



# Learning in non-avian reptiles 40 years on: advances and promising new directions

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## ABSTRACT

Recently, there has been a surge in cognition research using non-avian reptile systems. As a diverse group of animals, non-avian reptiles [turtles, the tuatara, crocodylians, and squamates (lizards, snakes and amphisbaenids)] are good model systems for answering questions related to cognitive ecology, from the role of the environment on the brain, behaviour and learning, to how social and life-history factors correlate with learning ability. Furthermore, given their variable social structure and degree of sociality, studies on reptiles have shown that group living is not a pre-condition for social learning. Past research has demonstrated that non-avian reptiles are capable of more than just instinctive reactions and basic cognition. Despite their ability to provide answers to fundamental questions in cognitive ecology, and a growing literature, there have been no recent systematic syntheses of research in this group. Here, we systematically, and comprehensively review studies on reptile learning. We identify 92 new studies investigating learning in reptiles not included in previous reviews on this topic – affording a unique opportunity to provide a more in-depth synthesis of existing work, its taxonomic distribution, the types of cognitive domains tested and methodologies that have been used. Our review therefore provides a major update on our current state of knowledge and ties the collective evidence together under nine umbrella research areas: (i) habituation of behaviour, (ii) animal training through conditioning, (iii) avoiding aversive stimuli, (iv) spatial learning and memory, (v) learning during foraging, (vi) quality and quantity discrimination, (vii) responding to change, (viii) solving novel problems, and (ix) social learning. Importantly, we identify knowledge gaps and propose themes which offer important future research opportunities including how cognitive ability might influence fitness and survival, testing cognition in ecologically relevant situations, comparing cognition in invasive and non-invasive populations of species, and social learning. To move the field forward, it will be immensely important to build upon the descriptive approach of testing whether a species can learn a task with experimental studies elucidating causal reasons for cognitive variation within and among species. With the appropriate methodology, this young but rapidly growing field of research should advance greatly in the coming years providing significant opportunities for addressing general questions in cognitive ecology and beyond.

*Key words:* Amphisbaenia, Chelonia, Crocodylia, Rhynchocephalia, Squamata, Serpentes, Sauria, cognition, integrative review

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## I. INTRODUCTION

Cognition, the process by which animals collect, store, and use information, is integral to fitness. It is essential for finding food and shelter, avoiding predators, finding and

distinguishing between conspecifics and potential mates and adapting when environmental conditions change (Shettleworth, 2010). 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 &

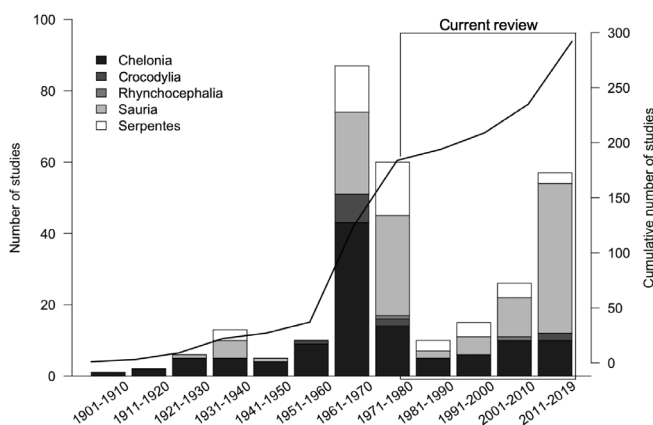
Guillette, 2018; Volter *et al.*, 2018), how learning and cognitive processes impact fitness (e.g. Thornton, Isden, & Madden, 2014; Huebner, Fichtel, & Kappeler, 2018; Madden *et al.*, 2018) and the underlying mechanistic basis for species differences in decision making and problem solving (e.g. Lefebvre, Reader, & Sol, 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 (henceforth reptiles), including turtles, crocodylians, tuatara and squamates (lizards, snakes and amphisbaenids), are starting to become model systems for addressing a host of questions in cognitive ecology. For example, because many squamates are egg layers it is possible to explore how early developmental environments (independent of maternal environment) impact learning. Incubation temperature affects sexual development (temperature-dependent sex determination; Warner, 2010), brain morphology (e.g. Amiel, Bao, & Shine, 2016), behaviour (e.g. Booth, 2006; Matsubara, Deeming, & Wilkinson, 2017) and learning (e.g. Amiel, Lindström, & Shine, 2014; Dayananda & Webb, 2017; Munch *et al.*, 2018a). Moreover, many reptiles are precocial and the juvenile brain is much more developmentally advanced at birth compared to altricial species (Grand, 1992; Charvet & Striedter, 2011) which impacts learning ability at an early age (Szabo *et al.*, 2019a). Reptiles also show individual variation in learning ability which has been linked to behavioural type, age, dominance status and sex (e.g. Carazo *et al.*, 2014; Noble, Byrne, & Whiting, 2014; Chung

*et al.*, 2017; Kar, Whiting, & Noble, 2017). Because some reptiles have evolved early forms of sociality (While *et al.*, 2015; Whiting & While, 2017) they have also been foundational in understanding how familiarity affects social learning ability (e.g. Whiting *et al.*, 2018; Munch *et al.*, 2018b).

Phylogenetically, reptiles (including birds) split from mammals about 320 million years ago and about 280 million years ago, the reptiles diverged into two clades: archosaurs (birds and crocodiles) and lepidosaurs [tuatara and squamates (lizards, amphisbaenids – which are deeply embedded within lizards – and snakes)] (Alföldi *et al.*, 2011). The position of turtles was long unclear but they are now considered a sister group to lepidosaurs (Güntürkün, Stacho, & Ströckens, 2017). The phylogenetic relationship of reptiles to mammals and birds makes them extremely interesting models to investigate the convergent evolution of cognitive ability such as sex differences in spatial learning (e.g. Carazo *et al.*, 2014). Furthermore, modern reptiles are the third most speciose group of vertebrates (11136 species as of December 2019; Uetz, Freed, & Hošek, 2019), inhabiting a wide range of different habitats, showing diversity in mating systems (monogamy to polygyny), feeding ecology, social organisation (solitary to groups of many individuals), reproductive tactics (parthenogenesis, oviparity or viviparity) and differ substantially in behaviour (Fox, McCoy, & Baird, 2003; Uller & Olsson, 2008; Reilly, McBrayer, & Miles, 2009; Whiting & While, 2017). As such, a diversity of questions regarding mechanisms underlying cognitive performance might be asked using reptile models and consequently we have seen a surge in work on reptile cognition (Fig. 1) given their potential to address fundamental questions in cognitive ecology.

Burghardt (1977) conducted the first major review on reptilian cognition as the field was developing. His review was critical in establishing and describing methods and providing an in depth 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 the existing cognitive work. Suboski (1992) developed the “releaser-induced recognition learning” model of reptilian and amphibian learning and reviewed all forms of conditioning, aversion learning and recognition in reptiles (and amphibians). More recently, Wilkinson & Huber (2012) provided an update on new developments including studies focusing on social learning – a novel direction in the study of reptilian cognition at that time. Finally, a review by Burghardt (2013) highlighted the empirical evidence supporting the diverse capabilities (cognitive and behavioural) of reptiles and the need for greater consideration of their welfare in captivity. While these have been important reviews, the explosion of recent research requires a more systematic approach to collating, reviewing and evaluating the current state of knowledge to provide a complete picture of current understanding of the field.



**Fig 1.** Number of studies from 1901 to 2019 (in 10-year intervals) on the main orders of reptiles; Squamates are split into Sauria (lizards) and Serpentes (snakes). The superimposed line is the cumulative number of studies (right-hand axis). Only studies conducted after 1977 and not included in Burghardt (1977) are included in this review.

Herein, we performed the first systematic review of cognition research (primarily learning) on non-avian reptiles conducted over the last 40 years. Contrary to conventional reviews, a systematic review uses standardized and transparent search methods to select relevant studies for inclusion [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 (1977). Importantly, we identify 118 new studies on reptile learning of which 26 were included in the updates (Suboski, 1992; Wilkinson & Huber, 2012; Burghardt, 2013) and none were included in Burghardt (1977). We intended our review to be thorough and as comprehensive as possible, functioning as a guide to enhance future work and identify critical gaps, and hopefully to inspire novel research questions in animal cognition, comparative psychology and cognitive ecology.

## II. SYSTEMATIC REVIEW AND LITERATURE COMPILATION

We searched *Web of Knowledge*, *Scopus*, *ProQuest Dissertation & Theses Global*, *Papers Library*, *GoogleScholar*, *PubMed* and *ScienceDirect* for publications on learning (using the key words ‘learning’, ‘cognition’, ‘behaviour’, ‘choice’ and ‘discrimination’) conducted in any non-avian reptile species (using the key word ‘reptile’). For all key words we accounted for differences in spelling. To focus our search on relevant publications only, we excluded publications containing the key words ‘bird’, ‘mammal’, ‘fish’, ‘fossil’, ‘parasite’, ‘frog’, ‘insect’, ‘morph’ and ‘chemi’. The initial search was conducted to collect data for a specific meta-analysis on sex-dependent learning (Szabo, Whiting, & Noble, 2019c); however, an additional search in *Web of Science* was conducted in 2019 to include more recent publications (until May 2019).

