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

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Word count: 10,996

## Abstract

## Introduction

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

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

Modern reptiles are the third most species rich group of vertebrates inhabiting a wide range of different habitats, showing diversity in mating systems (monogamy to polygynandry), feeding ecology, social structure (solitary to groups of many individuals), reproductive tactics (parthenogenesis, oviparity or viviparity) and differ substantially in behaviour (Whiting & While, 2017). For example, many reptiles exhibit oviparity without parental care representing a unique opportunity to study developmental effects on cognition not answerable using mammals or birds (Matsubara, 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 mammals about 280 million years ago (Macphail, 1982) and their brain exhibits several prototypic features (Nomura, Kawaguchi, Ono, & Murakami, 2013). Extant reptiles have, however, also experienced similar selective pressures as modern mammals since the split (Wilkinson & Huber, 2012). Expanding the taxonomic approach might give insight into a more prototypic vertebrate cognitive ability but can also help understand convergent evolution.

**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.

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

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

### Avoiding aversive stimuli

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

Undoubtedly, avoiding harmful food is important, escaping predators is, however, no less crucial for survival. In their natural habitat, curly-tailed lizards (*Leiocephalus schreibersii*) rapidly learnt to avoid capture. Females did so faster than males and after only one capture event (Marcellini & Jenssen, 1991). In male eastern fence lizardsescape behaviour was linked to corticosterone: compared to control animals, that showed increased flight initiation distance and decreased hiding time, males receiving 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 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 don’t just use pattern to choose a ‘safe’ refuge, they are similarly skilled using colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, escaped a simulated predator attack into a ‘safe’ refuge using location or colour (Chung et al., 2017). More lizards learnt when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang, Goulet, & Chapple, 2018). Besides population effects, developmental conditions can also alter escape behaviour. Hatchling White’s skins (*Liopholis whitii*) whose mothers received a low resource treatment were more likely to escape into a ‘safe’ refuge compared to hatchlings from mothers receiving a high resource treatment (Munch et al., 2018a). Thus, when escaping, reptiles can rely on a range of visual cues to find a safe refuge.

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

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

### Spatial cognition

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

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

Some studies use an open arena to test animals on their spatial learning ability. Sleepy lizards (*Tiliqua rugose*), for instance, preferred the location of familiar refuge sites within their enclosure. When brightness or shape were associated with the refuge, lizards preferred the familiar signal no matter its’ location (Zuri & Bull, 2000). For little brown skinks, 48h of experience with an arena was crucial to escaped under a randomly chosen correct refuge, without experience, they did not learn within the two days of testing (Paulissen, 2008). Furthermore, male Australian water skinks (*Eulamprus quoyii*) learnt to escape into a ‘safe’ refuge avoiding an ‘unsafe’ hide based on spatial location (Noble, Byrne, & Whiting, 2014) and male *Acanthodactylus boskianus* and A. *scutellatus*, differing in foraging strategies, both learnt to find a heated goal rock in a round arena. Unexpectedly, no difference in latency or spatial learning strategy were found between these species. When tested with a single local cue, however, the active forager, A. *boskianus*, took longer to learn pointing towards subtle species specific differences in spatial orientation (Day, Crews, & Wilczynski, 1999). In a related study, malewhiptail lizards (*Cnemidophorus inornatus*) navigated the same arena using no apparent spatial strategy. Lesions to the dorsal cortex slowed learning while damage to the medial cortex greatly impaired search efficiency by increasing time moving along the edge of the maze (Day, 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*) used extra-maze spatial cues to find the goal hole even after 180° rotation (LaDage, Roth, Cerjanic, Sinervo, & Pravosudov, 2012). Likewise, a group of juvenile corn snakes (*Elaphe guttata guttata*) successfully navigated the Barnes maze decreasing distance travelled and errors below chance on all trials (Holtzman, Harris, Aranguren, & Bostock, 1999). Whereas only half of a group of juvenile pythons (*Antaresia maculosa*) learnt to find the goal hole in the same task. Pythons did not decrease latency and no specific learning strategy could be identified. While corn snakes are terrestrial, pythons are usually arboreal. Habitat preference might explain these different findings (Stone, Ford, & Holtzman, 2000).

