracking, residential wild painted turtles (with knowledge of the habitat) and translocated animals (with no knowledge of the habitat) were tracked and their ability to find a water body assessed. The results show that experience, especially during the first few years of life, is crucial for these turtles to find a water body. While residential animals used specific routes back to the water, translocated turtles failed to find water (Roth & Krochmal, 2015).

Conditions during development can affect spatial learning similar to discrimination learning and the acquisition of a novel foraging behaviour. Hatchlings of the velvet gecko (*Oedura lesueurii*) incubated at ‘hot’ temperatures were slower at learning the location of a shelter compared to hatchling incubated at ‘cold’ temperatures. Furthermore, geckos with higher learning scores survived longer after being released at their mothers capture site indicating a lasting effect influencing survival (Dayananda, & Webb, 2017). Similarly, hatchling three lined skink (*Bassiana duperreyi*) incubated at ‘hot’ temperatures earned higher learning scores compared to ‘cold’ incubated lizards (Amiel, & Shine, 2012). Furthermore, hatchling *Eremias argus* incubated at hypoxic conditions were significantly less likely to located a save refuge compared to both normoxic and hyperoxic animals (Sun, Wang, Pike, Liang, & Du, 2014). Finally, in juvenile tree skinks (*Egernia striolata*) rearing environment (social or non-social) did not affect performance when solving a vertical maze with both intra- and extra-maze cues present (Riley, Noble, Byrne, & Whiting, 2016).

Summary paragraph

### The non-social social learning paradox

Social learning in general refers to learning from other individuals. These might be conspecifics, animals from the same species or even animals from a different species (Shettleworth, 2009). Most social learning studies have been conducted on animals that aggregate into social groups (Wilkinson & Huber, 2012) but less research has looked at how less social species use information provided by other animals. Especially in reptiles, we know little about their social behaviour, however, recent work has shown that even those ‘unsocial’ animals can learn from their conspecifics (Doody, Burghardt, & Dinets, 2013).

Solitary living red footed tortoises (*Chelonoidis carbonaria*) were the first reptile species to show social learning in a simple detour task (Wilkinson et al., 2010). Turtles observing a trained demonstrator before walking around a barrier learnt to detour to access a food reward themselves, while a control group did not learn. Follow-up experiments revealed that observers could generalise their knowledge to novel barriers (inverted V- and U-shaped) being significantly more successful than control animals (Wilkinson & Huber, 2012). Furthermore, bearded dragons (*Pogona vitticeps)*, a solitary, Australian lizard species learnt to open a sliding door in the same direction as a demonstrator by watching a video of a conspecific performing the task. A control group watching the door open on its own was not able to learn (Kis, Huber, & Wilkinson, 2015). Incubation treatment affected hatchlings performance on the same task. Cold incubated lizards opened the door significantly faster than hot incubated lizards. There was, however, no significant difference in the number of successful door openings between the incubation treatments (Siviter, Deeming, van Giezen, & Wilkinson, 2017). Moreover, Florida red-bellied cooters (*Pseudemys nelsoni*) showed stimulus enhancement during a black and white discrimination significantly matching the choice of a demonstrator turtle (Davis & Burghardt, 2011). It follows that social group living might not be a prerequisite for successful social information use. Social learning is viewed as a shortcut towards the acquisition of new information by avoiding costs of individual trial-and-error learning such as time and energy investment (Galef, & Laland, 2005), which can potentially benefit all animals.

In the water skink (*Eulamprus quoyii*) age affected the ability of lizards to learn a two-choice discrimination task from a trained conspecific, dominance status, however, influenced lizards social information use only marginally. Both old and young observers learnt to discriminate between two differently coloured lids, no matter if they watched a demonstration or not. Young males, however, used the social information more efficiently than older males; young observers learnt significantly faster than control lizards (Noble, Byrne, & Whiting, 2014). When dominance was taken into account, both observers and control lizards learnt the task, dominant social lizards, however, learnt faster than subordinate social lizards. In a subsequent reversal task, no effect of dominance was apparent (Kar, Whiting, & Noble, 2017). Although considered not social, water skinks are often found in high densities around water bodies (Cogger, 2014); socially provided information is therefore readily available.