We identified a total of 35,533 records (initial search: 35,210, recent search: 232 records) of which 1,741 were duplicates (the recent search did not produce duplicates) and 208 of these articles were selected based on title screening for words and/or expressions indicating that a learning experiment was conducted. From these 208 articles we conducted a backward literature search of their references, which produced an additional 92 records (82 original works, 10 reviews), and a forward search (citations of these articles) identifying a further 38 records (36 original studies and 2 reviews) to affirm completeness of the initial searches. We then screened the abstracts of the 338 (208 initially found plus 92 from the backwards search and 38 from the forward search) publications for learning experiments conducted on a non-avian reptile, identifying 201 papers for full-text screening. During full-text screening we looked for a description of any learning experiment (or learning task, defined as ‘the

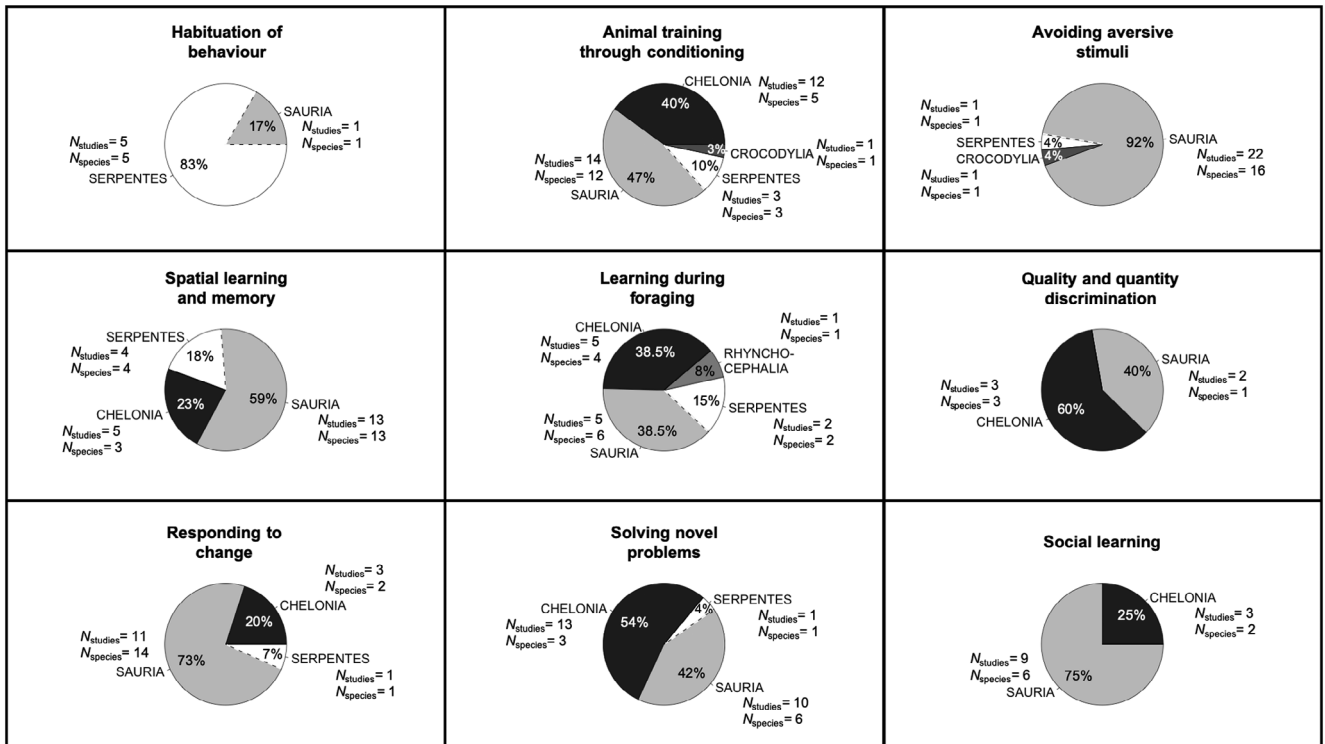
acquisition of a novel behaviour, novel behaviour sequence or novel application of existing behaviour’, including general associative learning, spatial learning, discrimination learning, avoidance learning, reinforcement learning, social or motor learning, taste aversion, habituation, conditioning, or maze learning; Shettleworth, 2010). Studies on, for example, gaze following or orientation mechanisms did not fit our criteria and were thus excluded from our review.

After scrutinizing papers based on their methods (describing a learning task as defined above) our final sample included 118 studies of which 92 were not included in previous reviews. In Section III, we group findings together under nine umbrella research areas: (i) habituation of behaviour; (ii) animal training through operant conditioning; (iii) avoiding aversive stimuli; (iv) spatial learning and memory; (v) learning during foraging; (vi) quality and quantity discrimination; (vii) responding to change; (viii) solving novel problems; and (ix) social learning (for an overview see Figs 2 and 3). Note that some studies are included under more than one category of learning. With this approach we were able to link results from different species and highlight methodological innovations and shortcomings. We provide a list of relevant studies on learning in non-avian reptiles as online Supporting Information (Table S1).

## III. WHAT HAVE WE LEARNED FROM THE LAST 40 YEARS OF STUDYING LEARNING IN REPTILES?

### (1) Habituation of behaviour

Habituation is considered one of the simplest forms of learning and occurs when an organism shows a decrease in reactivity after repeated exposure to a stimulus (without motor or sensory adaptation), allowing animals to filter out irrelevant information. Habituation is generally characterised as a short-term change in behaviour that at least partially reverts back to its original state after a certain period of time with no stimulation (Thorpe, 1963; Rankin *et al.*, 2009). Initially, habituation was thought only to occur in reflexes but it has since been shown that habituation can occur to responses that are not reflexes, including behaviour (Rankin *et al.*, 2009). One of the most famous examples of habituation is the decrease of the gill withdrawal reflex after repeated mechanical stimulation in the mollusc *Aplysia* (Carew, Pinsker, & Kandel, 1972) but habituation likely occurs across all animal taxa (Peeke & Herz, 1973) and has even been demonstrated in plants (Abramson & Chicas-Mosier, 2016). It is not surprising that habituation is widespread, because it is adaptive in many situations. For example, responding to all stimuli with defensive behaviour is a waste of energy, reducing the time available for other important behaviours such as foraging or reproduction. Across reptiles, the main focus of habituation studies is the habituation of anti-predator behaviour.



**Fig 2.** Pie charts summarising the proportion (% of studies) of reptilian taxa investigated since Burghardt (1977) for learning ability consolidated under nine umbrella research areas. Black, turtles and tortoises (Chelonia); dark grey, crocodiles (Crocodylia); medium grey, tuatara (Rhynchocephalia); light grey, lizards (Sauria); white, snakes (Serpentes). The dashed line separating lizards and snakes indicates that both belong to Squamates. Next to each taxon we provide the number of studies and number of species included in our review.

