# Taking the dragon by the horns: a review of learning in non-avian reptiles

Birgit Szaboa\*, Daniel W. A. Nobleb, c, Martin J. Whitinga

aDepartment of Biological Sciences, Macquarie University, Sydney, Australia

b University of New South Wales, School of Biological, Earth and Environmental Sciences, Ecology & Evolution Research Centre, Sydney, Australia

c Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, Australia

\*Corresponding author: Birgit Szabo, MSc, Department of Biological Sciences, Macquarie University, 209 Culloden Road, Building W19A, Marsfield, NSW 2122, Australia; mobile: +61 411 78 60 61; email: [birgit.szabo@gmx.at](mailto:birgit.szabo@gmx.at), ORCID: 0000000232268621

M.J. Whiting ORCID: 0000-0002-4662-0227

D.W.A. Noble ORDID: 0000-0001-9460-8743

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## Abstract

By definition, comparative cognition includes a wide range of species. Recently, there has been a surge in cognition research in previously unstudied groups such as non-avian reptiles. As a diverse group of animals, non-avian reptiles include squamates (lizards, snakes and amphisbaena), turtles, the tuatara, and crocodilians, all of which vary greatly in their habitat use, mating systems, feeding ecology, social structure, reproductive tactics, and behaviour. Importantly, reptiles are ectotherms and dependent on environmental temperature during development and throughout their lifetime. Consequently, they provide new opportunities to study learning processes in novel contexts. Furthermore, their brain exhibits several prototypic features and neural architecture not found in other vertebrates. After an comprehensive online literature search (part of the data collection for a meta-analysis) we identified 87 studies (published up to September 2018) investigating learning in a reptile species. Our review provides an up-to-date overview of the currently available data on learning in non-avian reptiles and ties the collected evidence together to form a comprehensive unit of knowledge. Non-avian reptiles show a diverse range of abilities including taste aversion, spatial and discrimination learning, non-symbolic quantity discrimination, behavioural flexibility, learning of novel foraging techniques, and social learning. Our synthesis revealed seven research areas for which we have significant knowledge gaps and which offer important future research opportunities. Taken together, research in the last 40 years has undoubtedly demonstrated that non-avian reptiles are capable of more than just instinctive reactions and basic cognition. 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, brain, Chelonia, cognition, Crocodilia, learning and memory, Reptilia, Rhynchocephalia, Serpentes, Squamata

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## Introduction

Cognition, the process by which animals collect, store, manipulate and use information, plays a pivotal role in their everyday life when, for example, searching for food and shelter or avoiding predators (Shettleworth, 2009). Hence, cognition is an important determinant of fitness (Thornton et al., 2014) 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 using a broader range of vertebrate and invertebrate species to test the generality of cognitive processes. Thus, the number of learning studies testing non-avian reptiles, from here on called reptiles (including turtles, crocodilians, tuatara and squamates - lizards, snakes and amphisbaenids), have increased within the last decade (Figure 1). The first major review of reptile learning ability was compiled by Gordon Burghardt (1978) in a book chapter “Learning processes in Reptiles” introducing the approach to the study of learning, describing methods and providing a detailed overview of reptile learning known up until the publication of the chapter. His 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. Over three decades later, Wilkinson and Huber (2012) provided an update on not only the development of reptilian cognitive abilities but highlighted the advancements in our understanding of cognitive processes by including accounts of the acquisition of novel behaviours, play behaviour and, importantly, social cognition, then a novel subject in the study of reptilian cognition. Since the start of the 21st century, the field of reptile cognition has become more structured and the steep increase of reptile learning studies in recent years calls for a comprehensive update.

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). 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 et al., 2017). Reptiles are ectotherms and temperature plays an important role during embryonal development of sex (temperature dependent sex determination, Warner, 2010) and phenotype including brain morphology and behaviour (e.g. Amiel et al., 2016; Booth, 2006) potentially resulting in cognitive differences between individuals. Furthermore, 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; Szabo et al., 2019). Importantly, reptiles diverged from mammals about 280 million years ago (Macphail, 1982) and their brain exhibits several prototypic features (Nomura et al., 2013). Expanding the taxonomic approach might give insight into a more prototypic vertebrate cognitive ability but can also help understand convergent evolution.

Our systematic literature search identified over 80 studies on reptile learning (Figure 1) not included in Burghardt (1978). 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 cognition (primarily learning) research conducted on non-avian reptiles over the past 40 years. We group findings from different species together under seven cognitive umbrella terms: avoiding aversive stimuli, spatial cognition, learning during foraging, quality and quantity discrimination, reacting to change, solving novel problems, social learning and memory expanding on the previous review by Wilkinson & Huber (2012). With this approach we are able to highlight methodological innovations and shortcomings by linking results from different species (some studies fall under more than one subheading). Lastly, we want to emphasise how appropriate study design in relation to a species biology can greatly improve results and their interpretation in relation to species ecology. Finally, we were able to identify a number of knowledge gaps and give some directions for fruitful future research endeavours.

