# Non-avian reptile learning 40 years on: advances, promises and potential

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## Abstract

Recently, there has been a surge in cognition research in non-avian reptiles. As a diverse group of animals, non-avian reptiles (turtles, the tuatara crocodilians, and squamates - lizards, snakes and amphisbaena), have proven good model systems. We now have a better understanding of how the environment during embryonal development alters learning ability. Moreover, they have been essential in showing that group living is unnecessary for animals to learning from conspecifics. Moreover, reptiles show a diverse range of spatial learning abilities and are able to acquire novel foraging techniques. Past research has undoubtedly demonstrated that non-avian reptiles are capable of more than just instinctive reactions and basic cognition. We identified over 90 studies investigating learning in reptiles during our systematic online literature search. Our review therefore provides an up-to-date overview of current knowledge by tying the collected evidence together under eight cognitive umbrella terms. Importantly, we were able to identify a number of knowledge gaps and propose six research themes which offer important future research opportunities. Overall, we belief that for the field to move forward and produce high quality research it will be immensely important to abandon the descriptive approach (testing if a species can learn a task) in favour of an experimental approach elucidating cognitive variation between and within species. With the appropriate methodology, this still young field of research should advance greatly in the coming years and represents a significant research opportunity.

*Keywords:* Amphisbaena, Chelonia, cognition, Crocodilia, integrative review, Reptilia, Rhynchocephalia, Serpentes, Squamata

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## Introduction

Cognition, the process by which animals collect, store, and use information, plays a pivotal role in their everyday life. It is integral to finding food and shelter, avoiding predators, finding and distinguishing between conspecifics and potential mates and adapting when environmental conditions suddenly change (Shettleworth, 2009). It is therefore not surprising that there has been immense interest in understanding what drives variation in cognition (e.g. Boogert et al., 2018; Dougherty & Guillette, 2018; Volter et al., 2018), how learning and cognitive processes impact fitness (e.g. Huebner et al., 2018; Madden et al., 2018; Thornton et al., 2014) and the underlying mechanistic basis for species differences in decision making and problem solving (e.g. Lefebvre et al., 2004; Mustafar et al., 2018; Volter et al., 2018). While we have seen a surge in cognitive studies, particularly a move towards those done in the wild, there has been a clear focus on particular taxonomic groups, such as birds and mammals. Only recently, has research begun to appreciate the diversity of cognitive variation across a broader range of animal groups and moved to take a more comprehensive comparative approach.

Non-avian reptiles, from here on called reptiles (including turtles, crocodilians, tuatara and squamates - lizards, snakes and amphisbaenids), have proven to be superb model systems in addressing developmental and age effects on learning (e.g. Amiel et al., 2014; Dayananda & Webb, 2017; Munch et al., 2018; Noble et al., 2014; Szabo et al., 2019), individual variation in learning (e.g. Carazo et al., 2014; Chung et al., 2017; Kar et al., 2017; Noble et al., 2014) and spatial cognition (e.g. Foa et al., 2009; Lopez et al., 2001; Wilkinson et al., 2009). As ectotherms, temperature plays an important role during embryonal development of phenotype including sex (temperature dependent sex determination, Warner, 2010), brain morphology and behaviour (e.g. Amiel et al., 2016; Booth, 2006; Matsubara et al., 2017). Furthermore, many reptiles are precocial and the juvenile brain is much more developmentally advanced at birth compared to altricial species (Charvet & Striedter, 2011; Grand, 1992; Szabo et al., 2019). Some reptiles have evolved rudimentary forms of sociality including long-term monogamy to big multi-generational family groups in which individuals delay dispersal sometimes into adulthood (While et al., 2015; Whiting & While, 2017). Importantly, reptiles diverged from mammals about 280 million years ago (Macphail, 1982) and their brain exhibits several prototypic features (Nomura et al., 2013). Modern reptiles are the third most species rich group of vertebrates (10,793 species as of July 2018, Uetz et al., 2019) 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 (Fox et al., 2003; Reilly et al., 2009; Uller & Olsson, 2008; Whiting & While, 2017). As such, we have seen a surge in work on reptile cognition (Figure 1) given their potential to address fundamental questions in cognitive ecology.

Gordon Burghardt (1978) introduced the first major review on reptiles as the field was only just developing. This review was critical in establishing and describing methods in the field and providing a preliminary overview of reptile learning. Burghardt’s review included over 70 species and described learning processes from simple habituation to different forms of conditioning, maze and detour learning and visual discrimination learning (including reversals) highlighting major limitations of existing cognitive work at the time. More recently, Wilkinson and Huber (2012) provided an update on new developments including accounts of social cognition – a novel direction in the study of reptilian cognition. Our systematic literature search identified over 90 studies on reptile learning (Figure 1) of which none were included in Burghardt (1978) and only 18 were included in Wilkinson & Huber (2012). Consequently, this calls for a comprehensive and systematic review to provide an unbiased update on the state of the field.

Here we conduct the first systematic review of cognition research (primarily learning) on non-avian reptiles over the last 40 years. A systematic review uses standardized and transparent search methods to select relevant studies to be included in the review (Stevens, 2001 cited by McGowan & Sampson, 2005; Higgins & Green, 2011). Multiple databases are searched and all articles are screened for relevance and inclusion based on well-defined criteria, making it less likely to miss important research and reducing biased representation of existing work.

Our aim was to present a detailed overview of the learning research done in reptiles since Burghardt (1978). We want our review to be thorough and as comprehensive as possible functioning as a guide of existing research to foster improvements that enhance future work. We identify a number of fruitful future research endeavours that are sure to inspire novel research questions in reptilian cognitive ecology.

I. Systematic Review and Literature Compilation

Wof their references (citations to these articles) ,After further scrutinizing papers based on their abstract our

We present the full table of relevant studies on non-avian reptiles in Table S1, Appendix I, and below we provide a discussion of this work relevant to each category of learning we defined above.

## 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. Conditioned taste aversion functions to avoiding toxic food with a potential noxious effect. It is a conserved ability demonstrated by a wide range of species that is highly adaptive because it aids survival (e.g. Bernstein, 1999). It is therefore not surprising to find that reptiles too, quickly learn to avoid food that either taste bitter or cause illness after ingestion. Mostly, research into taste aversion has focused on lizards. Only a single study tested a crocodilian and, to the best of our knowledge, it is still unclear if flavour aversion learning occurs in turtles. 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). These lizards rejected bitter prey but failed when the vomeronasal organ was blocked, highlighting their reliance on chemical cues (Stanger-Hall et al., 2001). Similarly, hatchling oriental garden lizards (*Calotes versicolor*) associated dish colour with prey taste. Independent cohorts of hatchlings received the same experience: neutral taste in non-painted dishes, sweet taste (from sucrose) in orange dishes and bitter taste (from chloroquine phosphate) in green dish. When presented with the same combinations they avoided dishes in the colour that had previously contained bitter prey. When lizards were presented with novel colour-taste combinations, however, they attacked bitter prey showing that they had associated dish colour with taste (Shanbhag et al., 2010). *Basiliskus vittatus*, *B*. *basiliscus*, *Eumeces schneideri* and *Eutropis multifasciata* avoided a novel food one week after a 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 skinks (*Tiliqua scincoides scincoides* and *T. s. intermedia*) fed cane toad sausages (*Rhinella marina*, a toxic invader) injected with LiCl avoided this food for seven weeks. A control group treated with saline showed little to no aversion and both groups accepted sausages of reptile feed nine weeks after illness (Price-Rees et al., 2011). These studies highlight how bitter tastes or illness are quickly avoided after only a few encounters, which was also demonstrated in the wild. Laurent's whiptail lizards (*Cnemidophorus murinus)* distinguished palatable (soaked in tomato juice) from unpalatable (soaked in quinine hydrochloride) sponges placed in their natural habitat based on visual (green - toxic versus red - sweet) and spatial (ground versus vegetation) cues (Schall, 2000). Conditioned taste aversion can also teach animals to avoid novel or invasive unpalatable prey. Hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*), for example, avoided freshly metamorphosed cane toads (*R. marina*) after training and were more likely to reject toads compared to naïve individuals (Somaweera et al., 2011). Conversely, juvenile eastern fence lizards (*Sceloporus undulatus*) from a population invaded by toxic fire ants (*Solenopsis invicta*) did not avoid ants when simultainously presented with a cricket (*Acheta domesticu*). They increased ant consumption similar to juveniles from a population uninvaded by ants (Robbins et al., 2013). Taken together, some species might be more apt to learn to avoid unpalatable or toxic prey, although differences in methodology might account for the mixed results.