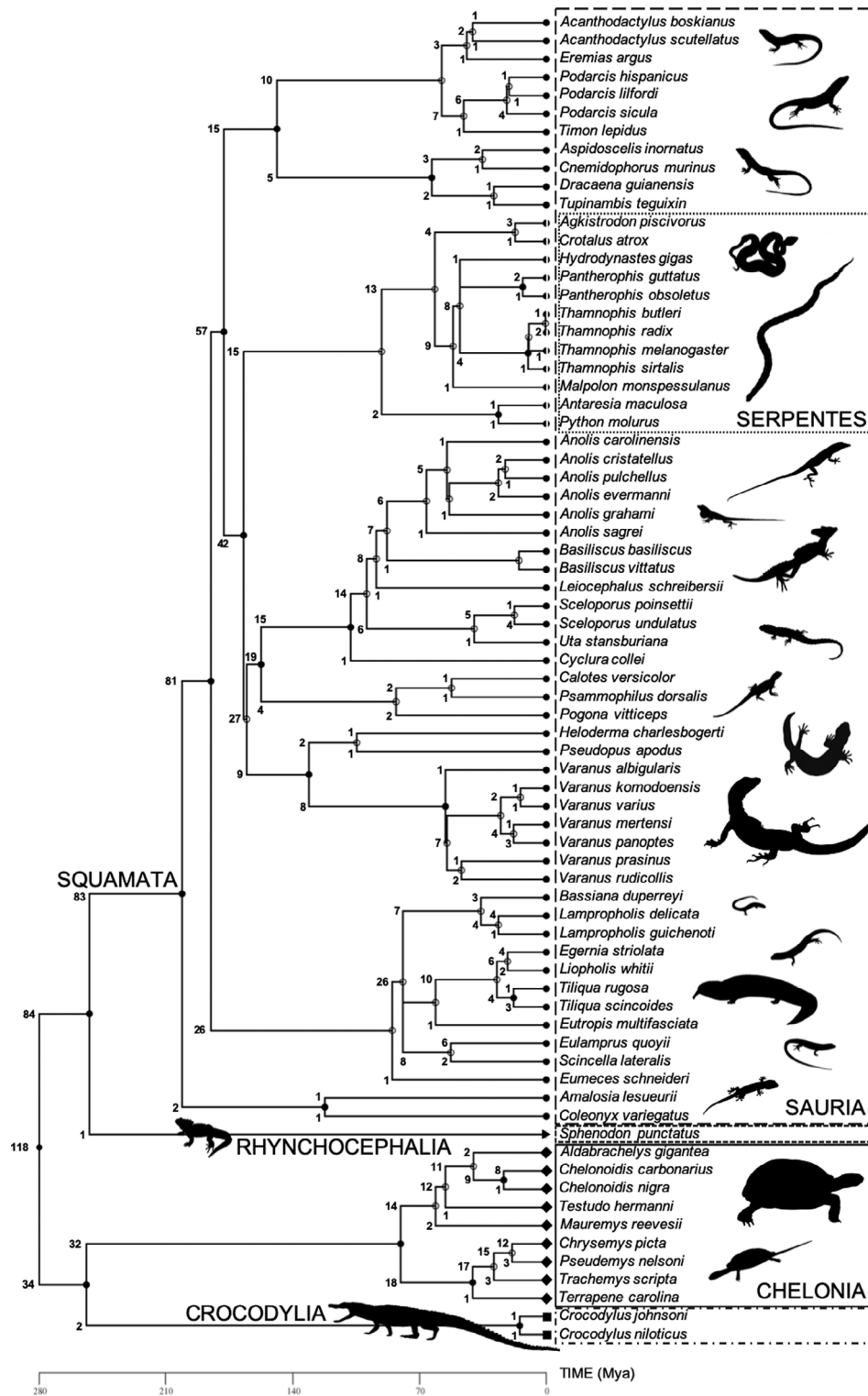
(a) Lizards

Iberian wall lizards (*Podarcis hispanicus*) were tested on how personality affects habituation to a simulated predator attack. Boldness, exploration and sociability were recorded for each individual and then groups of eight lizards were released into outdoor enclosures. Across 6 days, a human observer walked through each enclosure and flight initiation distance was recorded for each individual. The results show that ‘fast’ but less-social lizards habituated faster than slow-exploring but social individuals (Rodriguez-Prieto, Martin, & Fernandez-Juricic, 2011).

(b) Snakes

Neonatal common garter snakes (*Thamnophis sirtalis*) habituated their anti-predator response (movement and coiling of the body) towards the movement of a grey card overhead, demonstrating short-term habituation. Half of the animals responded again after a 15 min break and all showed anti-predator behaviour towards the card 24 h later. The number of presentations of the card until habituation decreased across 5 days, indicative of long-term habituation (Hampton & Gillingham, 1989). Neonatal Mexican garter snakes (*Thamnophis melanogaster*) but not Butler’s garter snakes

(*Thamnophis butleri*) habituated to both a moving and non-moving stimulus (the experimenter’s finger) across 5 days by decreasing attacks (strikes towards the stimulus) and fleeing across trials. 10 days after the last habituation trial, Mexican garter snakes once again responded to the experimenter’s finger (*T. butleri* was not tested). In both species, responses were stronger to the moving than non-moving stimulus and both exhibited individual differences in habituation. In Mexican garter snakes, more reactive snakes habituated faster and litter identity affected habituation. In Butler’s garter snake, sex as well as litter affected habituation. Juvenile Mexican garter snakes also habituated to both stimuli showing large individual differences but these were neither dependent on litter identity or sex (Herzog, Bowers, & Burghardt, 1989). Adult cottonmouths (*Agkistrodon piscivorus*) also habituated to an artificial predator (a leather glove with a snake tongue attached) decreasing defensive behaviour (a range of body movements) across 5 days. Eleven days with no stimulation later, however, their response had not fully recovered (Glaudas, 2004). In a second study on this species, adult snakes significantly decreased defensive striking at the artificial human hand, showing habituation, while neonate cottonmouths did not habituate (Glaudas, Winne, & Fedewa, 2006). This difference between age classes might reflect a difference in predation pressure in the wild: young snakes might have



**Fig 3.** Phylogenetic tree depicting our current understanding of the relationships among taxa included in this review. Numbers at node splits represent the number of studies included in our review (some studies included multiple species). Tree generated using <http://timetree.org> (Kumar *et al.*, 2017). Animal outlines from <http://www.phylopic.org/>; picture copyright: turtle & caiman, Scott Hartman; tortoise, Andrew A. Farke; anole, Sarah Werning; <https://creativecommons.org/licenses/by-nc-sa/3.0/>.

more predators and therefore benefit by habituating less easily. Western diamondback rattlesnakes (*Crotalus atrox*) showed habituation of the rattle response (anti-predator behaviour) in a rattle-box designed to stimulate snakes to rattle by repeated, automatic opening of the lid (Place, 2005). Rattlesnakes decreased rattling as well as latency and duration of rattling within and across four test days, however, individuals showed large variation in all these measures (Place, 2005; Place & Abramson, 2008).

### (c) Summary

Adult, juvenile and neonate snakes habituated to a simulated predator attack. In neonates, however, results show a species-specific effect; neonate cottonmouths were an exception and did not habituate to a simulated predator attack. These studies used different methodology and measured different behaviours. It is therefore hard to evaluate if the differences among species are species-specific effects or reflect the different methodologies. Prior research also investigated the habituation of defensive behaviour towards a shadow in turtles and of attack behaviour towards prey extracts and defensive behaviour in snakes (Burghardt, 1977). Studies investigating habituation of behaviour in lizards are rare with our review only identifying one such study. Burghardt (1977) commented on the paucity of habituation studies in reptiles and our updated review shows that this has continued to be the case. It might be argued that there is relatively little interest in habituation compared to other forms of learning in reptiles. It is, however, an important learning mechanism that likely has fitness consequences (although these have not been directly studied in reptiles) and, indeed, without habituation to experimental arenas and procedures more complex learning studies would not be possible.

## (2) Animal training through operant conditioning

Training procedures are increasingly used with reptiles in zoos as enrichment to improve welfare and to be able to perform veterinary procedures without excessive handling to reduce stress (Hellmuth *et al.*, 2012). However, training procedures can also be used in experimental studies, in which they are often termed reinforcement training. The goal of these procedures is to train an animal to perform a certain behaviour or behavioural sequence through operant/instrumental conditioning, which is a form of learning: a desired behaviour is reinforced within a certain context until the animal performs this behaviour reliably within that context. If complex behavioural sequences are the goal, then multiple small steps are usually trained by successive approximation until the more complex endpoint is achieved (Hellmuth *et al.*, 2012). In contrast to habituation, behaviour learned by conditioning is usually long term and sometimes permanent (Peeke & Herz, 1973). During the last 40 years a wide variety of training procedures have been used for almost all reptile groups in zoos and for research.

### (a) Turtles and tortoises

Turtles and tortoises demonstrate skill in learning different behavioural sequences frequently applied in other vertebrate groups, such as target training or the pushing of response keys (Hellmuth *et al.*, 2012). Aldabra tortoises (*Aldabrachelys gigantea*), for example, were successfully trained to associate the sound of a clicker (a commonly used bridge in animal training) with food and later this association was used to train tortoises to walk up to and touch a red target and then extend and lift their heads to make it possible to draw blood. With this target training procedure, animals could learn to move to their night quarters and walk up a ramp to a scale to be weighed, improving husbandry while simultaneously removing stress by excessive physical handling (Weiss & Wilson, 2003). Another group of Aldabra tortoises was successfully clicker trained and subsequently target trained to walk to, and then hold a blue-and-white dowel for 30 s. Both behaviours were used to facilitate husbandry and weighing (Gaalema & Benboe, 2008). Galápagos tortoise (*Chelonoidis nigra*) could be trained to extend their neck after touching by a keeper (finch response). For successful holding of the neck extended while touching occurred they received a food reward. This behaviour was subsequently used to facilitate the collection of regular blood samples (Bryant *et al.*, 2016).

Some experimental tests require animals to manipulate objects such as feeders or disks. Painted turtles (*Chrysemys picta*), were trained to push response keys to receive a reward. Animals first learned to eat from an automatic food dispenser and subsequently to push an illuminated plastic disk (key) to receive a food reward. The behaviour of pushing response keys was then used to test negative patterning as well as visual discrimination and reversal learning (Reiner & Powers, 1978, 1980, 1983; Cranney & Powers, 1983; Blau & Powers, 1989; Grisham & Powers, 1989, 1990; Yeh & Powers, 2005; Powers *et al.*, 2009) (see Sections III.5a and III.7a). Florida red-bellied cooters (*Pseudemys nelsoni*) and pond sliders (*Trachemys scripta*) both learned to exit water, climb a platform and tip plastic bottles to obtain food. First, animals were rewarded for approaching the platform, then for climbing the platform and finally for tipping the bottle. Tipping bottles was then used to test discrimination and social learning ability. Impressively, these animals remembered this trained behaviour for 7.5 months without contact with bottles, demonstrating that such training can result in behavioural changes that are long lasting (Davis & Burghardt, 2007, 2011, 2012).