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

### Avoiding aversive stimuli

Animals need to know what to eat, when to hide and which threats to avoid. Importantly, avoiding toxic food with a noxious effect aids survival. Reptiles, like other animals, show taste aversion learning (e.g. Bernstein, 1999). Male green anoles (*Anolis carolinensis*), for example, can distinguish between neutral, bitter (coated in quinine hydrochloride) and sweet (coated in Equal®) tasting crickets (a coloured dot improved discriminability). Lizards rejected bitter prey but failed when the vomeronasal organ was blocked, highlighting their reliance on 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: non-painted dish – neutral taste, orange dish – sweet taste from sucrose and green dish – bitter taste from chloroquine phosphate. When presented with the same combinations they avoided dishes in the colour previously containing bitter prey, but attacked the same prey during a transposition to novel colour-taste combinations (Shanbhag et al., 2010). Furthermore, *Basiliskus vittatus*, *B*. *basiliscus*, *Eumeces schneideri* and *Eutropis multifasciata* 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 skinks (*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 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. Bonaire island 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). Furthermore, conditioned taste aversion can teach animals to avoid novel or invasive unpalatable prey. Hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*), for example, avoided freshly metamorphosed cane toads after training and were more likely to reject toads compared to naïve individuals (Somaweera et al., 2011). Conversely, juvenile eastern fence lizards (*Sceloporus undulatus*) from a population invaded by toxic fire ants (*Solenopsis invicta*) had not adapted to avoid this novel prey. They increased ant consumption similar to juveniles from a population uninvaded by ants when presented with a choice between ants and crickets (*Acheta domesticu*) (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, 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 levels. Compared to control animals that increased their flight initiation distance (FID) 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 use pattern to choose a ‘safe’ refuge, they are similarly skilled using colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, escaped a simulated predator attack into a ‘safe’ refuge using location or colour (Chung et al., 2017). More lizards learnt when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang 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 to avoid 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). Furthermore, 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 are primarily used to test animals spatial abilities. They are easily constructed, modified and applied to many different species. Examples are the radial arm maze, made of eight arms, or plus- or X-shaped mazes with four arms. Red footed tortoise (*Chelonoidis carbonaria*), for instance, learnt to avoid previously food-depleted arms in the radial arm maze adopting a response-based strategy dependant on different spatial cues (Wilkinson 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 either use distal, extra-maze cues to find a goal in a plus-shaped maze or a single intra maze cue even when starting from a new location (Lopez et al., 2000). After lesions to the medial cortex, however, only cue-trained turtles (using a single intra -maze cue) learnt during a spatial reversal while turtles using a map like strategy (based on distal cues) were unable to stop responding to the previously correct location implicating the medial cortex in map representation and inhibition (Lopez et al., 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 et al., 1994).

The (Morris) water maze; a water filled pool containing a hidden goal platform, is another common spatial task. In a modified version with visible feeders, pond sliders used either a single local cue to guide them to the goal or a map based strategy based on distal, extra-maze cues (Lopez et al., 2001). Lesions to the medial cortex selectively impaired turtles using a map strategy affecting memory of the cognitive map when relearning to find the hidden food and when distal cues were partly concealed (Lopez et al., 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 wild or semi-natural enclosures 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 but not colour (red versus green) 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). Furthermore, male Australian 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 were 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 orientation (Day et al., 1999). In a related study, malewhiptail lizards (*Cnemidophorus inornatus*) navigated the same arena using no apparent spatial strategy. Lesions to the dorsal cortex slowed learning while damage to the medial cortex greatly impaired search efficiency by increasing time moving along the edge of the maze (Day et al., 2001).

A special case of a circular arena is the Barnes maze, a round open space with 10 holes equidistant along the edge. Male side-blotched lizards (*Uta stansburiana*) used extra-maze spatial cues to find the goal hole even after 180° rotation (LaDage et al., 2012). Likewise, a group of juvenile corn snakes (*Pantherophis guttatus*) successfully navigated the Barnes maze decreasing distance travelled and errors below chance on all trials (Holtzman et al., 1999). Whereas only half of a group of juvenile Spotted 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 diurnal and where very active exploring the arena, Spotted pythons are nocturnal and showed little exploration during trials which might explain these different findings (Stone et al., 2000).

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. Experience especially during the first few years of life proved crucial for these turtles to navigate successfully and find a water body. Follow-up experiments highlighted the importance of UV vision during navigation, while olfaction was not important (Roth & Krochmal, 2015). Furthermore, male eastern water skinks (*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.

Conditions experienced during development can also affect spatial learning, potentially influencing brain development. For example, hatchling 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). Furthermore, 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 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 these treatments prolonged influence on behaviour and survival.

