# 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 animals collect, store, manipulate and use information acquired from the environment, plays a pivotal role in their everyday life when, for example, 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 more comprehensive comparative approach utilising a broader range of species from all vertebrate and invertebrate taxa to test for the generality of cognitive processes. With this interest in more unusual model species the number of studies using non-avian reptiles (including turtles, crocodilians, tuatara and squamates - lizards, snakes and caecilians), from here on called reptiles, to study learning has surged within the last 10 years (Figure 1). A first account of reptile learning ability was compiled by Gordon Burghardt (1978) in his book section “Learning processes in Reptiles”. He gave a detailed description 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 are the third most species rich group of vertebrates. Many, in other animals well established learning concepts such as sex differences in spatial learning or executive function, have yet to be tested in reptiles. As a very diverse group of animals, reptiles inhabit a wide range of different habitats, show a range of mating systems (monogamy to polygynandry), feeding ecology, social structure (solitary to groups of many 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, 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 lineages leading to mammals about 280 million years ago (Macphail, 1982). Their brain exhibits several features with prototypic phenotypes (Nomura, Kawaguchi, Ono, & Murakami, 2013). Extant reptiles have, however, also experienced similar selective pressures as modern 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). These studies tested a wide range of learning abilities from taste aversion to discrimination and learning flexibility, number competencies, spatial orientation and social information use. Although a small number of these studies have been included in previous work (Whiting & Noble, 2018; Wilkinson & Huber, 2012), they are important contributions and are included here to give a full overview of the extent of the current knowledge. 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 from different species (some studies fall under more than one subheading). Lastly, we feel that it is of great importance for the field to move forward to pay 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 to hide and which threats to avoid. Avoiding potentially harmful stimuli encountered in the environment aids survival (Shettleworth, 2009). Groups of brown anoles (*Anolis sagrei*), 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 (inhibiting protein synthesis) in the basal forebrain, however, lizards failed to show any shock avoidance similar to findings in rodents (Punzo, 1985). This outdated practice using shock provides some evidence of the involvement of proteins in learning but with no link to ecological relevance.

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. A whole plethora of research has been dedicated to taste aversion learning (e.g. Bernstein, 1999) including research in reptiles. Male green anoles (*Anolis carolinensis*) can distinguish between 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, 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; they avoided dishes in the colour previously associated with bitter tasting prey (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). Likewise, Australian blue-tongue lizard (*Tiliqua scincoides scincoides* and *T. s. intermedia*) presented with cane toad meat (*Rhinella marina*, an invasive toxic toad) in the form of a sausage 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 receiving saline injections or eating meat treated with saline, however, showed little to no aversion and all lizards readily accepted sausages of reptile cow (pet feed) nine weeks after illness (Price-Rees, Webb, & Shine, 2011). These examples highlight how salient stimuli such as bitter tastes or illness aid learning and are quickly avoided after only a few encounters.

Three experiments used a more ecologically relevant approach testing taste aversion learning. Wild Bonaire island whiptail lizards (*Cnemidophorus murinus)* learnt to distinguish palatable from unpalatable artificial fruit (sponges soaked in sweet tomato juice versus toxic quinine hydrochloride) placed along their natural habitat based on visual (green - toxic versus red - sweet) and spatial (on the ground or in the vegetation) cues (Schall, 2000). Conditioned taste aversion can also be used to teach animals to avoid invasive unpalatable pray. 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). A more recent study investigated how populations of juvenile eastern 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 and can potentially increase fitness. Escaping predators is, however, no less important. 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). When threatened, male eastern fence lizardsescape into hiding. Escape behaviour was linked to corticosterone: compared to control animals, that 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 and escape a threat, they are similarly skilled at using colour and location cues when escaping. Male delicate skinks (*Lampropholis delicata*) 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 habitats. A greater proportion of lizards learnt when both colour and location stimuli were available than when only colour 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, 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., 2018a).

These examples provide a first glimpse into how reptiles use cues provided by the environment to learn and avoid harmful stimuli including potentially toxic food items and dangerous 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 for future research.

### 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 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. 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, male 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, Wilkinson, Hall, & Huber 2012).

Similar to the radial arm maze but with less possible entry points are plus- or X-shaped mazes. In the painted turtle (*Chrysemys picta*) the dorsal cortex and basal forebrain played an important role during spatial learning in a X-maze; after lesions to these brain areas turtles were impaired when relearning to navigate the same maze which was attributed to an impairment in memory (Petrillo, Ritter, & Powers, 1994). In the pond slider (*Trachemys scripta*), 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 cue trained turtles (using a single intra maze cue) were still able to learn the new goal location during a spatial reversal while turtles using a map like strategy (based on distal cues) were unable to inhibit responding to the previously correct location (Lopez, Gomez, Vargas, & Salas, 2003a).