### (b) Lizards

In a classical conditioning experiment using a shuttlebox, brown anoles (*Anolis sagrei*) learned to lift their tail to avoid a shock while a second group that received a shock whenever the first group was shocked, did not (Punzo, 1985). A second species, Graham's anoles (*Anolis grahami*), were conditioned to associate a sound with being pushed off their perch. Two out of three lizards avoided being pushed off by leaving the perch after hearing the sound (Rothblum, Watkins, &

Jenssen, 1979). Common golden tegus (*Tupinambis teguixin*) learned to associate a light combined with a buzzer to escape excessive heat into a goal chamber (Yori, 1978).

Similar to turtles, lizards can learn to perform a desired behaviour that can be used later to test questions regarding other learning abilities. Eight different studies used successive approximation procedures to teach lizards to remove lids from wells for a reward. First, lizards associated a test apparatus without lids with food. Thereafter, a lid was introduced and a food well gradually covered across sequential trials to teach lizards to remove the lid to access a reward. This behaviour was used in experimental settings to test visual discrimination and reversal learning. *Anolis evermanni*, *A. pulchellus* and *A. cristatellus* successfully learned lid removal, although the latter species was less successful compared to the other two and showed higher levels of neophobia (Leal & Powell, 2012; Powell, 2012). Hatchling three-lined skinks (*Bassiana duperreyi*) also learned lid removal but only 'hot'-incubated lizards acquired this behaviour while hatchlings incubated under 'cold' conditions did not (Clark *et al.*, 2014). Eastern water skinks (*Eulamprus quoyii*) and adult and juvenile tree skinks (*Egernia striolata*) removed lids but neither age class (young or old) or rearing environment (social or solitary) affected performance (Noble *et al.*, 2014; Riley *et al.*, 2018; Whiting *et al.*, 2018). Moreover, spatial learning proficiency did not predict lid-opening ability in water skinks (Qi *et al.*, 2018). Finally, Italian wall lizards (*Podarcis sicula*) and a closely related species *P. bocagei* learned the same lid-opening technique (Damas-Moreira *et al.*, 2018).

All the above examples used training procedures to test lizards later in learning experiments. Lizards have also been trained in zoo settings. Hellmuth *et al.* (2012) report that caiman lizards (*Dracaena guianensis*) were successfully trained to associate the sound of a clicker with food. Using this association animals later learned to touch and follow a target to enter a crate without human handling (Hellmuth *et al.*, 2012).

### (c) Snakes

Training procedures have also been used to condition snake species. False water cobras (*Hydrodynastes gigas*), for example, learned to follow a scented target from their exhibit enclosure to a separate place where they were fed (see Hellmuth *et al.*, 2012) and sub-adult Burmese pythons (*Python bivittatus*) were trained to associate a food dispenser with an automatic door with receiving food. Thereafter, these snakes learned to push a response key next to the door to open it and gain access to the reward (Emer *et al.*, 2015). Finally, Montpellier snakes (*Malpolon monspessulanus*) learned to move towards a compartment to receive a mouse after the activation of a light (Gavish, 1979).

### (d) Crocodiles

A Nile crocodile (*Crocodylus niloticus*) was successfully trained to expect food when hearing a clicker and this association was used for target training. The crocodile learned to

approach and touch a black, circular target first in water and later on land. This animal was later trained to allow the tail to be touched to facilitate blood withdrawal during veterinary procedures (Augustine & Baumer, 2012).

### (e) Summary

These examples provide evidence that conditioning can be used to teach novel behaviour, from target training to lid removal and the pushing of response keys. These examples also demonstrate that such training can be beneficial in both research and husbandry. Classical (Pavlovian) conditioning, in which a naturally occurring reflex (e.g. limb withdrawal after pain or salivation in the presence of food) is paired with a neutral stimulus (e.g. a bell or a smell), is missing from our review of recent work, but was heavily studied in reptiles in the past (Burghardt, 1977). This earlier work was important in establishing that reptiles can be conditioned much like other animals. Using various techniques earlier research explored dark adaptation, auditory thresholds, olfactory discrimination, colour vision and thermoregulation (Burghardt, 1977; Campbell, 1981). The application of electric shocks was common in the past, but we found only one more recent study that used such negative reinforcement methods (Punzo, 1985). Awareness of reptile welfare is rising (Burghardt, 2013), which likely has led to an increased use of positive reinforcement in animal training and a decrease of Pavlovian conditioning. Positive reinforcement was also used in the past, mostly to train animals to push levers or response keys (Burghardt, 1977). Burghardt (1977) predicted that the use of operant techniques would become more frequent and our review shows that this is certainly true, at least within zoo settings.

## (3) Avoiding aversive stimuli

Animals need to know what to eat, when to hide and which threats to avoid. Aversion learning functions to allow organisms to avoid toxic food with potential noxious effects or to avoid dangerous predators. Taste-aversion learning, for example, is a conserved ability demonstrated in a wide range of species that is highly adaptive because it aids survival (e.g. Bernstein, 1999). It is, therefore, not surprising that reptiles can learn to avoid food that either tastes bitter or causes illness after ingestion. Most reptilian research into aversion learning has focused on lizards (Fig. 2) with a single study on snakes and crocodylians each; it is still unclear if aversion learning occurs in turtles.

### (a) Lizards

Male green anoles (*Anolis carolinensis*) 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 to do so 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 dishes. When presented with the same combinations they avoided dishes of the colour that had previously contained bitter prey. When lizards were presented with novel colour–taste combinations, however, they attacked bitter prey confirming that they had associated dish colour with taste (Shanbhag, Ammann, & Saidapur, 2010). Brown basilisks (*Basiliscus vittatus*), common basilisks (*B. basiliscus*), Schneider's skinks (*Eumeces schneideri*) and common sun skinks (*Eutropis multifasciata*) avoided a novel food 1 week after a lithium chloride (LiCl) injection (inducing sickness). A second novel control food, however, was accepted 1 week after a saline injection (Paradis & Cabanac, 2004). Taste aversion has also been 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).

Aversion learning can also be used to train animals to avoid toxic prey. Australian blue-tongue skinks (*Tiliqua scincoides scincoides* and *T. s. intermedia*) fed cane toad sausages (*Rinella marina*, a toxic invader) in combination with a LiCl injection avoided this food for 7 weeks. A control group treated with saline showed little to no aversion and both groups accepted sausages of reptile feed 9 weeks after illness (Price-Rees, Webb, & Shine, 2011). In a follow-up study, wild-caught blue-tongue skinks (*T. s. intermedia*) were given experience with illness after ingesting a cane toad sausage laced with LiCl. These lizards were then released after recovering and were radio-tracked for several weeks. Trained lizards were more likely to survive in the wild after cane toads had invaded their habitat compared to naïve lizards without previous experience. Interestingly, low doses of LiCl that did not induce vomiting in skinks were less effective (Price-Rees, Webb, & Shine, 2013). Ward-Fear *et al.* (2017) trained wild-caught, adult yellow-spotted monitors (*Varanus panoptes*) to avoid cane toads by feeding a test group of lizards with cane toad sausages laced with LiCl, monitored their behaviour towards a live toad (within a mesh container) before and after training (eating chicken necks versus eating cane toad sausages) and compared the interest shown in the live toad to a control group fed chicken necks only. Test-group lizards showed significantly lower interest in the live toad after training. All lizards were then released back into the wild and followed to monitor their survival; however, trained lizards were not more likely to survive the toad invasion compared to control lizards. In a follow-up study Ward-Fear *et al.* (2016), fed small, juvenile cane toads to wild, free-ranging yellow-spotted monitors before toads had arrived in the test area, to teach them to avoid adult toads. After the arrival of the first toads at the study site, all naïve lizards died within the period of the study while half of the trained

lizards survived. In another study, wild, free-ranging yellow-spotted monitors from cane toad-free populations (Lizard Island, Australia) and from toad-invaded populations (Townsville, Australia) were offered both a dead native frog (rocket frog, *Litoria nasuta*) and a dead cane toad (with the parotoid gland that contains most of the toxin removed) and their behaviour (whether they swallowed the food and any negative reaction after swallowing) was recorded. Animals from the toad-free population also were retested 1–3 days later to see if they had developed any avoidance response towards the novel toxic toads. Naïve lizards, from the toad-free populations, responded similarly to both dead prey items; however, most experienced lizards from the invaded populations refused to consume the toad (with one exception), but ate the frog. Retesting revealed that none of the lizards from the toad-free population showed aversion to consuming dead cane toads; only a few animals, however, had showed signs of illness after ingesting toads (Llewelyn *et al.*, 2014). Contrary to these findings, lace monitors (*Varanus varius*) from toad-free populations experiencing training with dead toads avoided toads in later trials. Using a similar protocol, free-ranging lace monitors from toad-invaded and toad-free populations were simultaneously presented with a chicken neck, a dead cane toad (without glands) and a dead great barred-frog (*Mixophyes fasciolatus*) and their behaviour recorded. Animals from all populations were retested 1–3 days later, and toad-naïve lizards additionally were retested 30 days later. The results show that all lizards consumed the chicken neck and the frog but only lizards from toad-naïve populations consumed the toads. 1–3 days later most lizards consumed the frog but none consumed the toad and finally, 30 days later, animals still refused toads but readily ate frogs. Importantly, three-quarters of lizards that consumed toads showed signs of illness (Jolly, Shine, & Greenlees, 2016). Experience with strong illness after ingestion thus seems important for avoidance behaviour to develop towards cane toads and for the behaviour to be retained for extended periods.