Reptiles possess a range of spatial abilities using response-based strategies to avoid depleted food patches or map like representations of the environment to find either food or shelter. To this end, they can use landmarks or beacons (single local cues) to guide them and use the sun to navigate and previous experience with a habitat can be crucial for successful navigation. Importantly, species might show nuanced differences in their use of spatial information. Research in snakes demonstrated the importance of ecology in task design. Small differences between species such as activity level can affect results. More active species might encounter relevant stimuli at a higher rate and learn faster than less active species (e.g. bank voles versus wood mice; Galsworthy et al., 2005). Furthermore, in turtles, the basal forebrain and the dorsal and medial cortex store spatial information. In lizards the involvement of the dorsal and medial cortex is less clear, damage to the medial cortex, however, proved detrimental to spatial learning. Finally, incubation environment affects spatial learning although the effects are thus far species-specific. Overall, we still know little about spatial learning in reptiles. In particular, we have a poor understanding of how sex, spatial ecology or foraging strategy affect navigation.

### 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 when 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. 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 and transferred a rule (lighter or darker) 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; 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 a trained and three different 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. 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 unaffected (Powers et al., 2009; Yeh & Powers, 2005). Hence, reptiles can use multiple visual stimuli to find food while avoiding cues that indicate no food; however, not all experiments were successful. Invasive delicate skinks (*L. delicata*) and non-invasive common garden skinks (*Lampropholis* *guichenoti*) 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 et al., 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 tests one or two sequential discrimination stages; however, more sophisticated tests demonstrated that reptiles possess abilities previously unattributed to this group of animals including negative patterning and rule transfer. Furthermore, we still know little about how stimulus-reward relationships are processed in the reptile brain. A few studies in turtles provide some indication as to which brain regions are involved in discrimination learning.

### Quality and quantity discrimination

Judging non-symbolic 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), amphibians (e.g. Stancher et al, 2015; Uller et al., 2003) and reptiles are no exception. For example, after associating a stimulus with a specific reward quality or quantity, red-footed tortoises 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 Chinese pond 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). 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 et al., 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; 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 or 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). 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 et al., 2014).

Discrimination reversals are a common test used in reptiles applicable in different contexts (e.g. foraging or escape behaviour) and with various stimuli (e.g. spatial, visual or olfactory) while attentional set-shifting has only recently be adopted for reptile cognitive studies. Chinese pond turtles, for instance, reversed a simple left/ right discrimination; animals that were overtrained on the initial discrimination for an additional 100 trials, however, reversed slower (Ishida & Papini, 1997). Eastern water skinks learnt to locate a ‘safe’ refuge to escape an attack even after a spatial reversal in the lab (Noble et al., 2014) and in semi-natural conditions (Noble et al., 2012). Furthermore, whiptail lizards’ avoided a heat lamp using features (colour, brightness or pattern) or the location of a ‘safe’ refuge in a reversal; spatial cues, however, were more salient than visual cues during acquisition but not during reversals (Day et al., 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). Tree skinks (*Egernia 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 behavioural flexibility (Szabo et al., 2018).

Studies implicated the involvement of different brain areas during discrimination and reversal learning. The core nucleus, dorsal cortex and parts of the forebrain of the painted turtle process visual stimuli. Lesions to these regions slowed acquisition, reversals and extra-dimensional shifts from colour to pattern, whereas damage to the medial cortex had no impact (Blau & Powers, 1989; Cranney & Powers, 1983; Grisham & Powers, 1989; 1990; Reiner & Powers, 1980; 1983).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); 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). In hatchling three lined skinks, incubation treatment (‘hot’ versus ‘cold’) affected discrimination of lid colour; only ‘hot’ incubated lizards learnt the given tasks (Clark et al., 2014) indicating an effect of temperature on brain development, as to how, however, has not yet been studied.

A comparative approach testing multiple species with the same methodology can reveal subtle learning differences. A comparison between three anole species (A. *evermanni*, A. *cristatellus* and A. *pulchellus*) revealed less behavioural flexibility in a reversal task in *A.* *cristatellus* compared to A. *evermanni* and A. *pulchellus*. Differences were attributed to neophobia but sample sizes were small (Leal & Powell, 2012; Powell, 2012). Similarly, *Acanthodactylus* *boskianus*, an active forager, learnt faster during reversals applying the fork method (one spine holding the reward while the second spine provided 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).

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

### Solving novel problems

Some species are well known to be good complex problem-solvers. 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 developed a new technique for extracting pine seeds from 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 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 seven different studies 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). Hatchling three-lined skinks (species name) also learnt lid removal; however, only ‘hot’ incubated lizards acquired this behaviour (Clark et al., 2014). Furthermore, both water skinks (*E. quoyii*)and tree skinks (*E. striolata*) removed lids but neither age (young and old; Noble et al., 2014) nor rearing environment (social or solitary; Riley et al., 2018) affected performance. Moreover, spatial learning proficiency did not predict lid opening ability in water skinks (Qi et al., 2018) and finally, Italian wall lizards and a closely related specie *P. bocagei* learnt the same technique. Although training preceded the task, these are examples of reptiles solving a novel problem. In addition to lid opening and pressing response keys, Florida red-bellied cooters and pond sliders both exited water to climb a platform and tip bottles for food, which can also be interpreted as a novel foraging technique (Davis & Burghardt, 2007; 2011, 2012). Only a single study attempted to test a reptile on a puzzle box task. Black-throated monitors (*Varanus albigularis albigularis*) opened a plastic tube to retrieve a reward within 10 minutes of the first presentation and even solved this novel task faster during the second and third trial (Manrod et al., 2008). Little is still known about reptile capabilities in acquiring and/ or innovating novel foraging techniques. Further studying these innovative problem solvers could prove a fruitful undertaking in the context of invasion and range expansion. Moreover, a large comparative study of 39 carnivores revealed a significant relationship between relative brain size and problem solving ability on a puzzle box (Bendon-Amram et al., 2016), the relationship between brain size and cognitive ability in reptiles, however, is as of yet unexplored. Can you say anything about the Amiel, Tingley, Shine paper here?