While avoiding harmful food is important, escaping predators is no less crucial for survival. In their natural habitat, red-sided 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 lizards (*S. undulatus*)escape behaviour was linked to corticosterone levels. Compared to control animals that increased their flight initiation distance and decreased hiding time, males receiving a corticosterone blocker showed no change in these behaviours and no retention 24 h later (Thaker et al., 2010). Moreover, little brown skinks (*Scincella lateralis*) used horizontal and vertical stripes to find a ‘safe’ refuge but performed better when presented with vertical compared to horizontal lines, presumably because of the nature of sheltering sites, which are at the base of trees (Paulissen, 2014). Lizards do not just choose a ‘safe’ refuge based on patterns, they are similarly skilled using colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, escaped a simulated predator attack into a ‘safe’ refuge using location or colour (Chung et al., 2017). More lizards learnt when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang et al., 2018). Besides population effects, developmental conditions can also alter escape behaviour. Hatchling White’s skinks (*Liopholis whitii*) whose mothers received a low resource treatment were more likely to escape into a ‘safe’ refuge compared to hatchlings from mothers receiving a high resource treatment (Munch et al., 2018a).

Similarly significant for survival is the avoidance of potentially harmful environmental conditions such as excessive heat or shock (Shettleworth, 2009). Brown anoles (*Anolis sagrei*), 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). Moreover, two out of three *Anolis grahami* avoided being pushed off their perch by leaving the perch after hearing a sound (Rothblum, Watkins, & Jenssen, 1979).

### Spatial cognition

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

In rats (*Rattus rattus*) and mice (*Mus musculus*), spatial navigation and reference memory are frequently assessed using the Morris water maze, a water filled pool containing a hidden goal platform (e.g. Vorhees et al., 2006). Only two studies have, so far, used this well-established task to study spatial navigation in reptiles. In a modified version with visible feeders, pond sliders (*T. scripta*) 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). Similar to painted turtles (*C. picta*), lesions to the medial cortex selectively impaired turtles using a map strategy affecting memory of the cognitive map when relearning to find the hidden food and when distal cues were partly concealed (Lopez et al., 2003b). Apart from visual cues, reptiles might use the sun to navigate. 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).

A second commonly used task to asses spatial reference memory in rats is the Barnes maze, a round open space with 10 holes equidistant along the edge. The Barnes maze relies in rats’ innate impulse to escape brightly lit, open spaces into a dark escape hole (e.g. Harrison et al., 2006). Conversely, mice do not readily enter these holes and need additional training (e.g. Koopmans et al., 2003). Of the three squamate species (one lizard and two snakes) tested in the Barns maze, only two showed successful learning. Similar to mice, some species might be less well suited for testing in this maze. While male side-blotched lizards (*Uta stansburiana*) used extra-maze spatial cues to find the goal hole (even after 180° rotation; LaDage et al., 2012) and juvenile corn snakes (*Pantherophis guttatus*) similarly navigated the Barnes maze decreasing distance travelled and errors below chance on all trials (Holtzman et al., 1999), only half of a group of juvenile spotted pythons (*Antaresia maculosa*) learnt to find the goal. Pythons did not decrease latency and no specific learning strategy could be identified. While corn snakes are diurnal and were very active at exploring the arena, Spotted pythons are nocturnal and showed little exploration during trials which might explain these different findings (Stone et al., 2000).

Some studies use semi-natural enclosures to test spatial learning ability. These studies have demonstrated how lizards can use visual cues to find a refuge, how important it can be to have experience with the environment to escape a threat and that different species use different cues to learn which can sometimes be very subtle. 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 (*S. lateralis*), 48h of experience with an arena was crucial to escape under a randomly chosen correct refuge, without experience, they did not learn within the two days of testing (Paulissen, 2008). Male Australian eastern water skinks (*Eulamprus quoyii*) learnt to escape into a ‘safe’ refuge avoiding an ‘unsafe’ hide based on spatial location (Noble et al., 2014) and male *Acanthodactylus boskianus* and *A.* *scutellatus*, differing in foraging strategies (active versus ambush respectively), both learnt to find a heated goal rock in a round arena. Unexpectedly, no difference in latency or spatial learning strategy (such as a cognitive map or landmarks) was found between these species. When tested with a single local cue, however, the active forager, *A*. *boskianus*, took longer to learn suggesting subtle species-specific differences in spatial navigation (Day et al., 1999). In a related study, male little whiptail lizards (*Aspidoscelis* *inornatus*) navigated the same arena using no apparent spatial strategy. Lesions to the dorsal cortex slowed learning while damage to the medial cortex greatly impaired search efficiency by increasing time moving along the edge of the maze (Day et al., 2001).

Two studies investigated spatial learning in a naturalistic setting. Using radiotracking, only residential (with knowledge of the habitat) wild painted turtles (*C. picta*) used specific routes to find water, while translocated animals (with no knowledge of the habitat) failed this task. Importantly, follow-up tests showed that experience, especially during the first few years of life, proved crucial for these turtles to navigate successfully and find a water body. Furthermore, UV but not olfaction was important for spatial orientation (Roth & Krochmal, 2015). In lizards, male eastern water skinks (*E. quoyii*)located a ‘safe’ refuge out of three possible options within a semi-natural outdoor enclosure (Noble et al., 2012); which spatial strategy lizards used, however, was not assessed.

Unlike mammals, offspring of birds, fish and reptiles develop outside the parental body within eggs. Although many birds and fish protect and/ or incubate their eggs, most reptile species abandon their clutches after laying leaving them exposed to different environmental fluctuations potentially affecting embryonal development (morphology and performance; Deeming, 2004). In lizards, differences in incubation or oxygen levels resulted in differing learning performance, in one species, learning proficiency could even be linked to survival. Hatchling Lesueur's velvet geckos (*Amalosia lesueurii*) incubated at ‘cold’ temperatures were faster spatial learners compared to ‘hot’ incubated geckos. Furthermore, after release at their mother’s capture site, hatchlings with higher learning scores survived longer, indicating a lasting effect on survival (Dayananda & Webb, 2017). Conversely, hatchling three-lined skinks (*Bassiana duperreyi*) incubated under ‘hot’ conditions earned higher learning scores compared to ‘cold’ incubated lizards (Amiel & Shine, 2012). Moreover, hypoxic conditions during incubation decreased hatchling *Eremias argus’* probability to located a ‘safe’ refuge compared to both normoxic and hyperoxic animals (Sun et al., 2014). Finally, no effect of rearing environment (social or solitary) after birth was found in juvenile tree skinks (*E. striolata*) solving a vertical maze (Riley et al., 2016). Little is known about how incubation treatments or rearing environment alters the reptilian brain (but see Amiel et al., 2016). The examples above do, however, demonstrate prolonged influence on behaviour and survival of environmental effects.

### Learning during foraging

While foraging, it is important to discriminate food sources or patches providing food from those already depleted. To save time and energy during searching, animals need to recognise cues associated with food availability (optimal foraging theory; Pyke, 1984). During discrimination learning, animals are presented with a choice of at least two stimuli (such as two colours, patterns or light frequencies), one rewarded and the other not. Many reptiles have proven proficient in using visual cues such as colour and brightness to learn about stimulus-reward relationships. Florida red-bellied cooters (*Pseudemys nelsoni*), for instance, successfully discriminated two bottles based on a visible food pellet or bottle-brightness (black and white). Pond sliders (*T. scripta*) too, learnt the same black and white discrimination (Davis & Burghardt, 2007; 2012). Using coloured paddles, common box turtles (*Terrapene carolina*) successfully learnt to select the lighter or darker of two stimuli (out of five shades) and transferred this rule to novel stimuli of different colours (blue and green; Leighty et al., 2013), and similarly, rough-necked monitors (*Varanus rudicollis*) and a Komodo dragon (*Varanus komodoensis*) used paddle brightness (black and white) to obtain a food reward (Gaalema, 2007; 2011). Finally, male eastern water skinks (*E. quoyii*) relied on colour to solve a three-choice discrimination but no correlation was found between successful learning in the colour discrimination and a previously tested spatial learning task (Qi et al., 2018).