Fire ants (*Solenopsis invicta*) can be a threat to juvenile lizards because they can envenomate lizards during consumption, potentially leading to death, although the ants themselves are not poisonous. No avoidance of the consumption of fire ants was recorded in wild-caught juvenile eastern fence lizards (*Sceloporus undulatus*) from a population invaded by fire ants, when simultaneously presented with a cricket (*Acheta domesticus*). They increased ant consumption to a similar extent as juveniles from a non-invaded population (Robbins, Freidenfelds, & Langkilde, 2013). In a subsequent study, sub-adult lizards did not avoid toxic ants after direct exposure, 6 months after exposure as juveniles, or when they were sourced from a population invaded by fire ants for generations. Sub-adult lizards again increased ant consumption during the course of the experiment (Herr *et al.*, 2016). In a third study, naïve laboratory-born hatchling fence lizards were presented with (i) eight fire ants (100% treatment); (ii) four fire ants and four native ants (*Dorymyrmex bureni*; 50% treatments); or (iii) eight native ants (0% treatment) for five

consecutive days. Hatchlings from the 100% treatment showed clear aversion learning while individuals in the 50% treatment only avoided ants for 1 day (Venable, Adams, & Langkilde, 2019). Without a strong negative outcome, avoidance behaviour might only last a short amount of time. Additionally, fence lizards might learn how to avoid being stung by ants and subsequently incorporate them into their diet.

Escaping predators is another behaviour essential for survival. In their natural habitat, red-sided curly-tailed lizards (*Leiocephalus schreibersii*) rapidly learned to avoid capture. Females did so faster than males and after only one capture event (Marcellini & Jenssen, 1991). Faster predator avoidance could conceivably be more beneficial for females, for example, when gravid with eggs. 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 task retention 24 h later (Thaker *et al.*, 2010). In little brown skinks (*Scincella lateralis*), 48 h of experience with an arena was essential for escaping a simulated predator attack (a moving wall) by hiding under a 'safe' refuge. Lizards with no experience of the arena did not learn within the 2 days of testing (Paulissen, 2008). A second study showed that lizards could use horizontal and vertical stripes to find a 'safe' refuge but more individuals learned to find the refuge when vertical lines were present compared to horizontal lines, perhaps because natural sheltering sites tend to be at the base of trees (Paulissen, 2014). Lizards are similarly able to use colour and location cues when escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, learned to escape a simulated predator attack (tapping the base of the tail with a brush) into a 'safe' refuge using location or colour (Chung *et al.*, 2017). More lizards learned when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang, Goulet, & Chapple, 2018), possibly due to differences in the availability of sheltering sites between these populations. Finally, behaviour positively correlated with learning performance. Lizards with a 'fast' behavioural type (higher speed and activity, bolder and more sociable) made more errors, showed longer latencies to reach the shelter and took longer to reach the learning criterion, indicating a speed–accuracy trade-off in these males (Goulet *et al.*, 2018). Batabyal & Thaker (2019) quantified habitat composition of rural and urban habitats using satellite images and tested male South Indian rock agamas (*Psamophilus dorsalis*) sourced from these environments on their learning ability and learning flexibility when escaping a simulated predator attack (tapping the tail base). Urban habitats can differ extensively from natural habitats, and vegetation within these targeted urban habitats had decreased dramatically within only a few years. Lizards from the urban habitats learned better, making fewer errors compared to lizards collected from the rural areas. Developmental conditions can

also alter escape behaviour. Hatchling White's skinks (*Liopholis whitii*) whose mothers received a low-value diet (one *Tenebrio molitor* larva three times per week) were more likely to escape into a 'safe' refuge compared to hatchlings from mothers receiving a high-value diet (five larvae three times per week) while the reverse applied to a colour-discrimination task in a foraging context. One possible explanation proposed by the authors is that the conditions experienced during gestation prepare offspring for the conditions experienced after birth (Munch *et al.*, 2018a).

#### (b) Snakes

In plains garter snakes (*Thamnophis radix*) colouration enhances learning of chemosensory stimuli of noxious food. Food was presented to the snakes in forceps that were either plain, or had coloured (black, green and yellow-black) wings attached, and attack latencies were recorded. Results showed no innate avoidance of any of these visual stimuli. The snakes then were separated into three treatment groups: (i) aposematic prey colouration (yellow-black), (ii) non-aposematic colouration (green); and (iii) a control group (black) to test how visual and chemosensory cues (different food types) affect learned taste aversion. Fish pieces were offered and then illness was induced in the two test groups by injecting LiCl while control animals were injected with saline. After 7, 12, 17 and 22 days, the snakes were offered two pieces of fish and two earthworms (novel food) with forceps (coloured according to their group) and attack latencies were compared with those before training. Both test groups showed aversion learning to fish compared to controls, but the yellow-black-forceps group showed the strongest aversion. This effect disappeared by 22 days after training. To confirm this result, the same snakes were retested in two groups: (i) aposematic prey colouration (yellow-black) and (ii) non-aposematic prey colouration (green). Animals were again presented with fish in coloured forceps and illness was induced in both groups. Seven days later the animals were offered a piece of fish and an earthworm in both yellow-black and green forceps. Again, both groups showed aversion to fish but the aposematic group showed a stronger aversion (Terrick, Mumme, & Burghardt, 1995).

#### (c) Crocodiles

Crocodiles can be taught to avoid novel or invasive, unpalatable prey by using conditioned taste aversion. Hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*) given experience with freshly metamorphosed cane toads (*R. marina*) as prey were more likely to reject toads compared to naïve individuals (Somaweera *et al.*, 2011).

#### (d) Summary

These studies highlight how avoidance of bitter tastes or illness can take place after only a few encounters, and may be used effectively to train vulnerable species to avoid toxic

invaders, an important tool for conservation. Earlier studies also reported illness-induced aversion learning in snakes (Burghardt, 1977). Due to its success and value, it is not surprising that an increasing number of studies have investigated aversion learning in reptiles. When individuals are sampled from the wild or trained in the wild, care needs to be taken to consider sampling bias. It is well established that only part of a population is likely to be sampled with commonly used sampling techniques, often bolder individuals that are easier to catch (e.g. Carter *et al.*, 2012; Biro, 2013). Personality, amongst other traits, affects learning ability (e.g. Sih & Del Giudice, 2012; Boogert *et al.*, 2018; Dougherty & Guillette, 2018; Volter *et al.*, 2018) and behavioural morphs within the same population can show differences in brain volume (LaDage *et al.*, 2009). Thus, researchers should consider whether sampling bias could lead to data not representative of the abilities of the whole population.

Escaping predators has also been used successfully to elicit learning. One important factor that needs to be controlled for in such studies is experimenter bias caused by unconsciously influencing animals towards the 'correct' choice during trials, especially when tests are not conducted blind as to treatment groups (e.g. behavioural types, source population or sex) (Burghardt *et al.*, 2012). Researchers could avoid experimenter bias by using a movable wall to push lizards towards a choice apparatus as in Paulissen (2008, 2014). Such approaches would also help facilitate experiments being conducted blindly. As protocols involving chasing lizards into hiding have emerged only recently, little consideration has been given to evaluating their effectiveness and the degree to which experimenter bias could affect the results.

#### (4) Spatial learning and memory

Navigating the environment is essential when searching for food, shelter or mating partners. Resources and conspecifics are rarely found in the same location. Efficiently navigating, as opposed to moving randomly through space, may be accomplished by different cognitive processes or navigational strategies. Depending on the information available in the environment, animals employ different strategies such as remembering landmarks, or using path integration or cognitive maps (Shettleworth, 2010). A variety of studies have investigated the different spatial strategies and cues used by turtles, lizards and snakes to find food or shelter.