### Social learning

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

Solitary living red footed tortoises 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). Furthermore, 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 the door faster than ‘hot’ incubated lizards. There was, however, no significant difference between groups in the number of door openings (Siviter et al., 2017). Florida red-bellied cooters matched the choice of a demonstrator during a brightness discrimination, demonstrating stimulus enhancement (Davis & Burghardt, 2011). Thence social group living is not a prerequisite for social learning. As a shortcut towards the acquisition of new information it is beneficial even for non-social animals by avoiding costly trial-and-error learning and saving time and energy (Galef & Laland, 2005).

The relationship between individuals and factors such as age or sex can affect the probability with which animals employ socially provided information (Galef & Laland, 2005). In water skinks, age and dominance status predicted if lizards learnt a two-choice discrimination from a conspecific. Lizards selected the correct out of two coloured lids with and without a demonstration, young males, however, learnt faster than controls while older lizards did not (Noble et al., 2014). Furthermore, 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); socially provided information is therefore readily available.

Although most reptiles are considered mostly solitary, some Australian skinks live in social groups (Whiting & While, 2017). In monogamous White’s skinks (*Liopholis whitii*), familiarity improved 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, also a monogamous and family living 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. One explanation is that juvenile tree skinks experience a high risk of cannibalism from unrelated adult conspecifics and therefore, they may be less likely to use them as a source of social information. less important. Using parents as demonstrators might have led to different result. It did! No mention of the Frontiers paper? Whiting et al.

Typically, animals are tested with conspecific demonstrators but it can also be beneficial to learn from heterospecifics. How about saying that this has only been tested in one reptile. And then say that the basis for this study is that the lacertid lizard Podarcis sicula is commonly invasive across Europe. You could then say that it commonly co-occurs with other species of Podarcis, which creates a novel situation where they could exploit social information from a congeneric—lizards that are not dissimilar to themselves. This is a great situation where you can write a really interesting paragraph and give the full story. Otherwise, it’s just bean counting: this lizard does this…Accordingly, observer Italian wall lizards made fewer errors than individual learners in a colour discrimination when provided with information from a conspecific or a heterospecific species (*Podarcis bocagei*). Wall lizards are highly invasive and these results suggest a role for social learning when invading new habitats (Damas-Moreira et al., 2018).

The only non-lab study of cognition in lizards (or, all reptiles?) was conducted on wild *Podarcis lilfordi.* Lizards were presented with a choice between food with and without conspecifics present (including static copper models). Animals preferred locations with conspecifics present showing social enhancement when feeding; social attraction was also observed with no food present. *Podarcis lilfordi* occur in high densities, are generalist foragers and conspecifics can be a reliable source of information regarding foraging opportunities (Perez-Cembranos & Perez-Mellado, 2015). Again, this is a bit abrupt. Can you add a few more sentences to give more interpretation of the significance of this finding?

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

### 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, red-footed tortoises, common box turtles, and pond sliders can remember learnt stimuli or rules for up to 36 months after initial training (Davis & Burghardt, 2007; 2011; 2012; Leighty et al., 2013; Soldati et al., 2017), but lesions to 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. This is an area that is ripe for further study.

## Future directions

In the last 40 years, studies of reptile learning have undoubtedly demonstrated that these animals are capable of more than just instinctive reactions and basic cognition (Whiting & Noble, 2018). Due to the paucity of data, the evidence has as of yet to be strung together into a coherent story. In our review, we have attempted to link findings, present a comprehensive overview and clearly outline existing knowledge gaps to be filled by future investigations. This paragraph needs some work. In the process of this review, we have identified some key themes and questions that we believe are particularly interesting topics for future research.