Reptiles can also be trained to use light stimuli such as coloured light bulbs to find food. Wild crested anoles (*Anolis cristatellus*) first received food whenever a yellow or green bulb was raised and later preferred the trained colour during a simultaneous two-choice test (Shafir, 1995). Tuataras (*Sphenodon punctatus*) were able to discriminate between flicker frequencies in a simultaneous two-choice test (Woo et al., 2009) and painted turtles (*C. picta*) learnt to rely on illuminated response keys to receive a reward but showed impaired performance during negative patterning (testing for configural association learning of compound stimuli in which two single stimuli are reinforced but the compound made out of both stimuli is not reinforced) 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 blocking acetylcholine did not affect discrimination learning (of single elements) (Powers et al., 2009; Yeh & Powers, 2005). Hence, reptiles can use multiple visual stimuli to find food while avoiding cues that indicate no food. Not all experiments were, however, successful. Invasive delicate skinks (*L. delicata*) and non-invasive common garden skinks (*Lampropholis* *guichenoti*) failed to learn the correct arm in a Y-maze setup (one arm painted solid orange or blue, the other in orange or blue stripes) but common garden skinks reached the maze end faster (Bezzina et al., 2014).

### Quality and quantity discrimination

Judging quality and quantity are important capabilities during foraging, mate choice or when making decisions about joining a group (e.g. shoal choice in fish). Numerosity has been demonstrated in a wide range of animals from insects (e.g. Pahl et al, 2013) to fish (e.g. Agrillo & Bisazza, 2018), mammals (e.g. Abramson et al., 2011; Benson-Amram et al., 2018; Hanus & Call, 2007; Uller & Lewis, 2009), birds (e.g. Bogale et al., 2014; Garland et al., 2012; Rugani et al., 2018), and amphibians (e.g. Stancher et al, 2015; Uller et al., 2003). With the addition of data on three turtles and one lizards species numerical abilities have now been confirmed for all vertebrates. For example, after associating a stimulus with a specific reward quality or quantity, red-footed tortoises (*C. carbonarius*) selected the preferred food and larger quantity during the simultaneous presentation of two stimuli differing in value (Soldati et al., 2017). The speed with which Reeves’ turtles (*Mauremys reevesii*) moved down a runway was also contingent on the magnitude of food 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). Italian wall lizards (*P. sicula*) spontaneously discriminated between two food items differing in size (ratios 0.25 to 0.75) but did not select the larger of two quantities (Petrazzini et al., 2017). When the same species was later tested on a trained discrimination of both size and quantity, lizards discriminated between 1 versus 4 (N = 6/10) and 2 versus 4 (N = 1/6), but not between 2 versus 3 yellow disks and none were able to discriminate between two differently sized disks (ration of 0.25; Petrazzini et al., 2018). These conflicting results might be explained by differences in the stimuli used. Motivation to approach artificial stimuli might differ from motivation towards actual food items. Using a similar spontaneous discrimination test, Herman’s tortoises (*Testudo hermanni*) successfully chose the larger size/ quantity of tomato outperforming *P. sicula* on the quantity discrimination (1 vs 4, 2 vs 4, 2 vs 3 and 3 vs 4) but not on the size discrimination (Gazzola et al., 2018). Differences between species could be related to feeding ecology. Lizards feed on live, moving prey and tortoises mostly on vegetation. When optimising food intake during foraging, the number of moving prey might be less important compared to size. In contrast, when feeding on vegetation, number and size might both be important during patch selection (optimal foraging theory; Pyke, 1984). These studies demonstrate that reptiles have a sense of reward quality and size, and have numerical discrimination capacities. Artificial or naturalistic stimuli might be used to test for numerosity, however, both pose benefits and limitations (Agrillo & Bisazza, 2014).

### Responding to change

Flexibly responding to environmental stimuli and adapting to change quickly is important for survival especially in unpredictable environments (Tello-Ramos et al., 2018). Behavioural flexibility, the ability to adjust to environmental variation by adapting attention and behaviour and using existing skills to solve novel problems or existing problems in a new way, can be measured through different tests. One test is reversal learning, when a previously established stimulus-reward relationship changes (Brown & Tait, 2015). In recent years, reversal learning has become a somewhat standard test to investigate behavioural flexibility in reptiles. Reeves’ turtles (*M. reevesii*), for instance, reversed a simple left/ right discrimination. Turtles that were overtrained on the initial discrimination for an additional 100 trials, however, reversed slower (Ishida & Papini, 1997). Eastern water skinks (*E. quoyii*) 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). Little whiptail lizards’ (*A. inornatus*) avoided a heat lamp using features (colour, brightness or pattern) or the location of a ‘safe’ refuge in a reversal. During acquisition spatial cues were more salient to the lizards than visual cues but not during reversals (Day et al., 2003). Male rough-necked monitors (*V. rudicollis*) and one Komodo dragon (*V. komodoensis*) increased performance during a serial reversal (Gaalema, 2007; 2011) and red-footed tortoises (*C. 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). A comparative approach testing multiple species with the same methodology in 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 provided a visual cue) compared to *A. scutellatus*, a sit-and-wait forager. Active foraging might require better inhibitory skill, also crucial in reversal learning, to inspect prey before striking (Day et al., 1999). Taken together, all tested species demonstrated the ability to solve visual or spatial reversals. Given the general success rate, reversals alone might be a poor measure of behavioural flexibility in reptiles. Combining reversals with related tests of innovative problem solving (e.g. Auersperg et al., 2014; Leal & Powell, 2012) or attentional set-shifting (Szabo et al., 2018; 2019) could be a better way to investigate behavioural flexibility. If subjects use, for example, different techniques to solve a novel problem or quickly shift to a previously untrained attentional set (to a stimulus in a e.g. second, formerly irrelevant dimension; Brown & Tait, 2015) it could provide stronger evidence for behavioural flexibility. Tree skinks (*E. striolata*) were the first lizard species to be tested using an attentional intra-dimensional/ extra-dimensional (ID/ED) set-shifting approach. Unexpectedly, lizards did not establish an attentional-set but performed each set of two stages (discrimination and reversal of one stimulus pair) as if facing a new problem. Skinks, however, reversed four discriminations showing some degree of flexibility in response behaviour (Szabo et al., 2018).

The structure of the reptile brain exhibits several prototypic features (Nomura et al., 2013) and we still know little about how cognitive processes are mapped onto the reptilian brain. Only a few studies test how learning is processed in specific brain structures implicating the involvement of different brain areas during discrimination and reversal learning. In the case of turtles, region-specific processing has been studied in a single species of fresh water turtle, the North American painted turtle (*C. picta*). The core nucleus, dorsal cortex and parts of the forebrain 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). Similarly, only one study provides some insight into how learning is processed in the lizard brain. In European legless lizards (*Pseudopus apodus*), damage to the hippocampus and DVR (dorsal ventricular ridge) affected reversal performance (distinguishing between a triangle and a circle), however, both lesion groups took longer to learn compared to normal lizards. Results show that hippocampal lesions affect inhibition while lesions to the DVR affect visual processing (Ivazov, 1983).

As ectotherms, reptile rely in environmental temperature to reach optimal physiological function. Temperature also plays an important role during embryonic development. Many reptile species exhibit temperature dependent sex determination (Bull, 1980). Even in species with chromosomal sex determination, incubation temperature can alter brain morphology and consequently learning ability. For example, in hatchling three-lined skinks (*B. duperreyi*), incubation treatment (‘hot’ versus ‘cold’) affected discrimination of lid colour. Only ‘hot’ incubated lizards learnt the given tasks (Clark et al., 2014). These differences in performance were linked to differences in cortex size and structure. ‘Hot’ incubated lizards had smaller telencephalon but increased neuron density in certain cortical areas (Amiel et al., 2016).