Another popular maze is the (Morris) water maze; a pool filled with water in which a goal platform is hidden. In a slightly modified version containing four visible feeders, pond sliders 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 (Lopez et al., 2001). After lesions to the medial cortex, turtles using a map strategy were impaired when relearning to find the hidden food and when distal cues were partly concealed while a control group was unimpaired (Lopez, Vargas, Gomez, & Salas, 2003b). Furthermore, male Italian wall lizards (*Podarcis sicula*) used a sun compass to locate a hidden goal platform in the Morris water maze; covering the parietal eye (a photoreceptive third eye found on the head) revealed that it was 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 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 Australian water skinks (*Eulamprus quoyii*) learnt to escape into a ‘safe’ refuge and to avoid an ‘unsafe’ hide based on spatial location (Noble, Byrne, & Whiting, 2014) and 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. Contrary expectations, they 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 indicating some differences in spatial orientation between the tested species (Day, Crews, & Wilczynski, 1999). In a related study, malewhiptail lizards (*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 while damage to the medial cortex greatly slowed learning and strongly interfered with navigation by decreasing search efficiency and increasing time spent walking around the edge of the maze (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. Male 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, Roth, Cerjanic, Sinervo, & Pravosudov, 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, Harris, Aranguren, & Bostock, 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 two studies investigated a reptiles spatial learning ability in a naturalistic 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 navigate successfully and find a water body. While residential animals used specific routes back to the water, translocated turtles failed to find water (Roth & Krochmal, 2015). Furthermore, male eastern water skinks learnt to locate a ‘safe’ refuge out of three possible hides within a semi-natural outdoor enclosure (Noble, Carazo, & Whiting, 2012) which spatial learning strategy lizards’ used, however, was not investigated.

Conditions during development, potentially influencing brain development, can have an effect on spatial learning. Hatchlings of the velvet gecko (*Oedura lesueurii*) incubated at ‘cold’ temperatures were faster at learning the location of a shelter compared to hatchling incubated at ‘hot’ 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). Contrary, 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 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). Little is known about how incubation treatments or rearing environment alters the reptilian brain. The examples above do, however, demonstrate how conditions during embryonal development affect behaviour shown after hatching and that this change can have prolonged consequences for survival.

Together these studies show that 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 towards a goal and use the sun to navigate. Previous work has also indicated that experience with a habitat is crucial for successful navigation and that even closely related species show nuanced differences in their use of spatial information. Importantly, the studies in snakes clearly demonstrate the importance of considering a species ecology to apply the most appropriate task. Furthermore, evidence in turtles suggest the involvement of the basal forebrain, the dorsal and medial cortex in spatial navigation, lesions differentially impair memory associated with navigational strategy; the involvement of the dorsal and medial cortex in lizard navigation is, however, less clear. Finally, incubation environment affects spatial learning although differently in different species. 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.

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

While foraging it is important to identify food sources or patches that are still providing food and are not already depleted. To save time and energy when searching patches, animals have to learn to recognise specific cues associated with the availability of food (optimal foraging theory, Pyke, 1984). Discrimination learning can be used to find out which cues are salient to animals by confronting them with at least two stimulus choices (such as two colours or brightness, patterns or light flicker frequencies) of which one is rewarded and the other is 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) to gain a reward (Leighty, Grand, Courte, Maloney, & Bettinger, 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).

Reptiles can also be trained to use light stimuli such as coloured light bulbs. Wild crested anoles (*Anolis cristatellus*) were first trained to receive food whenever a yellow or green bulb was raised, later, they 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 using food rewards (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. No effect was found during discrimination learning (Powers et al., 2009; Yeh & Powers, 2005). The evidence provided above demonstrate that reptiles can use different visual cues to find a reward and simultaneously avoid a second stimulus which does not provide food, however, not all experiments were successful. Both delicate skinks, an invasive species, and common garden skinks (*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; common garden skinks, however, reached the end of a maze arm faster (Bezzina, Amiel, & Shine, 2014).