### “Invader-smart” reptiles

Studies demonstrated how A single aversive event can prevent reptiles from consuming novel toxic invaders (e.g. Price-Rees et al., 2011; Somaweera et al., 2011) which can have detrimental effects on naïve native species. For example, the northern quoll (*Dasyurus hallucatus*) has drastically declined because of a variety of factors, including the invasive toxic cane toad. Some populations, however, coexist with the invader. These toad-smart quolls avoid toads and genetically pass this behaviour on to their offspring which can be utilised as a protective measure for the remaining wild population (Indigo et al., 2018; Kelly & Phillips, 2017; 2018). If behaviour is heritable in reptiles has not yet been investigated. Taste aversion could also be socially transmitted to naïve individuals. Previous work demonstrated information transmission through enhancement and facilitation (e.g. Davis & Burghardt, 2011; Perez-Cembranos & Perez-Mellado, 2015) even in wild animals (e.g. Schall, 2000). Conservation interventions might benefit from adopting a behaviour centred approach by incorporating species-specific cognitive ability. It’s not really clear to me what you are advocating here? Given that this is about future directions, you need to be prescriptive. What about all of Isabel’s work?!! This is kind of what I was expecting when I saw this heading. She will be so mad at you!

### 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 (Kimura, 1992; 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) despite known sex differences in home range sizes (Stamps, 1977). Furthermore, the sexes might use different learning strategies similar to humans. Women, for example, can memorise more landmarks while men show better mental rotation skills (Kimura, 1992). Venturing in this unexplored research field will likely produce novel insights into spatial navigation and how sexual selection shapes spatial learning. I would mention that we already have evidence in sex-specific differences (Eulamprus) and this could be quite common given that males defend territories or search for females. We therefore need more studies of species with distinct male and female tactics and it would be interesting to compare this to species in which there is less conflict such as family-living species. (High vs low sexual conflict in which space use patterns differ.)

### 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 (Brown & Tait, 2015; Diamond, 2013) which have been demonstrated in reptiles (e.g. Leal & Powell, 2012, Powell, 2012; Szabo et al., 2018; Wilkinson & Huber, 2012). Impairments in executive function are linked to diseases such as Alzheimer’s, Parkinson's or Schizophrenia (e.g. Royall et al., 2002). Understanding how executive function is processed in reptile brains which differ from mammals in neurological architecture (Nomura et al., 2013) might aid the development of better treatments for these diseases. I think this argument needs developing..

### Innovative problem solving

In lizards, sit-and-wait foragers ambush passing prey, do not use chemical cues and rely heavily on vison while active foragers typically move through the habitat while tongue-flicking to detect hidden prey. Concealed prey are often detected by vomerolfaction followed by digging or removing debris(Whiting & Noble, 2018). Previous examples demonstrated lizards’ capability to acquire novel foraging techniques and to solve complex problems such as puzzle boxes. It is our firm belief that lizards can apply behaviour in new ways when facing novel problems. Active foragers might be especially suited, and in Australia, varanids (considered ‘smart’ lizards) are frequently found in picnic areas habituated to humans (Whiting & Noble, 2018) representing a great opportunity to study wild lizards on different problems (Whiting & Noble, 2018). This pg needs more meat to it. You don’t really explain how foraging behaviour links to innovative problem solving. And be clear about what needs to be investigated.

### Social learning in social reptiles

Social learning is usually studied in group living animals (Wilkinson & Huber, 2012) because it is hypothesised that the demands of group living act as a selective pressure to improve cognition to cope with these demands (Social Intelligence Hypothesis: Byrne & Whiten, 1988; Social Brain Hypothesis: Reader & Laland, 2002). Solitary and 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). A comparison between related species differing in social complexity might reveal which aspects of cognition are affected by sociality. Furthermore, with the available smart phone technology, video demonstrations (e.g. Siviter et al., 2017; Kis et al., 2015) could be adapted to test wild reptiles; a novel opportunity to study social information use in an ecologically relevant, naturalistic setting. Could you be specific about this? Otherwise it sounds like we should be walking around with smart phones at the ready, but to what end?

### Cognition in ecologically relevant contexts

Only a 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) or link findings to fitness and/ or survival (e.g. Dayananda & Webb, 2017). Furthermore, disregarding a species’ ecology can dramatically affect study results. For example, 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). Considering species ecology and life history could enhance the value of cognitive studies and testing cognition in the wild would make results more biologically relevant, although we appreciate how challenging this can be with reptiles (see also Whiting & Noble, 2018). Although some questions can only be tested within a controlled laboratory setting, using wild-caught individuals could be a suitable alternative. In certain cases, a comparative approach might be recommendable to better answer how cognition relates to ecology. The field of reptile cognition is advancing rapidly, carefully considering ecology ensures high quality research output in the future. Is there anywhere in the review where we mention the importance of reporting the animals’ history? For example, how many studies actually report whether their animals were captive bred or wild caught and if the latter, how long they have been in captivity and how they have been maintained (e.g. outdoors vs indoors)?