Typically, animals are tested with demonstrators of their own species. It can, however, be beneficial to learn from another species if this information is beneficial. Invasive Italian wall lizards (*Podarcis sicula*) made less errors when socially learning to discriminate between differently coloured lids than individual learners. Furthermore, they were able to use information provided from a conspecific as well as an unfamiliar heterospecific species (*Podarcis bocagei*). These results indicate that social information use might benefit invasive species when invading unfamiliar, new habitats (Damas-Moreira et al., 2018).

The only non-lab study was conducted on wild *Podarcis lilfordi.* Lizards were presented with two choices between food with and without conspecifics including static copper models. When feeding, wild *Podarcis lilfordi* prefer locations with conspecifics present showing social enhancement in their feeding behaviour, social attraction was also observed when no food was present. *Podarcis lilfordi* occur in high densities, are generalist foragers and experience low predation pressure. In this system, conspecifics can act as a reliable source of information regarding foraging opportunities (Perez-Cembranos & Perez-Mellado, 2015).

The *Egernia* group is a group of Australian skinks including species with varying degree of social complexity (Whiting & While, 2017). Two monogamous species from this group have been the focus of social learning. In the White’s skink (*Liopholis whitii*), familiarity plays an important role during reversal learning but not in a simple discrimination task. Observers in three treatment groups were tested: Individuals observing their mating partner, an unfamiliar conspecific, or a control lizard providing no social information. No significant differences were found during the initial discrimination. During reversals, lizards observing a familiar mate learnt significantly faster than control lizards (Munch, Noble, Wapstra, & While, 2018). Contrary to White’s skinks, the closely related tree skink (*Egernia striolata*) does not use social information to learn a similar task. Furthermore, rearing treatment (social or solitary) did not affect learning a discrimination or reversal task (Riley et al., 2018).

Although generally considered as solitary animals, reptiles show a variety of social structures from simple social tolerance to group living (Whiting & While, 2018). So far, some studies indicate that both more solitary species such as the bearded dragon (Kis et al., 2015) or red footed tortoise (Wilkinson et al., 2010; Wilkinson & Huber, 2012) can still use socially provided information to solve different tasks. When sociality was taken into account such as in the White’s skink, familiarity significantly affected learning especially in a more complex task such as a reversal (Munch et al., 2018). In the closely related tree skink no performance increase through social information use was detected. These studies provide a first glimpse into how reptiles use information provided by conspecifics and future studies could potentially reveal some important new insights into the difference in social information use between species with varying degree of sociality.

### Memory

Memory, the retention of information through time 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 (*Pseudemys nelsoni*), red footed tortoises (*Chelonoidis carbonaria*), common box turtles (*Terrapene carolina*) and pond sliders (*Trachemys scripta*) 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). In lizards studies specifically investigating memory retention are rare. Crevice spiny lizards (*Sceloporus poinsettii*) were tested on their associative learning and memory ability. Animals were trained to find food in four specific locations within an arena. Test trials were divided into two phases: First none of the dishes provided food and the location each lizard inspected first was recorded. In the second phase, food was provided in only one dish. During phase one, lizards preferentially visited the location food was provided the day before (phase 2) indicating a memory for cues associated with successful foraging (Punzo, 2002).

Some degree of memory retention is imperative for fitness and survival (Shettleworth, 2009). Memory, however, has been little studies in reptiles although many species can live for long periods of time (e.g. Crocodiles: up to 100 years, tuatara: around 60 years, big lizards: more than 50 years, snakes: more than 40 years and turtles: up to 100 years; ). Previous research has shown long term and short term memory in reptiles. Importantly, all forms of learning involve some degree of memory and all studies included in this review together are an account of the memory capacity present in reptiles. Furthermore, we still know almost nothing about how memory is processed in the reptilian brain which could be a promising new venture for future research. In the painted turtle the dorsal cortex and especially Acetylcholine play an important role during spatial learning in a X-maze; treatment turtles were impaired when relearning to navigate the maze after surgery which was attributed to an impairment in memory (Petrillo, Ritter, & Powers, 1994).

## Conclusions and future directions

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