Using all these different, simple cues, reptiles can be trained to discriminate visual stimuli using a range of methods and show similar learning patterns as previously found in other taxa (Shettleworth, 2009). 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. 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

To understand if and how animals count can help better understand if our own mathematical abilities are a unique result of our language use or based on a common neural basis present in all vertebrates. Previously, a number of species demonstrated numerical abilities discriminating 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, 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 (*Mauremys reevesii*) moved down a runway was also contingent on the magnitude 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 trained with less reward. Furthermore, Italian wall lizards 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 differently sized stimuli with a ration of 0.25 (Petrazzini, Bertolucci, & Foa, 2018). According to the distance effect (increased discriminability the more distance between two numbers or the greater the ratio between), 0.25 might have been too small for the lizards to discriminate (Agrillo & Bisazza, 2014). 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, can be measured through different tests. One simple way is reversal learning, when a previously established stimulus-reward relationship changes (Brown & Tait, 2015). 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.

Chinese pond turtles 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 eastern water skink learnt the location of a ‘safe’ refuge and to escape a simulated predator 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 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 and one Comodo dragon 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). Discrimination reversals are a common and easily implemented test which can be applied in different contexts (e.g. foraging or escape behaviour) and with a wide range of stimuli (e.g. spatial, visual or olfactory).

Some studies have implicated the involvement of different brain areas when processing discrimination learning and reversals. Studies in the painted turtle revealed that the core nucleus, dorsal cortex and parts of the forebrain are involved in processing visual stimuli. 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; 1990; Reiner & Powers, 1980; 1983). Furthermore, in the European legless lizard (*Ophisaurus apodus*), damage to the hippocampus and DVR (dorsal ventricular ridge) affected reversal performance (distinguishing between a triangle and a circle); both lesion groups took significantly longer to learn compared to normal lizards. The results indicate that lesions to the hippocampus affect inhibition while lesions to the DVR affect visual processing (Ivazov, 1983). Moreover, in hatchling three lined skinks, incubation treatment (‘hot’ versus ‘cold’) did effect learning using lid covered food wells in different colours; only hot incubated lizards learned throughout the experiment including the reversal (Clark, Amiel, Shine, Noble, & Whiting, 2014) indicating that incubation temperature affected brain development, as to how, however, has not yet been studies.

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 using, again, 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 (one spine holding the reward while the second spine providing a visual cue), 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 et al., 1999).

Only one study, so far, looked at behavioural flexibility using an attentional intra-dimensional/ extra-dimensional (ID/ED) set-shifting approach. Tree skinks (*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. Contrary to the authors expectations, 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 compiled evidence provides ample support for the existence of behavioural flexibility in reptiles. Research in turtles indicated the involvement of the medial cortex in visual processing and in a lizard lesions to the hippocampus and DVR impaired reversal learning, albeit differently. One study revealed how developmental conditions can affect learning which represents a promising avenue for future research especially in the context of climate change. Furthermore, sophisticated behavioural flexibility might only be adaptive in certain ecological conditions, for example in harsh or highly unstable habitats (Tello-Ramos et al., 2018) or for certain hunting strategies (Day et al., 1999). A broad taxonomic approach comparing species differing in their social complexity, habitat preference, diet or hunting strategy could improve our understanding of how behavioural flexibility might increase fitness in different contexts.

### 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 as well as sub-adult Burmese pythons (*Python molurus bivittatus*) could both 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* were all successful in learning the novel technique removing lids, *A. cristatellus,* however, were less successful compared to the other two species. Although *A. cristatellus* is an invasive Anole which is often linked to higher levels of flexibility, individuals of this species showed greater neophobia which might partly explain the results (Leal, & Powell, 2012; Powell, 2012). Hatchling three lined skink 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 et al., 2014). Furthermore, both water skinks and tree skinks were able to learn how to remove a lid from a food well. Neither age (young and old; Noble et al., 2014) nor rearing environment (social or solitary; Riley et al., 2018) affected performance in these two species, respectively. Finally, Italian wall lizards and a closely related specie *P. bocagei* were also able to learn to remove lids from dishes to reach a reward. 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, 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). We still know little about reptiles capabilities in acquiring and/ or innovating novel foraging techniques and why some species learn novel behaviours quickly while others do not. Studying these innovative problem solver species in greater detail could prove a fruitful undertaking especially in the context of invasion and range expansion.

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). 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, Dantzer, Stricker, Swanson, & Holekamp, 2016). The relationship between brain size and cognitive ability is as of yet unexplored in reptiles.

### 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 heterospecifics, 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 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 receiving no demonstration 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 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) and is potentially beneficial even for animals that do not live in stable social groups.