### The reptile brain and cognition

Brain correlates of learning have intrigued researchers for many years. What are the neural substrates of cognitive processes? What measure explains the difference between species best: absolute or relative brain size, the size of specific regions or neural complexity (Chittka & Niven, 2009; Healy & Rowe, 2007; 2013)? We still have unsatisfactory answers to these questions (Benson-Amram et al., 2016; Reader & Laland, 2002). Furthermore, the available data are taxonomically biased towards primates, selective mammals and birds (Reader & Laland, 2002); consequently, we know little about reptile brains in general or how cognitive abilities map onto the reptilian brain. Only a few reptile learning studies looked at how learning is processed in specific brain structures (e.g. Day et al., 2001; Ivazov, 1983; Punzo, 1985) and these 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). Furthermore, reptiles provide a unique opportunity to study environmental effects on brain development during incubation which can not be tested in mammals or birds. Some previous studies have already shown how incubation temperature can affect cognitive ability in lizards (e.g. Amiel & Shine, 2012; Clark et al., 2014; Dayananda & Webb, 2017; Siviter et al., 2017). In the context of climate change, this research approach can give novel insights into how brain development in poikilotherms could be affected by future conditions and what fitness consequences might arise from these changes. I’m not really sure this section adds much. No mention of Dan Hoops et al recent paper providing an atlas of the lizard brain (a major online resource). No mention of how sexual selection drives differences in brain morphology: Dan Hoops et al J Evol Biol paper and Lara LaDage papers on Uta. You either need to beef this up or just get rid of it.

## Conclusions

1. Our knowledge of reptile learning has greatly advanced, especially in the last decade. Increasingly, researchers become interested in these neglected animals because of the need for a more comprehensive, wide taxonomic approach to the study of learning. Most studies included here were conducted on lizards and turtles but little is known about learning ability in snakes, tuatara and crocodilians. Our review emphasises the general paucity of learning studies in reptiles and the need for the application of a broader taxonomic range within reptiles (Figure 1).
2. Our systematic review provides an up-to-date overview of the currently available data. Although we identified a number of existing knowledge gaps to hopefully be closed in the near future, we highlight seven research avenues which might be of special interest in the near future such as invader-smart reptiles or temperature dependent developmental changes in learning affecting fitness and survival especially in the context of climate change.
3. The field has reached a point in which it will be important to carefully consider methodological design appropriate for reptiles to ensure 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. For further reading on methodological considerations see Matsubara et al. (2017) and Whiting & Noble (2018).

To be honest I did not get much from this conclusions section. I suggest a single pg that wraps things up, focusing on the key points. I found myself reading points that I had read only a few pages back.

## Acknowledgements

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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 are summarised in Appendix Table 1. Could you be specific about what data is included?

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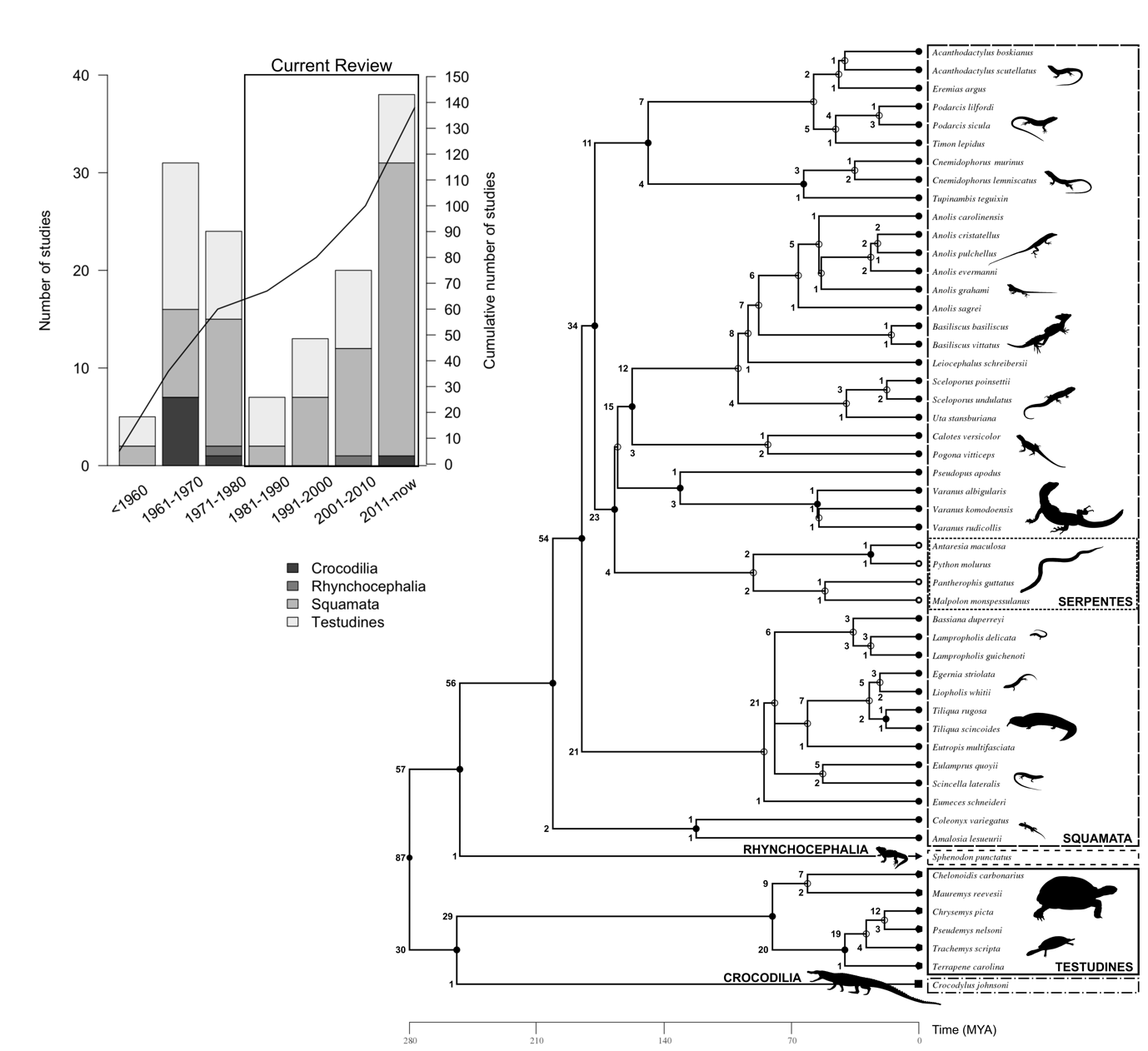
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## Appendix