### Solving novel problems

Some species are known to be good at solving complex problems. For example, New Caledonian crows (*Corvus moneduloides*) bending wires into hooks in order to extract a reward-containing basket from within a well (Weir et al., 2002), or black rats (*Rattus rattus*) that develop new techniques for extracting pine seeds from cones when little other food is available (Zohar & Terkel, 1991) are just two examples of innovation and problem solving skills. Reptiles, as well, can learn novel foraging techniques. Painted turtles (*C. picta*) and sub-adult Burmese pythons (*Python bivitattus*), for example, both learnt to push response keys (Blau & Powers, 1989; Cranney & Powers, 1983; Emer et al., 2015; Grisham & Powers, 1989; 1990; Powers et al., 2009; Reiner & Schade Powers, 1978; Reiner & Powers, 1980; 1983; Yeh & Powers, 2005) and eight different studies have trained lizards to remove lids from wells for a reward. *Anolis evermanni*, *A*. *pulchellus and A. cristatellus* learnt lid removal*.* The latter,however, were less successful compared to the other two species showing higher levels of neophobia which may explain low performance (Leal, & Powell, 2012; Powell, 2012). This is a surprising result because *A. cristatellus* is invasive and invasion success was previously linked to increased behavioural flexibility (Sol et al., 2002) of which one measure is innovative problem solving (Auersperg et al., 2014). Hatchling three-lined skinks (*B. duperreyi*) also learnt lid removal but only ‘hot’ incubated lizards acquired this behaviour (Clark et al., 2014). Both eastern water skinks (*E. quoyii*) and adult (Whiting et al., 2018) and juvenile tree skinks (*E. striolata*) are known to remove lids but neither age (young and old; Noble et al., 2014) nor rearing environment (social or solitary; Riley et al., 2018), respectively, affected performance. Moreover, spatial learning proficiency did not predict lid opening ability in water skinks (Qi et al., 2018). Finally, Italian wall lizards (*P. sicula*) and a closely related specie *P. bocagei* learnt the same opening technique (Damas-Moreira et al., 2018). Although training preceded the tasks, these are examples of reptiles solving a novel problem. In addition to lid opening and pressing response keys, Florida red-bellied cooters (*P. nelsoni*) and pond sliders (*T. scripta*) both exited water to climb a platform and tip bottles for food, which can also be interpreted as a novel foraging technique (Davis & Burghardt, 2007; 2011, 2012). Only a single study attempted to test a reptile on a puzzle box task. Black-throated monitors (*Varanus albigularis albigularis*) opened a plastic tube to retrieve a reward within 10 minutes of the first presentation and even solved this novel task faster during the second and third trial (Manrod et al., 2008).

### Social learning

Social learning refers to learning from other individuals (conspecifics or heterospecifics) used as a shortcut to solve novel problems and in the process, avoid costly trial-and-error learning. Social learning comprises several abilities from simple enhancement and facilitation to imitation and emulation (Byrne, 1994; Heyes, 1994) and can be beneficial for social species as well as more solitary animals (Galef & Laland, 2005; Shettleworth, 2009). Nonetheless, research has focused mainly on group living animals’ social learning ability, much less is known about less social species’ social information use (Galef & Laland, 2005). Recent work has shown that even ‘non-social’ reptiles can learn from their conspecifics (Doody et al., 2013). So far, social learning has only been studied in six lizard and two turtle species and it is likely to be more common in reptiles than previously believed. Solitary living red-footed tortoises (*C. carbonarius*) were the first reptile species to show social learning in a detour task (Wilkinson et al., 2010). Tortoises that observed a demonstrator walking around a barrier learnt to detour for a reward, while a control group with no demonstration did not. During follow-up experiments, observers were able to generalise to novel barriers (inverted V- and U-shaped) and were more successful than control turtles (Wilkinson & Huber, 2012). Solitary bearded dragons (*Pogona vitticeps)* opened a sliding door in the same direction as a demonstrator after watching a video of a conspecific’s performance. A control group watching a ghost control (door opening by itself) did not learn to open the door, indicating some involvement of socially facilitated enhancement (Kis et al., 2015). Interestingly, ‘cold’ incubated hatchling bearded dragons opened a door faster than ‘hot’ incubated lizards. There was, however, no significant difference between groups in the number of successful door openings (Siviter et al., 2017). Moreover, Florida red-bellied cooters (*P. nelsoni*) matched the choice of a demonstrator during a brightness discrimination, demonstrating stimulus enhancement (Davis & Burghardt, 2011) and wild *Podarcis lilfordi* preferred locations with conspecifics present when presented with a choice between food with and without conspecifics (including static copper models). Lizards also preferred to aggregate with conspecifics (trapped in a glass jar) instead of an empty glass jar when no food was 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).

Age or sex can affect the probability with which animals employ social information (Galef & Laland, 2005). In eastern water skinks (*E. quoyii*), age but not 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 older lizards did not (Noble et al., 2014). Although dominance status did not affect the probability of social learning, dominant observers learnt faster than subordinate observers during task acquisition but not during reversals (Kar et al., 2017). Water skinks are often found in high densities around water bodies (Cogger, 2014) and social information is therefore readily available.

Social learning improves acquisition of crucial information which is essential for naïve individuals including juveniles or when facing novel challenges (Galef & Laland, 2005). Although reptiles are considered mostly solitary, Australia is home to an exceptional group of skinks, the *Egernia* group (including nine genera), with species varying in their degree of social complexity from solitary species to monogamous species living in multi-generational family groups (Chapple, 2003; Gardner et al., 2008; While et al., 2015). One such species is the monogamous White’s skinks (*L. whitii*), in which familiarity can improve social information use during reversal learning but not during acquisition. In this study, three treatment groups were tested: Individuals observing their mating partner, an unfamiliar conspecific, or a non-demonstrator. Lizards observing their mate reversed faster than controls (Munch et al., 2018b). Reversals might be more challenging and social information more valuable for this task. Conversely, juvenile tree skinks (*E. striolata*), also a monogamous and family living *Egernia* species, did not use information provided by an adult in a similar discrimination task. Furthermore, rearing treatment (social or solitary) did not affect discrimination or reversal learning (Riley et al., 2018). Although tree skink families stay together for at least one season (Whiting & While, 2017) and juveniles have opportunity to learn from parents, learning from just any adult might be costly because juveniles experience a high risk of cannibalism from unrelated adult conspecifics (REF) and therefore, they may be less likely to use them as a source of social information. Adult females of the same species do readily learn a two-choice discrimination from other, familiar females showing a decrease in errors and faster learning compared to a control group (Whiting et al., 2018). Using a familiar parent as demonstrator for juveniles might lead to different results.

Typically, animals are tested with conspecific demonstrators but it can also be beneficial to learn from heterospecifics which has been tested in one reptile species, the Italian wall lizard (*P. sicula*). This species has been introduced to a number of regions outside its natural distribution all over the globe (CABI, 2018) including regions with other species of the genus *Podarcis*. This situation creates a novel opportunity to test if *P. sicula* exploit social information from congeneric lizards that are not dissimilar to themselves. Accordingly, when tested on a colour discrimination task in which information was provided either from a conspecific or a heterospecific species (*Podarcis bocagei*), observer lizards made fewer errors regardless of demonstrator species compared to individual learners (Damas-Moreira et al., 2018). These results suggest that social information use might play some role during the establishment in a novel habitat.

### Memory

Memory can be important for survival especially if information stays relevant for extended periods of time and a good memory is energetically cheaper compared to relearning (Shettleworth, 2009). Turtles are generally long-lived and are good models for studying long-term memory. Florida red-bellied cooters (*P. nelsoni*), red-footed tortoises (*C. carbonarius*), common box turtles (*T. carolina*), and pond sliders (*T. scripta*) can remember learnt stimuli or rules for up to 36 months after initial training (Davis & Burghardt, 2007; 2011; 2012; Leighty et al., 2013; Soldati et al., 2017), but lesions to the 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 food patch 24 h later (Punzo, 2002). Some degree of retention is imperative for fitness and survival (Shettleworth, 2009). Memory, however, is little studied in reptiles, although life span can exceed 50 years in some taxa (Bull , 1995; World life expectancy, 2019). Previous research has demonstrated both 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 rare.