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

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

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

### Learning during foraging

While foraging it is important to discriminate food sources or patches providing food from those that are depleted. To save time and energy when searching, it is important to recognise cues associated with food availability (optimal foraging theory, Pyke, 1984). During discrimination learning, animals are confronted with at least two stimulus choices (such as two colours, patterns or light frequencies), one rewarded and the other not. Florida red-bellied cooters (*Pseudemys nelsoni*), for instance, successfully discriminated between two bottles based on a visible food pellet or bottle-brightness (black and white). Pond sliders too, learnt the same black and white discrimination (Davis & Burghardt, 2007; 2012). Using coloured paddles, common box turtles (*Terrapene carolina*) successfully learnt and transferred a rule (lighter or darker) to novel stimuli of different colours (blue and green; Leighty, 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). Finally, male eastern water skinks relied on colour to solve a three-choice discrimination; no correlation was found between successful learning in the colour discrimination and a previously tested spatial learning task. Reptiles can also be trained to use light stimuli such as coloured light bulbs to find food. Wild crested anoles (*Anolis cristatellus*) first received food whenever a yellow or green bulb was raised, 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 (Woo et al., 2009) and painted turtles learnt to rely on illuminated response keys to receive a reward. Turtles showed impaired performance during negative patterning (testing for configural association learning of compound stimuli) after blocking of nitric oxide and acetylcholine in the dorsal cortex. While blocking nitric oxide affected responses towards single elements, blocking acetylcholine affected responses towards the non-reinforced compound stimulus but discrimination learning was not affected (Powers et al., 2009; Yeh & Powers, 2005). Hence, reptiles can use many visual stimuli to find food while avoiding cues indicating no food, however, not all experiments were successful. Invasive delicate skinks and non-invasive common garden skinks (*L. guachenoti)* failed to learn which arm in a Y-maze setup (one arm painted solid orange or blue, the other in orange or blue stripes) provided a reward; common garden skinks, however, reached the maze end faster (Bezzina, Amiel, & Shine, 2014).

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

### Quality and quantity discrimination

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

### Reacting to change

Flexibly responding to environmental stimuli and adapting to change quickly is important for survival especially in unpredictable environments (Tello-Ramos, 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 test is reversal learning, when a previously established stimulus-reward relationship changes (Brown & Tait, 2015). Another is attentional set-formation and shift, during which an animal is first trained to recognise an attentional set (a rewarded stimulus set) that is later shifted (to a stimulus in a different set, e.g. a second, formerly irrelevant dimension; Brown & Tait, 2015). Furthermore, innovation frequency or problem solving skill might also represent behavioural (or cognitive) flexibility (Auersperg, Gajdon, & von Bayern, 2014).

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

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

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

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

### Solving novel problems

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

### Social learning

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

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

The relationship between individuals and factors such as age or sex can affect the probability with which animals employ socially provided information (Galef & Laland, 2005). In water skinks age and dominance status predicted if lizards learnt a two-choice discrimination from a conspecific. Lizards selected the correct out of two coloured lids with and without a demonstration, young males, however, learnt faster than controls while old lizards did not (Noble et al., 2014). Furthermore, dominant observers learnt faster than subordinate observers during task acquisition but not during reversals (Kar, Whiting, & Noble, 2017). Water skinks are often found in high densities around water bodies (Cogger, 2014); socially provided information is therefore readily available. As one expetion to the rule, some Australian skinks exhibit social group living (Whiting & While, 2017). In monogamous White’s skinks, familiarity improves social information use during reversal learning but not during acquisition. Three treatment groups were tested: Individuals observing their mating partner, an unfamiliar conspecific, or a non-demonstrator. Lizards observing their mate reversed faster than controls (Munch, Noble, Wapstra, & While, 2018b). Reversals might be more challenging and social information more valuable for this task. Contrary juvenile tree skinks, also a monogamous species, did not use information provided by an adult in a similar discrimination task. Furthermore, rearing treatment (social or solitary) did not affect discrimination or reversal learning (Riley et al., 2018). Although families stay together for at least one season (Whiting & While, 2017) and juveniles have opportunity to learn from parents, learning from any adult might be less important. Using parents as demonstrators might have led to different result.

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

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

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

### Memory

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

## Future directions

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

### “Invader” smart reptiles

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

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

## Conclusions

What work best

Cite Whiting and Noble and Matsubara, S., Deeming, D. C., & Wilkinson, A. (2017 for further reading on suggested improvements

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