**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 | *Cnemidophorus inornatus* | Adult | Wild | Day et al., 2001 |
| 16 | Spatial | 2-choice | Arena | Multiple | Shelter | 2x6/8 | *Cnemidophorus 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 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  16 trials | *Eremias*  *argus* | Hatchling | Captive | Sun et al., 2014 |
| 23 | Reversal | 3-choice | Arena | Location | Shelter | 5/5 | *Eulamprus*  *quoyii* | Adult | Wild | Noble et al., 2012 |
| Spatial | 3-choice | Arena |
| 24 | Spatial | 2-choice | Arena | Location | Shelter | Significant  performance | *Eulamprus*  *quoyii* | Adult | Wild | Carazo et al., 2014 |
| 25 | 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 |
| 26 | Social | Discrimination | Wells | Multiple | Food | 5/6 | *Eulamprus*  *quoyii* | Adult | Wild | Kar et al., 2017 |
| Social | Reversal | Wells |
| 27 | 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 |
| 28 | 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* |
| 29 | Spatial | 2-choice | Arena | Location | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Chung et al., 2017 |
| 30 | Discrimination | 2-choice | Y-Maze | Multiple | Shelter | 5/6 | *Lampropholis*  *delicata* | Adult | Wild | Kang et al., 2018 |
| Discrimination | 2-choice | Y-Maze | Colour |
| 31 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | Defence reaction | *Leiocephalus schreibersii* | Adult | Wild | Marcellini & Jenssen, 1991 |
| 32 | Social | Discrimination | Wells | Multiple | Food | 7/8 | *Liopholis*  *whitii* | Adult | Wild | Munch et al., 2018 |
| Social | Reversal | Wells |
| 33 | Discrimination | 2-choice | Wells | Multiple | Food | No criterion,  20 trials | *Liopholis*  *whitii* | Juvenile | Captive | Munch et al., 2018 |
| Spatial | 2-choice | Arena | Location | Shelter |
| 34 | Conditioning | 1-choice | Key | Light | Food | No criterion,  20 trials | *\* Malpolon monspessulanus* | Not Given | Not Given | Gavish, 1979 |
| 35 | Spatial | 8-choice | Arena | Location | Shelter | No criterion,  latency measured | *\* Pantherophis*  *guttatus* | Juvenile | Captive | Holtzman et al., 1999 |
| 36 | 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 |
| 37 | Spatial | 1-choice | Water Maze | Location | Escape | >6 for two  sessions | *Podarcis*  *sicula* | Adult | Wild | Foa et al., 2009 |
| 38 | 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 |
| 39 | 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 |
| 40 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Kis et al., 2015 |
| 41 | Social | Bidirectional | Door | Direction | Food | No criterion,  10 trials | *Pogona*  *vitticeps* | Adult | Captive | Siviter et al., 2017 |
| 42 | Discrimination | 2-choice | Arena | Shape | Food | Minimum 5/6 | *Pseudopus*  *apodus* | Adult | Wild | Ivazov, 1983 |
| 43 | Conditioning | 1-choice | Key | Light | Food | No criterion,  latency measured | *\* Python*  *molurus* | Mixed | Mixed | Emer et al., 2015 |
| 44 | Spatial | 4-choice | Arena | Location | Food | No criterion | *Sceloporus*  *poinsettii* | Adult | Captive | Punzo, 2002 |
| 45 | Avoidance | n-choice | Natural Habitat | Threat | Shelter | No criterion, hiding time and FID | *Sceloporus*  *undulatus* | Adult | Wild | Thaker et al., 2010 |
| 46 | Taste Aversion | 2-choice | Arena | Taste | Food | No criterion | *Sceloporus*  *undulatus* | Juvenile | Wild | Robbins et al., 2013 |
| 47 | Spatial | 2-choice | Arena | Location | Shelter | No criterion,  latency measured | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2008 |
| Spatial | 2-choice | Arena | Location +  Experience |
| 48 | Discrimination | 2-choice | Arena | Pattern | Shelter | 5/5 | *Scincella*  *lateralis* | Adult | Wild | Paulissen, 2014 |
| 49 | Discrimination | 2-choice | Arena | Multiple | Shelter | No criterion,  time at location | *Tiliqua*  *rugosa* | Adult | Wild | Zuri & Bull, 2000 |
| 50 | Taste Aversion | 1-choice | Arena | Taste | Food | No criterion,  remaining food | *Tiliqua*  *scincoides* | Adult/  Subadult | Mixed | Price-Rees et al., 2011 |
|
| 51 | 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 |