## Future directions

In the last 40 years, since Burghardts’ (1978) first detailed review on reptile learning, we have seen an explosion in reptile cognition research – gaining a better understanding of reptile cognitive abilities more generally. This advancement was first highlighted by Wilkinson and Huber (2012). Together with our systematic review we can now move towards testing contemporary questions regarding the role of cognition in conservation or how differences in cognition relate to species ecology and invasion success. Furthermore, cognitive processes such as executive function or sex-based spatial learning have yet to be investigated in reptiles. Here, we present some key themes and questions that we believe are particularly interesting topics for future research that have emerged as key components missing from our synthesis.

### Cognition in ecologically relevant contexts

The proficiency with which a species learns about certain stimuli depends on the degree to which selection has operated on a given cognitive process in the wild (Shettleworth, 2009). Few studies covered in our review attempted to test learning in the wild (e.g. Marcellini & Jenssen, 1991; Roth & Krochmal, 2015; Schall, 2000; Shafir, 1995), or even in ecologically relevant contexts in the lab/ captivity (e.g. Foa et al., 2009; Price-Rees et al., 2011; Robbins et al., 2013; Somaweera et al., 2011). Additionally, even fewer attempt to link findings to fitness and/ or survival (e.g. Dayananda & Webb, 2017). Inadequate attention to a species’ ecology can dramatically affect study results. For example, while corn snakes (*P. guttatus*) successfully learned to escape a Barnes maze, spotted pythons (*A. maculosa*) showed little learning in the same maze. Pythons are nocturnal, spending their days mostly curled up while corn snakes are diurnal and active during the day, which may explain differences between the studies given tests were done during the day for both species (Holtzman et al., 1999; Stone et al., 2000).

Considering species ecology and life history will enhance the value of cognitive studies and testing cognition in the wild will make results more biologically relevant, although we appreciate how challenging this can be with reptiles (see also Whiting & Noble, 2018). For questions that are only testable within a controlled laboratory setting (as compared to studies in the wild), using wild-caught individuals could be a suitable alternative (accounting for prolonged negative effects of captivity, e.g. Mohammed et al., 2002). Adequate reporting of the origin of animals is high in studies testing squamates while in turtles more than half did not report the origin of test animals (Appendix Table 1). Furthermore, information on the duration animals were maintained in captivity is scare. Overall, we encourage researchers to improve on reporting of critical study details and to select species considering ecology and life history appropriate for the research question. For example, nocturnal species should be tested in the dark under red light and as ectotherms reptiles depend on the temperature of the environment to heat their body to reach optimal physiological function which can have a major impact on response time and motivation (Whiting, & Noble, 2018). For active foragers, that rely on prey odour during foraging, task design needs to control for olfactory cues while it is less important for sit-and-wait foragers because they rely more heavily on vison (Cooper, 1995). These are just a few parameters that need to be considered when designing laboratory studies in reptiles and for more details see Whiting & Noble (2018).

### How do cognition and behaviour assist invasive species

Introduced species outside their natural range can have detrimental effects on the local species community (e.g. Reaser et al., 2007). Mechanisms favouring the successful invasion of a species into a new habitat have become of major interest but, unfortunately, traits benefiting the establishment of new populations are inconsistent between taxonomic groups (Hayes & Barry, 2008; Kolar & Lodge, 2001). Success and failure during invasion have been linked to behaviour and personality (Chapple et al.,2012) but how learning benefits individuals has received little attention (Avargue`s-Weber et al., 2013). Social learning and behavioural flexibility might play an important role during the early stages of establishment when animals frequently face novel predators or prey. Using information from congeneric species or flexibly changing behaviour could be key to survival (Sol et al., 2002; Wright et al., 2010). It has already been demonstrated that invasive lizards are able to effectively use information provided by heterospecifcs. Italian wall lizards (*P. sicula*) learnt both from individuals of their own species and a different species (*P. bocagei*; Damas-Moreira et al., 2018). This study, however, is only a first step in understanding which abilities might benefit invasive species when conquering novel challenges. Future research could focus on comparing performance in different tasks (foraging, social and spatial learning) between species known to be successful and unsuccessful invaders.

### Social learning in social reptiles

Social learning is usually studied in group living animals (Galef & Laland, 2005) because it is hypothesised that the demands of group living act as a selective pressure to improve cognition (and increase brain size) to cope with these demands (Humphrey, 1976; Jolly, 1966; Reader & Laland, 2002). Less social reptiles, however, are also capable of social learning (e.g. Noble et al., 2014; Wilkinson et al., 2010). We agree that testing non-social species is an important research endeavour, but we want to encourage researchers to also test social reptiles (Whiting & While, 2018). With available smart phone technology, video demonstrations (e.g. Siviter et al., 2017; Kis et al., 2015) could be adapted to test wild animals. Although reptiles have demonstrated the ability to learn from conspecifics in controlled lab-setups, it is less clear if such social information use also occurs in the wild. It would be interesting to see how wild reptiles react to a conspecific trying, for example, some unusual prey or using a novel technique to gain access to a previously inaccessible food source. By using video recordings researchers can exert control over task parameters and gain insight into which information is passed on. Comparing results between social and less social species might then in turn reveal differences in the used information a previously completely unexplored research endeavour.

### Avoidance of harmful invasive prey species

A single aversive event can prevent reptiles from consuming novel toxic invaders (e.g. Price-Rees et al., 2011; Somaweera et al., 2011) that can have detrimental effects on naïve native species (e.g. Indigo et al., 2018). Crocodiles (*C. johnstoni*) and blue-tongue lizards (*T. scincoides*) have been successfully trained to avoid toxic novel prey (cane toad, *R. marina*). Follow-up experiments could investigate if this behaviour is heritable (Kelly & Phillips, 2017; 2018) and/ or if avoidance behaviour can 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 reptiles (e.g. Schall, 2000). Conservation interventions will benefit from adopting a more behaviour centred approach by incorporating species-specific cognitive abilities in avoidance learning and social information use. Training a subset of individuals to spread valuable information (genetically or through social transmission) might prove effective and relatively cheap which will help conservation efforts.

### Executive function

Core executive function comprise inhibitory skills, selective attention, associated memory, and flexibility in cognition. These processes prevent automatic responses to make informed decisions. Tests for executive function include reversal learning, set-shifting, or detour tasks which are well studied in mammals (Brown & Tait, 2015; Diamond, 2013) but less well in other vertebrates. In reptiles, behavioural flexibility has been investigated using reversal learning, however, how inhibition is exerted during reversals has received little attention. Recently, eastern water skinks (*E. quoyii*) demonstrated context specific inhibitory skills in a discrimination and cylinder detour task. Lizards that successfully discriminated between two visual stimuli showed significantly worse inhibitory skills during the detour task compared to individuals that did not learn the discrimination. Previously, red-footed tortoises (*C. carbonarius*) socially learnt to detour a barrier (Wilkinson et al., 2010; Wilkinson & Huber, 2012) but how response inhibition was exerted in this species was not investigated. Furthermore, two studies, one in painted turtles (*C. picta*; Cranney & Powers, 1983) and one in tree skinks (*E. striolata*; Szabo et al., 2018), presented animals with an extra-dimensional shift testing for attentional flexibility. Both species learnt during the shift but only in tree skinks could performance on the shift be compared to a previous intra-dimensional stage to investigate if an attentional-set was formed. Skinks formed no attentional-set but learnt each new set of stimuli as if presented with a new problem. How the turtles solved the shift is unclear. Importantly, memory capacity has largely been unexplored except for five studies in turtles and one in lizards (Davis & Burghardt, 2007; 2011; 2012; Leighty et al., 2013; Punzo, 2002; Soldati et al., 2017). Executive function comprise layers of cognitive processing, forming the basis of higher order abilities such as planning and problem solving (Diamond, 2013). To understand if reptiles do, for example, plan their actions we need to establish if they possess basic executive function underlying these complex, higher-order abilities.