##### (a) Turtles and tortoises

A red-footed tortoise (*Chelonoidis carbonaria*) adjusted its navigational strategy in a radial-arm maze (a common maze used for testing spatial memory) according to the visual cues available in the surrounding environment. In a cue-rich environment, the tortoises used visual cues to find their way around the maze, avoiding already visited, food-depleted arms (Wilkinson, Chan, & Hall, 2007). By contrast, in an environment with little visual structure (when the maze was

surrounded by a curtain), the animal used a response-based strategy by entering the arm adjacent to the last-exited arm. Interestingly, when complex visual cues again became available, the animal switched back to using these cues to navigate. The specific features of the environment that were used by the tortoise, however, remain unclear (Wilkinson, Coward, & Hall, 2009). These results suggest that the spatial strategy depends on the most useful information available. In another study, pond sliders (*T. scripta*) were presented with a single intra-maze cue acting as a beacon to locate a goal within a plus-shaped maze. The turtles reliably used this landmark to find the goal as confirmed by transfer trials, in which individuals started from novel positions. When the beacon was removed, the turtles were unable to find the goal. A second group of sliders were trained to use an array of extra-maze cues to navigate. Contrary to the cue-trained group, these turtles formed a map-like representation of the maze. Animals were able to find the goal starting from new locations when some of the extra-maze cues were concealed but not when all extra-maze cues were removed (Lopez *et al.*, 2000). Unfortunately, no data are available to establish which of these spatial strategies the turtles prefer when both intra- and extra-maze cues are available. Painted turtles (*C. picta*) were able to learn to navigate an X-shaped maze with three choice arms. Although extra-maze cues were provided the authors did not assess if turtles used these to find the goal (Petrillo, Ritter, & Powers, 1994). In another study, painted turtles (*C. picta*) transferred a position habit from a T-maze to a X-maze although they started from a different position (Avigan & Powers, 1995).

In rats (*Rattus rattus*) and mice (*Mus musculus*), spatial learning and reference memory are frequently assessed using the Morris water maze, a water-filled pool containing a hidden goal platform (e.g. Vorhees & Williams, 2006). In a modified version of this task 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 extra-maze cues (Lopez *et al.*, 2001).

By studying spatial learning in a natural setting using radiotracking, Roth 2nd & Krochmal (2015) showed that only resident wild painted turtles (*C. picta*) with knowledge of the habitat used specific routes to find water, while translocated animals failed this task. Importantly, follow-up tests showed that experience, especially during the first few years of life, was necessary for these turtles to navigate successfully to a water body. Furthermore, ultraviolet (UV) reflectance but not olfaction was important for spatial orientation in a Y-maze.

##### (b) Lizards

A male jewelled lizard (*Timon lepidus*) navigated a radial-arm maze using a response-based strategy despite a complex cue environment (Mueller-Paul *et al.*, 2012). Male Italian wall lizards (*P. sicula*) located a hidden goal platform in a Morris water maze using a sun compass. When lizards experienced a clock-shift of 6 h, their search direction shifted accordingly,

confirming that they used the sun to navigate the maze. Covering the parietal eye, a photoreceptive organ on the head, established that it was essential for successful navigation (Foa *et al.*, 2009).

Another task commonly used to assess spatial reference memory is the Barnes maze, a round open arena with 10 exit holes spaced equidistant along its circumference. Male side-blotched lizards (*Uta stansburiana*) used extra-maze spatial cues to find the correct hole in a Barnes maze even after 180° rotation (LaDage *et al.*, 2012). When tested in a round arena including four possible goal rocks similar to a traditional Barnes maze, male Bosk's fringe-fingered lizards (*Acanthodactylus boskianus*) and male Nidua fringe-fingered lizards (*A. scutellatus*) both learned to find a goal, as indicated by decreasing time to find a heated rock. Detailed analysis of the lizards search behaviour during training and probe trials revealed that *A. scutellatus* used slight markings on the arena wall as local cues to guide their search rather than distal extra-maze cues, while *A. boskianus* did not use either. In a second experiment providing lizards with distant intra-maze cues, both species again learned to find the goal, however, probe trials were inconclusive as to the strategy used. Finally, when a single visual intra-maze cue (a red light) indicated the location of the goal rock, both species learned the task but *A. scutellatus* outperformed *A. boskianus*. As an ambush forager, *A. scutellatus* is likely to rely more heavily on visual cues compared to *A. boskianus*, an active hunter that uses chemical cues to find prey, potentially providing a biological basis for the observed differences in information use (Day, Crews, & Wilczynski, 1999). In a related study, male little whiptail lizards (*Aspidoscelis inornatus*) navigated the same arena; however, the strategy used to find the goal rock could not be determined. Probe trials suggest that they did not learn through trial-and-error learning or use local, configurational, or spatial cues (Day, Crews, & Wilczynski, 2001).

Some studies use semi-natural enclosures to test spatial navigation. Sleepy lizards (*Tiliqua rugosa*) preferred the location of familiar refuge sites within their enclosure. However, when brightness or shape cues were associated with the refuge, lizards preferred the familiar cue over its spatial location (Zuri & Bull, 2000). Crevice spiny lizards (*Sceloporus poinsettii*) remembered the location of a food patch 24 h later (Punzo, 2002) and male eastern water skinks (*E. quoyii*) learned to escape into a 'safe' refuge avoiding an 'unsafe' hide based on spatial location in a semi-natural outdoor enclosure (Noble, Carazo, & Whiting, 2012); however, the spatial strategy they used was not assessed. In a related study, differences in spatial learning ability were linked to behavioural type and sex. Bold as well as shy water skinks (measured by the time taken to bask after a simulated predator attack) were more likely to solve a spatial task compared to intermediate-type lizards. Furthermore, more males than females learned within a given number of trials and males were more likely to choose the 'safe' refuge initially although this difference disappeared by the end of the experiments (Carazo *et al.*, 2014). While all of these studies demonstrate that lizards can learn the location of a refuge, they did not

investigate the underlying mechanisms. Only one study on lizards (Carazo *et al.*, 2014) investigated spatial learning differences between males and females, which are commonly found in other taxa [e.g. great panda (*Ailuropoda melanoleuca*; Perdue *et al.*, 2011); hummingbirds (*Sephanoides sephanoides*; Gonzalez-Gomez *et al.*, 2014); túngara frog (*Engystomops pustulosus*; Liu & Burmeister, 2017)]. Such differences are likely to be common in reptiles, especially lizards, where sex-specific mating tactics are present (e.g. Stamps, 1977, 1983), as these could be linked to differences in spatial memory proficiency ('range size hypothesis'; Jones, Braithwaite, & Healy, 2003).

In egg-laying species, developing embryos are particularly vulnerable to the developmental environment. Variable environmental conditions can affect embryonic development resulting in changes in morphology and performance (Noble, Stenhouse, & Schwanz, 2018; While *et al.*, 2018). For example, differences in incubation temperature or oxygen levels can result in different spatial learning performance, and learning proficiency could be linked with survival. Hatchling Lesueur's velvet geckos (*Amalosa lesueurii*) incubated at 'cold' temperatures were faster spatial learners compared to 'hot'-incubated geckos. 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 (*B. duperreyi*) incubated under 'hot' conditions earned higher spatial learning scores compared to 'cold'-incubated lizards (Amiel & Shine, 2012). Hypoxic conditions during incubation decreased the probability that hatchling racerunner lizards' (*Eremias argus*) could locate a 'safe' refuge compared to both normoxic- and hyperoxic-incubated animals. However, error rates were not affected (Sun *et al.*, 2014). While abiotic conditions seem to affect learning, no effect of social rearing environment (social or solitary) 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 alter the reptilian brain (but see Amiel *et al.*, 2016), but these examples do demonstrate a prolonged influence of early environmental conditions on behaviour and survival.

### (c) Snakes

Three snake species have been tested for their spatial reference memory in a Barnes maze but only two showed successful learning. In the Barnes maze animals need to find one exit hole among 10 at the edge of a round, open arena. Juvenile corn snakes (*Pantherophis guttatus*) learned successfully to navigate a Barnes maze, decreasing the distance travelled and number of errors to below chance over the trials (Holtzman *et al.*, 1999), however, only half of a group of juvenile spotted pythons (*Antaresia maculosa*) learned to find the goal. Pythons did not decrease latency and no specific learning strategy could be identified. The Barnes maze was developed for rats and relies on their innate impulse to escape from brightly lit, open spaces into a dark escape hole (e.g. Harrison

*et al.*, 2006). However, mice do not readily enter these holes and need additional training (e.g. Koopmans *et al.*, 2003). While corn snakes are diurnal and actively explored the arena, spotted pythons are nocturnal and showed little exploration during trials which might explain these different findings (Stone, Ford, & Holtzman, 2000). Rat snakes (*Pantherophis obsoletus*) decreased the time to escape a 12 hole Barnes maze, but individuals that had been kept in an enriched environment escaped the maze faster than snakes kept under standard conditions. Snakes were provided with intra- as well as extra-maze cues but the cues they used were not assessed. In some trials prey scent was added to the arena floor which marginally improved performance (Almli & Burghardt, 2006). In a modified version of the traditional Barnes maze using shelters instead of holes, adult corn snakes (*P. guttatus*) readily used a prominent intra-maze cue fixed to the inner wall to locate an open shelter amongst four possibilities. During training, all snakes decreased their latency to find the goal shelter and increasingly used a more direct path with less searching behaviour. When the intra-maze cue was moved to a new location within the arena, snakes changed their behaviour accordingly, searching for the goal shelter in the location predicted by the cue (Holtzman, 1998). Similarly, juvenile cottonmouths (*A. piscivorus*) learned to locate a goal shelter out of four choices within a round arena, with a white card provided as a visual cue. The snakes learned the location of the goal during the first day (four trials), decreasing both the time to locate the shelter and the distance travelled. Males took 2.5 times longer to locate the goal shelter compared to females and travelled a longer distance than females. The cues used again were not assessed (Friesen, 2017).