It is well known that the relationship between individuals as well as other factors such as age or sex affect the probability with which animals use information provided by other individuals (Galef & Laland, 2005). In the water skink 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 et al., 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. 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 tested on their social learning ability. In the White’s skink, familiarity played 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, 2018b). Reversals might be more challenging and observers might have been more apt to utilised socially provided information to solve the task. Contrary to White’s skinks, in the closely related tree skink juveniles do not use social information provided from an adult to learn a similar colour discrimination task. Furthermore, rearing treatment (social or solitary) did not affect learning a discrimination or reversal task (Riley et al., 2018). Although juveniles tree skinks stay with their parents for at least one season (Whiting & While, 2017) and should have opportunity to learn from them, learning from adults in general might be less important. Using parents as demonstrators might have led to different results.

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 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).

Although generally considered as solitary animals, reptiles live in a range of social groupings exhibiting simple social tolerance to family 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., 2018b). In the closely related tree skink no performance increase through social information use was detected. These studies provide some indication 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, 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). Lesions to the basal forebrain, medial and dorsal cortex of turtles impair memory of previously learnt tasks (Petrillo et al., 1994, Lopez et al., 2003a; 2003b). 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; REF). 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 research in the research.

## Conclusions and future directions

The last 40 years of the study of reptile learning have undoubtedly demonstrated that these animals are capable of more than just instinctive reactions and simple forms of cognition (Whiting & Noble, 2018). Reptiles show a great variety in ability, which, due to the paucity of data, has as of yet to be strung together into a coherent body of evidence. In our review we have attempted to link findings to develop a more comprehensive overview and be able to clearly outline existing knowledge gabs to be filled by future investigations. We recommend the following topics to be the most fruitful future research endeavours.

### “Invader” smart reptiles

Studies on taste aversion learning in reptiles demonstrated how a single aversive event can prevent animals from consuming novel toxic invaders (e.g. Price-Rees et al., 2011; Somaweera et al., 2011). Toxic invasive species can had detrimental effects on naïve native animal populations. For example, in the northern quoll, an Australian marsupial, numbers have drastically declined due to quolls attacking invasive toxic cane toads. However, some populations exhibit reduced attack behaviour successfully coexisting with the invasive amphibian. In these toad-smart individuals avoidance behaviour is heritable meaning their offspring show the same behaviour. Toad-smart individuals can, therefore, be released into the wild to protect the remaining population from extinction (Indigo, Smith, Webb, & Phillips, 2018; Kelly & Phillips, 2017; 2018). If learned taste avoidance is heritable in reptiles has not yet been investigated. Another possibility is to test if taste aversion can be socially transmitted between smart and naïve individuals. Previous work has shown how social information can affect reptiles choice through enhancement and facilitation (e.g. Davis & Burghardt, 2011; Perez-Cembranos & Perez-Mellado, 2015). Conservation interventions might be greatly enhanced by adopting a behaviour centred approach by incorporating species cognitive ability. Furthermore, taste aversion in reptiles can be studied in the wild, as has been previously shown (e.g. Schall, 2000). Investigating which stimuli are most salient in different species can further our ability to improve methodological approaches and efficiently train wild individuals.

Sexual selection in the context of spatial cognition

Based on the Adaptive Specialisation Hypothesis (Kimura, 1992; Alcock, 1998), differences in ecological demands between the sexes and resulting differences in selective pressures can lead to related specialisations including cognitive abilities. Males of promiscuous mammalian species, for example, show greater spatial memory ability compared to females which was linked to greater spatial demands in males. Contrary, males and females of monogamous species, with similar spatial demands, showed no such difference (Gaulin & Fitzgerald, 1989; Perdue, Snyder, Zhihe, Marr, & Maple, 2011). A large portion of the existing studies on spatial learning, especially in lizards, focuses on male individuals only (e.g. Day et al., 1999; 2001; Foa et al., 2009; LaDage et al., 2012; Mueller-Paul et al., 2012) and those studies testing both sexes rarely look for a sex difference in performance (e.g. Lopez et al., 2000; 2001; Zuri & Bull, 2000). In many lizard species, males and females have different home range sizes (Stamps, 1977) and we would expect similar differences in spatial learning ability as previously found in mammals. Furthermore, the sexes might use different learning strategies similar to humans. Women, for example, can memorise a greater number of 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 cognitions.

Executive function

Core executive function comprise inhibitory skills, selective attention, associated memory and flexibility in cognition. These processes act against instinctive or automatic reactions to enable animals to make informed decisions. A plethora of methods exist to test for executive function including reversal learning and set-shifting testing for behavioural flexibility (Brown & Tait, 2015; Diamond, 2013) which have previously been successfully applied in reptiles (e.g. Leal & Powell, 2012, Powell, 2012; Mueller-Paul et al., 2014; Szabo et al., 2018). Impairment in executive function have been linked to diseases such as Alzheimer’s, Parkinson's or Schizophrenia (e.g. Royall et al., 2002). Understanding how executive functions are processed in reptile brains which exhibit a different neurological architecture compared to mammals (Nomura et al., 2013) might aid the understanding of how these diseases affect the human brain and help develop better treatments.