### Spatial cognition in the context of sexual selection

Sex-specific differences in ecological demands and the resulting selective pressures can lead to adaptive specialisation, including in cognitive ability (Alcock, 1998). For example, when spatial demands differ between males and females, promiscuous mammals differ in spatial memory ability while monogamous species do not (Gaulin & Fitzgerald, 1989; Perdue et al., 2011). Most studies on spatial learning, especially in lizards, have tested only males (e.g. Day et al., 1999; 2001; Foa et al., 2009; LaDage et al., 2012; Mueller-Paul et al., 2012) and studies investigating both sexes rarely considered sex during analyses (e.g. Lopez et al., 2000; 2001; Zuri & Bull, 2000). Only a single study *a priori* considered sex as a possible factor explaining individual variation in learning performance and subsequently uncovered a significant sex-based difference in spatial learning. Twice as many male eastern water skins (*E. quoyii*) learnt the location of a ‘safe’ refuge learning faster than females (Carazo et al., 2014). This could be quite common given that males and females of many lizard species differ in home range size (Stamps, 1977). Differences in space use patterns can arise with increased sexual selection, when males defend territories or actively search for females (Cummings, 2018). It would be quite interesting to compare male and female learning performance between species with high and low levels of sexual selection such as polygamous versus monogamous (respectively) lizards. Venturing in this unexplored research field will likely produce novel insights into reptile spatial navigation and how sexual selection shapes spatial learning.

## Conclusions

1. Our knowledge of reptile learning has greatly advanced, especially in the last decade. Most studies included here were conducted on lizards and turtles and little is known about learning abilities in snakes, tuatara and crocodilians. Our review therefore emphasises the need for the application of a broader taxonomic range within reptiles.
2. We provides an up-to-date overview of the currently available knowledge on reptile learning. We provide information on over 90 studies showing how reptiles avoid aversive stimuli including flavour aversion learning and escaping predators, which stimuli they use during spatial learning as well as foraging, their numerical abilities and their ability to learn novel foraging techniques, how they cope with change and what we know about their social learning ability and memory capacity.
3. We highlight six contemporary research themes and avenues which we believe will be of special interest in the near future:

* Social learning of avoidance behaviour could be used to teach reptiles to avoid harmful invasive prey species by spreading this knowledge to naïve individuals.
* Reptiles show a great range in ecology, life-history and behaviour. It is therefore important to consider these traits to select appropriate model species.
* Behaviour and learning might be important attributes for invasive species when invading a new environment. A comparison in a variety of tasks between invasive and non-invasive species can further our knowledge of what makes a successful invader.
* Although most reptiles are considered unsocial some species have evolved rudimentary sociality showing different levels of kin-based grouping behaviour. Testing these lizards social learning ability could disentangle which cognitive abilities are affected by sociality.
* Reasoning and planning are higher order processes which require executive function such as inhibition, attention and memory. These processes are badly understood in reptiles but could provide novel insights into the evolution of intelligence.
* When ecological demands differ between the sexes, males and females might show different adaptive specialisations such as differences in spatial learning strategy and performance. This has been well studies in mammals and some birds and fish but has largely been ignored in reptiles.

1. The field has reached a point in which it will be important to move from descriptive studies testing if a species can learn a task towards a more experimental approach to elucidate the drivers of cognitive variation within and between species. This will ensure that the field will move forward and produce high quality research in the future. Furthermore, a more ecologically adapted approach will produce higher quality data better interpretable in relation to fitness. We want to encourage researcher to venture into this young and promising field and to be more bold in applying complex methodologies.

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## Supporting information

Due to the large number of studies our review focused on the main results. Further details on each study including task specifics, stimuli and reward used during testing, learning criteria as well as age and origin of animals are summarised in Appendix Table 1.

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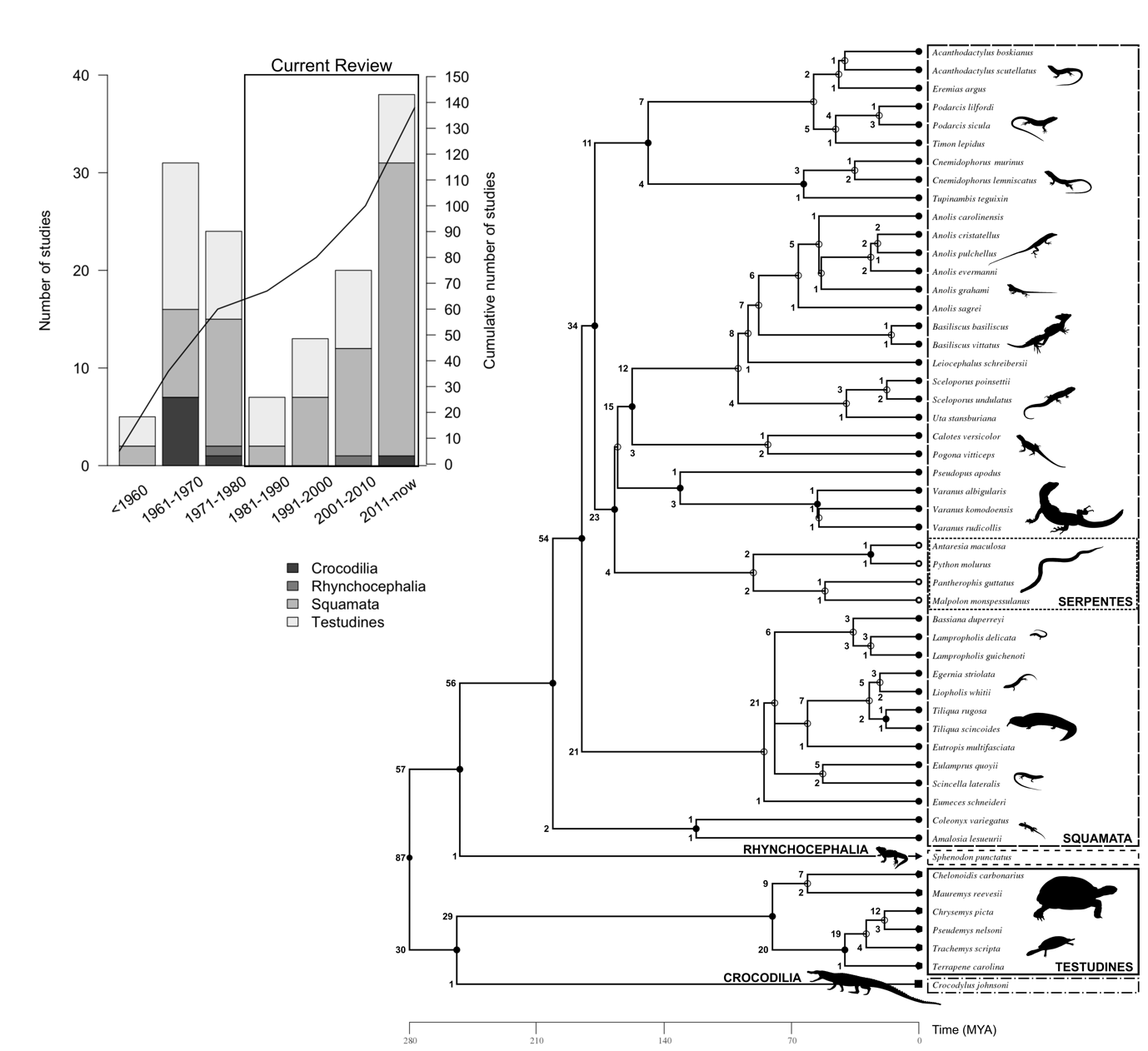
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## Appendix