#### (d) Summary

While many studies have utilised open arenas or mazes to investigate spatial learning in reptiles, few investigated the strategies used by the test animals to learn the given task. Interestingly, as noted by Burghardt (1977), many reptiles seem to use vision during navigation. In recent years, the use of mazes has decreased compared with earlier work (Burghardt, 1977) and complex mazes, such as the Lashley maze that includes a number of culs-de-sac, are not used any more. A few studies have investigated the involvement of different brain areas or neuroreceptors and neurotransmitters in spatial learning and navigation in reptiles, which is reviewed elsewhere (Roth 2nd, Krochmal, & LaDage, 2019). The reviewed studies demonstrate that reptiles can use response-based strategies, that they can rely on local as well as distant visual cues to find a goal and that in a cue-rich environment they might use map-like strategies to navigate. They show that experience with the environment can be important to escape a threat, that different species can use different cues to learn (which can sometimes be very subtle) and that differences might even arise within species according to sex and behavioural types. Contrary to earlier

work showing only limited learning ability in snakes (Burghardt, 1977), more recent research shows that these animals can learn successfully in laboratory settings, hopefully leading to more comparative work in the future.

### (5) Learning during foraging

While foraging, it is important to discriminate food sources or patches providing food from those already depleted. To allocate time and energy during searching, animals thus 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-flicker frequencies), only one of which is rewarded. Many reptiles are proficient in using visual cues including hue, luminance, or shapes and patterns to learn about stimulus–reward relationships.

#### (a) Turtles and tortoises

Florida red-bellied cooters (*P. nelsoni*) successfully learned to discriminate a bottle including a visual pellet from a bottle without a pellet and retained this ability for 12 months (Davis & Burghardt, 2007) and subsequently for 24 months with no interaction with the task (Davis & Burghardt, 2012). They were also able to discriminate between a black and a white bottle, retaining this ability for 3.5 months with no further training (Davis & Burghardt, 2012). Pond sliders (*T. scripta*) learned the same black/white discrimination and retained this for 3.5 months (Davis & Burghardt, 2012). Red-footed tortoises (*C. carbonaria*) recognise the similarity between real objects and their photographs, confusing real objects with pictures when presented simultaneously (Wilkinson, Mueller-Paul, & Huber, 2013). Common box turtles (*Terrapene carolina*) successfully learned to select the lighter or darker of two coloured paddles (out of five shades) and transferred this rule to novel stimuli of different colours (blue and green; Leighty *et al.*, 2013). Painted turtles (*C. picta*) were tested in a negative patterning test for configurational associative learning of compound stimuli in which two single stimuli are reinforced but the compound stimulus is not. Turtles were first trained on two single elements, a red and a black-and-white-striped response key. When the compound (white stripes on a red background) was introduced, individuals gradually decreased their response to the compound while continuing to respond to the single elements. In a second experiment testing two-choice discrimination of the single elements, turtles learned easily to discriminate between the two stimuli (Powers *et al.*, 2009).

#### (b) Lizards

Rough-necked monitors (*Varanus rudicollis*) and a Komodo dragon (*V. komodoensis*) used paddle brightness (black and white) to obtain a food reward (Gaalema, 2007, 2011). Male

eastern water skinks (*E. quoyii*) relied on colour to solve a three-choice discrimination task but no correlation was found between successful learning and a previously tested spatial learning task, indicating that learning ability is domain specific in these lizards (Qi *et al.*, 2018). In another study, eastern water skinks demonstrated task-specific inhibitory skills. Half of the tested lizards had to discriminate between two blue stimuli (different shades), the other half had to discriminate between two shape stimuli to find a reward. However, some lizards from both groups did not learn this discrimination due to a strong side bias. Importantly, learning success in the discrimination task was negatively correlated with success on a detour task. ‘Learners’ (those individuals without a side bias) made more errors in the detour task compared to ‘non-learners’ (individuals with a side bias) (Szabo, Noble, & Whiting, 2019b).

Lizards can also be trained to use light stimuli such as coloured light bulbs to find food. Wild crested anoles (*A. 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 & Roughgarden, 1994). Not all experiments were successful. Invasive delicate skinks (*L. delicata*) and non-invasive common garden skinks (*Lampropholis guichenoti*) failed to learn the correct arm in a Y-maze (one arm painted solid orange or blue, the other in orange or blue stripes) but common garden skinks showed shorter latencies to reach the goal (Bezzina, Amiel, & Shine, 2014).

#### (c) Snakes

Juvenile and adult plains garter snakes (*T. radix*) learned to discriminate lemon-scented pine chips from non-scented chips within 100 trials. Later, adult male snakes were tested in a Y-maze setting in which amyl acetate was diffused into one arm. For some individuals the odour indicated the correct arm, while for others it indicated the incorrect arm. The latter group reached the learning criterion in fewer trials (Begun *et al.*, 1988). Juvenile cottonmouths (*A. piscivorus*) learned to rely on a red card to find food. Animals were tested in two groups: in the test group the red card predicted in which food bowl a live fish could be found, while in the control group the card was randomly allocated and therefore did not predict the presence of the fish. After 14 days of training, test-group animals showed foraging postures in front of the bowl indicated by the red card only, while control-group animals performed at chance level. After 25 days with no further training, test-group animals performed similar to control-group snakes indicating the absence of a long-lasting memory of this task (Friesen, 2017).

#### (d) Tuatara

A single study tested discrimination learning using a simultaneous two-choice test in 17 juvenile tuataras (*Sphenodon punctatus*). Animals were able to discriminate between a constant

light and light flickering at frequencies of 14.08, 25.06 and 45.61 Hz but failed to discriminate between a constant light and a light flickering at a frequency of 65.09 Hz (Woo *et al.*, 2009).

#### (e) Summary

Reptiles are able to discriminate between a wide range of visual stimuli in two-choice experiments and turtles can remember such learned discriminations for long periods of time. Memory studies are, however, rare in other reptile groups. In some studies, rather complex learning rules were used, such as in tasks of negative patterning (Powers *et al.*, 2009), knowledge transfer between real objects and pictures (Wilkinson *et al.*, 2013) or discrimination based on lighter/darker colour (Leighty *et al.*, 2013). Patterns, shapes, coloured paper or coloured light were also used in earlier work, although mainly with a focus on the investigation of colour vision, visual acuity and visual thresholds (Burghardt, 1977). Knowledge transfer, generalisation and rule learning were also demonstrated previously in reptiles (Burghardt, 1977), but the lack of evidence for learning reported by Burghardt (1977) has certainly changed with recent work. Many species included in Burghardt’s (1977) review required hundreds of trials to reach a learning criterion, with the biggest issue being the development of position habits (a side bias). It is not clear why some animals develop side biases while others do not, but stimulus type might be relevant. If animals are unable to perceive a stimulus properly or are unlikely to consider it a cue then a one-sided response might be an appropriate strategy. It is therefore very important to consider stimulus type carefully in learning tasks. The focus of research in recent years has shifted towards how reptiles learn rather than whether they can discriminate. Discrimination learning in snakes was largely ignored in the past (Burghardt, 1977) and even now, such research is relatively rare.

#### (6) 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; e.g. Buckingham, Wong, & Rosenthal, 2007). Quantity discrimination has been demonstrated in a wide range of animals from insects (e.g. Pahl, Si, & Zhang, 2013) to fishes (e.g. Agrillo & Bisazza, 2018), mammals (e.g. Hanus & Call, 2007; Uller & Lewis, 2009; Abramson *et al.*, 2011; Benson-Amram, Gilfillan, & McComb, 2018), birds (e.g. Rugani, Regolin, & Vallortigara, 2008; Garland, Low, & Burns, 2012; Bogale, Aoyama, & Sugita, 2014), and amphibians (e.g. Uller *et al.*, 2003; Stancher *et al.*, 2015). With the addition of data on three turtles and one lizard species, basic numerical abilities (judging differences in quantity) have now been confirmed for all vertebrates.