Innovative problem solving in lizards

In lizards, body shape is a strong indicator of ecology. While sit-and-wait forager ambush passing prey, use little olfactory cues and rely heavily on vison, active foragers typically move through the habitat searching for prey by tongue flicking to detect odour cues emitted by hidden prey. Concealed prey is often uncovered by removing debris, leaves or soil (Whiting & Noble, 2018). Previous examples have already demonstrated that lizards are able to learn novel foraging techniques and some species are even capable of solving more complex problems such as puzzle boxes. It is our firm believe that lizards possess the ability to invent behaviour or apply existing behaviour in new ways when facing novel problems. Active foragers might be especially suited to look for innovative behaviour. Varanids, for example, are considered as ‘smart’ reptiles and in Australia, these lizards can be frequently found in picnic areas already habituated to human presence (Whiting & Noble, 2018) which represents a great opportunity to study Varanids on similar puzzle boxes or more complex arrangements in the wild (Whiting & Noble, 2018).

Social learning in social reptiles

As previously described, most social learning studies have been conducted on animals that aggregate into social groups (Wilkinson & Huber, 2012). This focus was mainly based on the hypothesis that the demands of social group living act as a selective pressure and improve cognition for individuals to cope with these demands (Social Intelligence Hypothesis: Byrne & Whiten, 1988; Social Brain Hypothesis: Reader & Laland, 2002). Reptiles, as mostly solitary animals have, however, demonstrated that social grouping is not necessarily a prerequisite for good social information use (e.g. Noble et al., 2014; Wilkinson et al., 2010). Although we agree that testing non-social species on their social information use is an important research endeavour, we want to strongly encourage researchers to also test social reptiles (Whiting & While, 2018). A direct comparison between closely related species differing in their social complexity might give interesting insights into how sociality affects social information use in reptiles. Furthermore, utilising videos of conspecifics demonstrating a task (e.g. Siviter et al., 2017; Kis et al., 2015) could potentially be adapted to test individuals in the wild. With the currently available smart phone technology videos can be easily created and played back in the field presenting a novel opportunity to study social information use in a more ecologically relevant, naturalistic setting.

Cognition in ecologically relevant contexts

When considering the research covered in our review only a few studies have attempted to test learning ability 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 has already shown how a failure to consider a 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). Taking into account species ecology and life history could greatly enhance results obtained from cognitive studies. Additionally, testing cognition in the wild would make results easier to relate to ecology. We are aware of the difficulty of cognitive studies in wild population (see also Whiting & Noble, 2018), some questions can only be tested within a controlled laboratory setting and the use of wild caught individuals can be a suitable alternative to studies in wild populations. Within this context, species adaptations in ecology and behaviour should always be considered before attempting study design. Researchers should carefully select relevant stimuli and consider the context in which a certain ability is tested. In certain cases a comparative approach in more than one species might be recommendable to answer certain questions. Currently, the field of reptile cognition is rapidly advancing, taking the aforementioned considerations into account will ensure high quality research output in this young field of study.

Do big brains make smart reptiles?

Brain correlates of cognition have intrigued researchers for many years. What are the neural substrates that differ between species that lead to differing cognitive performance? What measure explains the difference between species: Absolute brain size, relative brain size, size of specific regions, neural complexity (Chittka & Niven, 2009; Healy & Rowe, 2007; 2013)? We still have no conclusive answer to these questions (Benson-Amram et al., 2016; Reader & Laland, 2002). Furthermore, available data is taxonomically biased towards primates, selective other mammals such as carnivores and birds (Reader & Laland, 2002). So far, we know little about reptile brains in general, how cognitive abilities map onto the reptilian brain and if there is a similar link between measurements of brain morphology and cognitive ability as found in other animals. Only a few studies have looked at how specific brain structures are involved in different learning processes in reptiles (e.g. Day et al., 2001; Ivazov, 1983; Punzo, 1985) and those studies mainly 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). Experimentally assessing the relationship between cognition and brain measurements is challenging across animals because each species is uniquely adapted to their particular ecological niche (Benson-Amram et al., 2016).

This might seem overly generous, but nevertheless we

shouldn’t be dismissive of insect’s often impressive abilities

just because they have small brains. Chittka & Niven, 2009

Final remarks

What work best

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