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

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| SQUAMATA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 1 | Spatial | 8-choice | Arena | Distal Cues | Heat | No criterion,  latency measured | *Acanthodactylus boskianus* | Adult | Wild | Day et al., 1999 |
| Local Cue |
| Light |
| Discrimination | 2-choice | Fork | Multiple | Food | 10/12 |
| Spatial | 8-choice | Arena | Distal Cues | Heat | No criterion,  latency measured | *Acanthodactylus scutellatus* |
| Local Cue |
| Light |
| Discrimination | 2-choice | Fork | Multiple | Food | 10/12 |
| 2 | Spatial | 2-choice | Arena | Location | Shelter | No criterion | *Amalosia*  *lesueurii* | Hatchling | Captive | Dayananda & Webb, 2017 |
| 3 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  eaten or not | *Anolis*  *carolinensis* | Adult | Captive | Stanger-Hall et al., 2001 |
| 4 | Conditioning | 1-choice | Runway | Colour | Food | No criterion,  proportion correct | *Anolis*  *cristatellus* | Adult/  Subadult | Wild | Shafir, 1995 |
| Discrimination | 2-choice | T-Maze |
| 5 | Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *cristatellus* | Adult | Wild | Powell, 2012 |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *evermanni* |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| Motor Task | 1-choice | Wells | Multiple | Food | 6/6 | *Anolis*  *pulchellus* |
| Discrimination | 2-choice | Wells | Colour |
| Reversal | 2-choice | Wells |
| 6 | Discrimination | 2-choice | Wells | Colour | Food | 6/6 | *Anolis*  *evermanni* | Adult | Wild | Leal & Powell, 2012 |
| Reversal | 2-choice | Wells |
| 7 | Conditioning | 1-choice | Arena | Sound | Escape | No criterion,  80 trials | *Anolis*  *grahami* | Adult | Not Given | Rothblum et al., 1979 |
| 8 | Avoidance | 1-choice | Box | Shock | Relieve | No criterion,  number of shocks | *Anolis*  *sagrei* | Adult | Captive | Punzo, 1985 |
| 9 | Spatial | 8-choice | Arena | Multiple | Shelter | 8/10 | *\* Antaresia*  *Maculosa* | Juvenile | Captive | Stone et al., 2000 |
| 10 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  remaining food  weighed | *Basiliscus*  *vittatus* | Subadult | Not Given | Paradis & Cabanac,  2004 |
| *Basiliscus*  *basiliscus* |
| *Eumeces*  *schneideri* |
| *Eutropis*  *multifasciata* |
| 11 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  16 trials | *Bassiana*  *duperreyi* | Hatchling | Captive | Amiel & Shine, 2012 |
| 12 | Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion,  15 trials | *Bassiana*  *duperreyi* | Hatchling | Captive | Amiel et al., 2014 |
| 13 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Bassiana*  *duperreyi* | Hatchling | Captive | Clark et al., 2014 |
| Discrimination | 3-choice | Wells |
| Discrimination | 3-choice | Wells | Colour |
| Reversal | 3-choice | Wells |
| 14 | Discrimination | 2-choice | Arena | Colour | Food | No criterion,  number consumes | *Calotes*  *versicolor* | Hatchling | Captive | Shanbhag et al., 2010 |
| 15 | Spatial | 4-choice | Arena | Local Cues | Heat | No criterion,  latency measured | *Aspidoscelis inornatus* | Adult | Wild | Day et al., 2001 |
| 16 | Spatial | 2-choice | Arena | Multiple | Shelter | 2x6/8 | *Aspidoscelis inornatus* | Adult | Wild | Day et al., 2003 |
| 17 | Discrimination | n-choice | Natural Habitat | Colour | Food | No criterion,  volume and  damage recorded | *Cnemidophorus murinus* | Adult | Wild | Schall, 2000 |
| Location |
| 18 | Reversal | 2-choice | Y-Maze | Position | Food | 16/20 | *Coleonyx*  *variegatus* | Adult | Not Given | Kirkish et al., 1979 |
| Spatial | 2-choice | Y-Maze |
| 19 | Spatial | 3-choice | Vertical Maze | Multiple | Food | 5/6 | *Egernia*  *striolata* | Juvenile | Captive | Riley et al., 2016 |
| 20 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Egernia*  *striolata* | Juvenile | Captive | Riley et al., 2018 |
| Social | Discrimination | Wells | Multiple | Food | 7/8 |
| Social | Reversal | Wells |
| 21 | Discrimination | 2-choice | Wells | Multiple | Food | 6/6 or 7/8 | *Egernia*  *striolata* | Adult | Wild | Szabo et al., 2018 |
| Reversal | 2-choice | Wells |
| 22 | Discrimination | 2-choice | Wells | Colour | Food | 7/8 | *Egernia*  *striolata* | Adult | Wild | Whiting et al., 2018 |
| 23 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  16 trials | *Eremias*  *argus* | Hatchling | Captive | Sun et al., 2014 |
| 24 | Reversal | 3-choice | Arena | Location | Shelter | 5/5 | *Eulamprus*  *quoyii* | Adult | Wild | Noble et al., 2012 |
| Spatial | 3-choice | Arena |
| 25 | Spatial | 2-choice | Arena | Location | Shelter | Significant  performance | *Eulamprus*  *quoyii* | Adult | Wild | Carazo et al., 2014 |
| 26 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Noble et al., 2014 |
| Discrimination | 2-choice | Wells |
| Social | 2-choice | Wells |
| 27 | Social | Discrimination | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Kar et al., 2017 |
| Social | Reversal | Wells |
| 28 | Motor Task | 1-choice | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Qi et al., 2018 |
| Discrimination | 3-choice | Wells | Multiple |
| Discrimination | 3-choice | Wells | Colour |
| 29 | Discrimination | 2-choice | Wells | Multiple | Food | 6/6 or 7/8 | *Eulamprus*  *quoyii* | Adult | Wild | Szabo et al., 2019 |
| Detour | 1-choice | Cylinder | Multiple | Food | 4/5 |
| Detour | 1-choice | Cylinder | Multiple | Food | correct out of 10 |
| 30 | Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion, 15 trials | *Lampropholis*  *delicata* | Adult | Wild | Bezzina et al., 2014 |
| Discrimination | 2-choice | Y-Maze | Multiple | Food | No criterion, 15 trials | *Lampropholis guichenoti* |
| 31 | Spatial | 2-choice | Arena | Location | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Chung et al., 2017 |
| 32 | Discrimination | 2-choice | Y-Maze | Multiple | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Kang et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Colour |
| 33 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | Defence reaction | *Leiocephalus schreibersii* | Adult | Wild | Marcellini & Jenssen, 1991 |
| 34 | Social | Discrimination | Wells | Multiple | Food | 7/8 | *Liopholis*  *whitii* | Adult | Wild | Munch et al., 2018 |
| Social | Reversal | Wells |
| 35 | Discrimination | 2-choice | Wells | Multiple | Food | No criterion,  20 trials | *Liopholis*  *whitii* | Juvenile | Captive | Munch et al., 2018 |
| Spatial | 2-choice | Arena | Location | Shelter |
| 36 | Conditioning | 1-choice | Key | Light | Food | No criterion,  20 trials | *\* Malpolon monspessulanus* | Not Given | Not Given | Gavish, 1979 |
| 37 | Spatial | 8-choice | Arena | Location | Shelter | No criterion,  latency measured | *\* Pantherophis*  *guttatus* | Juvenile | Captive | Holtzman et al., 1999 |
| 38 | Social | Enhancement | Arena | Multiple | Food | No criterion,  number of  individuals | *Podarcis*  *lilfordi* | Adult | Wild | Perez-Cembranos &  Perez-Mellado, 2015 |
| Social | Enhancement | Arena | Multiple | Conspecifics |
| Social | Enhancement | Arena | Multiple | Models |
| 39 | Spatial | 1-choice | Water Maze | Location | Escape | >6 for two  sessions | *Podarcis*  *sicula* | Adult | Wild | Foa et al., 2009 |
| 40 | Discrimination | 2-choice | Y-Maze | Quantity | Food | 75% correct 2  days, >chance  120 trials | *Podarcis*  *sicula* | Adult | Wild | Petrazzini et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Size |
| 41 | Motor Task | 1-choice | Wells | Multiple | Food | 7/7 or 7/8 | *Podarcis*  *sicula* | Adult | Wild | Damas-Moreira et al., 2018 |
| Discrimination | 3-choice | Wells | Colour |
| Social | 3-choice | Wells |
| 42 | Discrimination | 2-chocie | Y-Maze | Quantity | Food | No criterion, 64 trials | *Podarcis*  *sicula* | Adult | Wild | Petrazzini et al., 2017 |
| Discrimination | 2-chocie | Y-Maze | Size |
