# Taking the dragon by the horns: Towards a comprehensive 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, plays a pivotal role in their everyday life when, for example, searching for food or 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 reptile, 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 such 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 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 (Stanger-Hall, Zelmer, Bergren, & Burns, 2001) highlighting their reliance on olfactory cues. 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* as well as *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. Informed crocodiles 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 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 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 (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 different 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. Example 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 inhibit responding to the previously correct location (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 maze. In a modified version applying feeders, pond sliders usd 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 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 was 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). 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 was found. When tested with a single local cue, 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 to. 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 the maze was rotated 180° (LaDage, Roth, Cerjanic, Sinervo, & Pravosudov, 2012). Likewise, a group of juvenile corn snakes (*Elaphe guttata guttata*) all successfully navigated the Barnes 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 back to the water, translocated animals (with no knowledge of the habitat) failed to find water. Experience especially during the first few years of life, was crucial for these turtles to navigate successfully and find a water body (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 have an effect on spatial learning, potentially by affecting brain development. 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* probaility to located a save refuge compared to both normoxic and hyperoxic animals (Sun, Wang, Pike, Liang, & Du, 2014). Finally, rearing environment (social or non-social) after birth did not affect juvenile tree skinks performance 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 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.

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

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 re 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. 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 cstimuli 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) demonstrate 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 a 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).

Chinese pond turtles 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 making 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). Discrimination reversals are a common test applicable in different contexts (e.g. foraging or escape behaviour) and various stimuli (e.g. spatial, visual or olfactory).

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 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).

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).

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, higher order behavioural flexibility (set-shifting) 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 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*) both learnt to push response keys to receive 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 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 (REF), 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. Not all species, however, could be trained. White’s skinks were unable to learn this behaviour (personal conversation). 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). Little is still known about reptiles capabilities in acquiring and/ or innovating novel foraging techniques and why some species learn novel behaviours quickly while others do not. Further studying these innovative problem solvers could prove a fruitful undertaking in the context of invasion and range expansion.

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). 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 structure and even less about their social organisation (Whiting & While, 2017), 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 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 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.

## 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

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

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