| 52 | Avoidance | 1-choice | Shuttle Box | Light | Relieve | Mean %  avoidance | *Tupinambis*  *teguixin* | Juvenile | Not Given | Yori, 1978 |
| 53 | Spatial | 10-choices | Barnes Maze | Location | Shelter | 3/3 | *Uta*  *stansburiana* | Subadult | Captive | LaDage et al., 2012 |
| 54 | Problem Solving | 1-choice | Puzzle  Box | Visual | Food | No criterion,  3 trials | *Varanus*  *albigularis* | Juvenile | Captive | Manrod et al., 2008 |
| 55 | Discrimination | 2-choice | Target | Brightness | Food | 2x8/10 | *Varanus komodoensis* | Adult | Captive | Gaalema, 2007 |
| Reversal | 2-choice | Target |
| Reversal | 2-choice | Target |
| 56 | 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 |
| 57 | 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 |
| 58 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2007 |
| 59 | Spatial | 8-choice | Radial  Arm Maze | Location | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Adult | Captive | Wilkinson et al., 2009 |
| 60 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson et al., 2010 |
| 61 | Social | Detour | Arena | Multiple | Food | No criterion,  goal reached | *Chelonoidis carbonaria* | Juvenile/  Subadult | Not Given | Wilkinson & Huber, 2012 |
| 62 | Discrimination | 2-choice | Arena | Visual | Food | No criterion,  number correct | *Chelonoidis carbonaria* | Subadult | Captive | Wilkinson et al., 2013 |
|
| 63 | 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 |
| 64 | Discrimination | 2-choice | Arena | Quantity | Food | no criterion | *Chelonoidis carbonaria* | Subadult | Captive | Soldati et al., 2017 |
| 65 | 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 |
| 66 | 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 |
| 67 | 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 |
| 68 | 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 |
| 69 | Discrimination | 2-choice | Keys | Pattern | Food | Mean latency  difference of  48s for 4 days | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1989 |
| 70 | Discrimination | 2-choice | Keys | Pattern | Food | 17/20 | *Chrysemys*  *picta* | Adult | Not Given | Blau & Powers, 1989 |
| 71 | Discrimination | 2-choice | Keys | Position | Food | 2x17/20 | *Chrysemys*  *picta* | Adult | Not Given | Grisham & Powers, 1990 |
| Reversal | 2-choice | Keys |
| 72 | Spatial | 3-choice | X-Maze | Location | Water | 67% 2 days | *Chrysemys*  *picta* | Adult | Not Given | Petrillo et al., 1994 |
|
| 73 | Discrimination | 2-choice | T-Maze | Position | Food | 2/3 for 2 days | *Chrysemys*  *picta* | Adult | Not Given | Avigan & Powers, 1995 |
| 74 | Discrimination | 3-choice | Keys | Multiple | Food | Probability  of response | *Chrysemys*  *picta* | Adult | Not Given | Yeh & Powers, 2005 |
| 75 | 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 |
| 76 | 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 |
| 77 | Conditioning | 1-choice | Runway | Quantity | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Papini & Ishida, 1994 |
| 78 | Conditioning | 1-choice | Runway | Location | Food | No criterion,  latency measured | *Mauremys*  *reevesii* | Adult | Not Given | Ishida & Papini, 1997 |
| 79 | Discrimination | 2-choice | Bottles | Visual | Food | No criterion,  latency measured | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2007 |
| 80 | Social | Discrimination | Bottles | Brightness | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2011 |
| 81 | Discrimination | 2-choice | Bottles | Food Pellet | Food | 6/6 | *Pseudemys*  *nelsoni* | Adult | Captive | Davis & Burghardt, 2012 |
| 82 | 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 |
| 83 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2000 |
| Local Cue |
| 84 | Spatial | 4-choice | Water Maze | Distal Cues | Food | 9/18 | *Trachemys*  *scripta* | Subadult | Not Given | Lopez et al., 2001 |
| Local Cue |
| 85 | Spatial | 4-choice | 4-Arm Maze | Distal Cues | Food | 13/15 | *Trachemys*  *scripta* | Juvenile | Not Given | Lopez et al., 2003a |
| Local Cue |
| 86 | 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 |
| 87 | 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/>