| 43 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Kis et al., 2015 |
| 44 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Siviter et al., 2017 |
| 45 | Discrimination | 2-choice | Arena | Shape | Food | Minimum 5/6 | *Pseudopus*  *apodus* | Adult | Wild | Ivazov, 1983 |
| 46 | Conditioning | 1-choice | Key | Light | Food | No criterion,  latency measured | *\* Python*  *molurus* | Mixed | Mixed | Emer et al., 2015 |
| 47 | Spatial | 4-choice | Arena | Location | Food | No criterion | *Sceloporus*  *poinsettii* | Adult | Captive | Punzo, 2002 |
| 48 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | No criterion, hiding time and FID | *Sceloporus*  *undulatus* | Adult | Wild | Thaker et al., 2010 |
| 49 | Taste Aversion | 2-choice | Arena | Taste | Food | No criterion | *Sceloporus*  *undulatus* | Juvenile | Wild | Robbins et al., 2013 |
| 50 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  latency measured | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2008 |
| Spatial | 2-choice | Arena | Location +  Experience |
| 51 | Discrimination | 2-choice | Arena | Pattern | Shelter | 5/5 | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2014 |
| 52 | Discrimination | 2-choice | Arena | Multiple | Shelter | No criterion,  time at location | *Tiliqua*  *rugosa* | Adult | Wild | Zuri & Bull, 2000 |
| 53 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  remaining food | *Tiliqua*  *scincoides* | Adult/  Subadult | Mixed | Price-Rees et al., 2011 |
|
| 54 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | 40 trial 6/18 correct  in last 20 trials | *Timon*  *lepidus* | Adult/  Subadult | Captive | Mueller-Paul et al., 2012 |
| 55 | Avoidance | 1-choice | Shuttle Box | Light | Relieve | Mean %  avoidance | *Tupinambis*  *teguixin* | Juvenile | Not Given | Yori, 1978 |
| 56 | Spatial | 10-choices | Barnes Maze | Location | Shelter | 3/3 | *Uta*  *stansburiana* | Subadult | Captive | LaDage et al., 2012 |
| 57 | Problem Solving | 1-choice | Puzzle  Box | Visual | Food | No criterion,  3 trials | *Varanus*  *albigularis* | Juvenile | Captive | Manrod et al., 2008 |
| 58 | Discrimination | 2-choice | Target | Brightness | Food | 2x8/10 | *Varanus komodoensis* | Adult | Captive | Gaalema, 2007 |
| Reversal | 2-choice | Target |
| Reversal | 2-choice | Target |
| 59 | Discrimination | 2-choice | Target | Brightness | Food | 2x8/10 | *Varanus*  *rudicollis* | Adult | Not Given | Gaalema, 2011 |
| Reversal | 2-choice | Target |
| Reversal | 2-choice | Target |
| RHYNCHOCEPHALIA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 60 | Discrimination | 2-choice | Arena | Frequency | Food | No criterion | *Sphenodon*  *punctatus* | Juvenile | Captive | Woo et al., 2009 |
| TESTUDINES | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 61 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2007 |
| 62 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2009 |
| 63 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson et al., 2010 |
| 64 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson & Huber, 2012 |
| 65 | Discrimination | 2-choice | Arena | Visual | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Subadult | Captive | Wilkinson et al., 2013 |
|
| 66 | Discrimination | 2-choice | Touch Screen | Position | Food | Last 3 blocks  above chance | *Chelonoidis carbonaria* | Juvenile | Captive | Mueller-Paul et al., 2014 |
| Discrimination | 2-choice | Arena | Position | Food | No criterion,  20 trials |
| Reversal | 2-choice | Touch Screen | Position | Food | Last 3 blocks  above chance |
| Reversal | 2-choice | Arena | Position | Food | No criterion,  20 trials |
| 67 | Discrimination | 2-choice | Arena | Quantity | Food | no criterion | *Chelonoidis carbonaria* | Subadult | Captive | Soldati et al., 2017 |
| 68 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Reiner &  Schade Powers, 1978 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 69 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Not Given | Not Given | Reiner & Powers, 1980 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 70 | Discrimination | 2-choice | Keys | Multiple | Food | 17/20 | *Chrysemys*  *picta* | Adult | Not Given | Cranney & Powers,  1983 |
| Reversal | 2-choice | Keys |
| ED Shifts | 2-choice | Keys |
| 71 | Discrimination | 2-choice | Keys | Intensity | Food | 80% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Reiner & Powers, 1983 |
| Discrimination | 2-choice | Keys | Pattern | Food | 90% 2 days |
| 72 | Discrimination | 2-choice | Keys | Pattern | Food | Mean latency  difference of  48s for 4 days | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1989 |
| 73 | Discrimination | 2-choice | Keys | Pattern | Food | 17/20 | *Chrysemys*  *picta* | Adult | Not Given | Blau & Powers, 1989 |
| 74 | Discrimination | 2-choice | Keys | Position | Food | 2x17/20 | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1990 |
| Reversal | 2-choice | Keys |
| 75 | Spatial | 3-choice | X-Maze | Location | Water | 67% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Petrillo et al., 1994 |
|
| 76 | Discrimination | 2-choice | T-Maze | Position | Food | 2/3 for 2 days | *Chrysemys*  *picta* | Adult | Not Given | Avigan & Powers, 1995 |
| 77 | Discrimination | 3-choice | Keys | Multiple | Food | Probability  of response | *Chrysemys*  *picta* | Adult | Not Given | Yeh & Powers, 2005 |
| 78 | Discrimination | 2-choice | Keys | Multiple | Food | No criterion, responses  per day | *Chrysemys*  *picta* | Subadult | Not Given | Powers et a., 2009 |
| Negative Patterning | 3-choice | Keys |
| 79 | Spatial | n-choice | Natural Habitat | Multiple | None | No criterion | *Chrysemys*  *picta* | Adults/  Juveniles | Mixed | Roth & Krochmal, 2015 |
| Discrimination | 2-choice | Y-Maze | UV | None | No criterion, proportion correct |
| Odour |
| 80 | Conditioning | 1-choice | Runway | Quantity | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Papini & Ishida, 1994 |
| 81 | Conditioning | 1-choice | Runway | Location | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Ishida & Papini, 1997 |
| 82 | Discrimination | 2-choice | Bottles | Visual | Food | No criterion,  latency measured | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2007 |
| 83 | Social | Discrimination | Bottles | Brightness | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2011 |
| 84 | Discrimination | 2-choice | Bottles | Food Pellet | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2012 |
| 85 | Discrimination | 2-choice | Target | Brightness | Food | 9/10 for 5  sessions | *Terrapene*  *carolina* | Adult | Captive | Leighty et al., 2013 |
| Discrimination | 2-choice | Target | Brightness | Food | 11/12 for 5 sessions |
| Discrimination | 2-choice | Target | Brightness | Food | No criterion |
| Discrimination | 2-choice | Target | Brightness | Food | 9/10 for  5 sessions |
| 86 | Discrimination | 2-choice | Y-Maze | Quantity | Food | No criterion, 60 trials | *Testudo hermanni* | Adult | Wild | Gazzola et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Size |
| 87 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2000 |
| Local Cue |
| 88 | Spatial | 4-choice | Water Maze | Distal Cues | Food | 9/18 | *Trachemys*  *scripta* | Subadult | Not Given | Lopez et al., 2001 |
| Local Cue |
| 89 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2003a |
| Local Cue |
| 90 | Spatial | 4-choice | Water Maze | Distal Cues | Food | 9/18 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2003b |
| CROCODILIA | | | | | | | | | | |
| # | Learning task | | | Stimuli | Reward | Criterion | Species | Age-class | Origin | Source |
| 91 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  eaten or not | *Crocodylus*  *johnstoni* | Juvenile | Wild | Somaweera et al., 2011 |

**Figures**



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