*(a) Turtles and tortoises*

After associating a stimulus with a specific reward quality or quantity, red-footed tortoises (*C. carbonarius*) selected the larger quantity during the simultaneous presentation of two stimuli differing in value. The tortoises remembered these relative quantities/qualities for 18 months (Soldati *et al.*, 2017). Turtles are generally long-lived species that are good models for studying long-term memory. The speed with which Reeves' turtles (*Mauremys reevesii*) moved down a runway was contingent on the magnitude of food reward provided at the end. Turtles receiving 24 pellets per trial moved faster than turtles receiving only two pellets. During extinction trials, with no food present, animals previously receiving large quantities took longer to cease responding than animals previously trained with less reward (Papini & Ishida, 1994). In a spontaneous discrimination test, Hermann's tortoises (*Testudo hermanni*) successfully chose the larger size and quantity of tomato (Gazzola, Vallortigara, & Pellitteri-Rosa, 2018) in four different combinations: 1 *versus* 4, 2 *versus* 4, 2 *versus* 3 and 3 *versus* 4 (in ratios 0.25, 0.5, 0.67 and 0.75, respectively). Performance followed a ratio effect, with a better accuracy in choosing the larger quantity/size of food for smaller ratios.

*(b) Lizards*

Italian wall lizards (*P. sicula*) spontaneously discriminated between two food items (dead fly larvae) differing in size (ratios 0.25–0.75). They did, however, not select the larger of two quantities but performance in the size-discrimination test followed a ratio effect (Petrazzini *et al.*, 2017). When the same species was later tested on a trained discrimination of both size and number, some 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 (ratio of 0.25; Petrazzini, Bertolucci, & Foa, 2018). These conflicting results might be explained by differences in the stimuli used: motivation to approach artificial stimuli might differ from motivation to approach actual food items.

*(c) Summary*

Quantity discrimination is likely to be important for survival, and it is therefore not surprising that reptiles possess at least rudimentary abilities to discriminate based on food quantity and quality. From the few studies available, it is clear that there are differences among species that require further investigation. Tests of quantity discrimination are relatively recent, and knowledge remains very limited in reptiles compared to other vertebrates (Agrillo, 2015). Future studies of both spontaneous and trained quantity discrimination will be of great value (Agrillo & Bisazza, 2014). In reptiles, the use of artificial stimuli during trained quantity discrimination may be less successful than using natural stimuli such as food items during spontaneous quantity discrimination. Some reptiles can recognise food items from photographs

(Wilkinson *et al.*, 2013), which could be a possible experimental tool.

**(7) Responding to change**

Responding flexibly to environmental stimuli and adapting rapidly to change is important for survival in unpredictable environments (Lefebvre *et al.*, 2004). 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 in different ways. One index of behavioural flexibility is a test of reversal learning ability, when a previously established stimulus–reward relationship changes (Brown & Tait, 2015). Another index of behavioural flexibility is attentional set shifting (Roberts, Robbins, & Everitt, 1988; Brown & Tait, 2015). Attentional set-shifting tasks usually incorporate multiple two-choice discrimination stages (including reversals) of multi-dimensional stimuli. Animals first learn to rely on one dimension to receive a reward, and to disregard the other dimensions (development of an attentional set). The stimulus–reward relationship is then moved to a previously unimportant dimension and animals need to shift their attention towards this dimension (Brown & Tait, 2015). A final category, innovative problem-solving tasks (Auersperg, Gajdon, & von Bayern, 2014), has not yet been used to investigate behavioural flexibility in reptiles.

*(a) Turtles and tortoises*

Reeves' turtles (*M. reevesii*) could reverse a simple left/right discrimination, although turtles that were over-trained on the initial discrimination for an additional 100 trials reversed more slowly (Ishida & Papini, 1997). Red-footed tortoises (*C. carbonaria*) transferred knowledge about a food patch (left/right food bowl) acquired on a touchscreen to a real-life arrangement, but did not transfer knowledge about a reversal trained on a real-life arrangement back to the touchscreen (Mueller-Paul *et al.*, 2014). When tested on a visual (colour plus shape) discrimination in a Y-maze, red-footed tortoises developed a side bias during reversals, although a pilot study indicated no strong tendency to choose one side over another. Despite this bias, tortoises successfully learned during four successive reversals, and trials to criterion decreased to training performance (initial acquisition) by the second reversal (Bridgeman & Tattersall, 2019). Finally, painted turtles (*C. picta*) performed multiple reversals and extra-dimensional shifts of colour and pattern (stripes) stimuli. Colour reversals appeared to be most difficult for the animals to achieve (Cranney & Powers, 1983).

*(b) Lizards*

Male rough-necked monitors (*V. rudicollis*), a Komodo dragon (*V. komodoensis*; Gaalema, 2007, 2011) and five western banded geckos (*Coleonyx variegatus*; Kirkish, Fobes, &

Richardson, 1979) increased performance during serial reversals. In rock agamas (*P. dorsalis*), habitat features (vegetation cover) affect reversal learning proficiency. Lizards learned to escape into a 'safe' refuge during a spatial reversal conducted in a controlled laboratory setting but animals collected from urban areas made fewer errors compared to lizards from rural areas (Batabyal & Thaker, 2019). Wild eastern water skinks (*E. quoyii*) likewise learned to locate a 'safe' refuge to escape a simulated attack after a spatial reversal in semi-natural conditions (Noble *et al.*, 2012), and 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 these lizards than visual cues but not during the reversal (Day, Ismail, & Wilczynski, 2003).

A test of multiple species with the same methodology in three anoles (*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). *A. boskianus*, an active forager, learned faster during a reversal applying the fork method (in which one spine had the reward while the second spine provided a visual cue) compared to *A. scutellatus*, a sit-and-wait forager. Active foraging might require better inhibition, important in reversal learning, to allow prey inspection before striking (Day *et al.*, 1999).

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. These skinks, however, successfully reversed four discriminations, showing some degree of flexibility in response behaviour (Szabo *et al.*, 2018). In a subsequent study using the same methodology in blue-tongue lizards (*T. s. scincoides*), no evidence of set formation was detected. The study revealed that juveniles learned at adult levels throughout all set-shifting stages, demonstrating adult-level cognitive abilities in young precocial lizards. This result suggests that juvenile precocial skinks might be born with enhanced cognitive abilities that may be advantageous during early life in the absence of parental care (Szabo *et al.*, 2019a); however, data from lizard species with rudimentary forms of parental care (e.g. species that live in family groups; see Whiting & While, 2017) are needed to confirm this hypothesis.

European glass lizards (*Pseudopus apodus*) with damage to the hippocampus and lizards with lesions to the dorsal ventricular ridge (DVR) took longer to learn a reversal (distinguishing between a triangle and a circle) compared to normal lizards. The results show that hippocampal lesions affect inhibition while lesions to the DVR affect visual processing (Ivazov, 1983).

As ectotherms, reptiles rely on 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, deviations from normal incubation temperatures can alter brain morphology and, consequently, learning ability. In hatchling three-lined skinks (*B. duperreyi*), incubation treatment ('hot' versus 'cold') affected discrimination of colour. Only 'hot'-incubated lizards learned the given tasks including a choice reversal (Clark *et al.*, 2014). These differences in performance were linked to differences in cortex size and structure: 'hot'-incubated lizards had a smaller telencephalon but increased neuron density in certain cortical areas (Amiel *et al.*, 2016).

### (c) Snakes

Juvenile and adult plains garter snakes (*T. radix*) reversed an initially learned discrimination between lemon and unscented pine chips within 50 trials. Before the reversal, snakes chose the lemon-scented compartment at a level of about 80% correct while directly after the reversal, choices decreased to chance level. Thereafter, the snakes gradually increased their choice of the compartment with the unscented pine chips, with 70% correct choices by the end of 50 trials (Begun *et al.*, 1988).

### (d) Summary

In recent years, reversal learning has increasingly been used to test behavioural flexibility in reptiles. Reversal learning performance was originally viewed as a measure of intelligence that could be compared across species (Bitterman, 1975), although this view has now changed because most species tested are capable of reversal learning. Combining reversals with related tests of innovative problem solving (e.g. Leal & Powell, 2012; Auersperg *et al.*, 2014) or attentional-set shifting (Szabo *et al.*, 2018, 2019a) could represent a more robust approach to the investigation of behavioural flexibility. For example, use of different techniques to solve a novel problem or rapid shifting to a previously untrained attentional set in a different dimension (Brown & Tait, 2015) could provide stronger evidence for behavioural flexibility. Tests of serial reversal learning also might prove informative with regard to learning-set formation. Serial reversal tasks have, however, become less popular compared with tests of a single reversal. Importantly, cue modality can greatly affect performance. For example, rats show poorer visual reversal performance compared to monkeys and pigeons but outperform them in odour reversals (Slotnick, 2001). No data on reversal learning was available for snakes until recently, perhaps indicating a trend towards testing of a phylogenetically wider range of species. Researchers are starting to use the methods of comparative psychology (Szabo *et al.*, 2018, 2019a). Such interdisciplinary work will likely become more frequent and will help us understand behavioural flexibility better in reptiles while also enabling comparisons with other vertebrates.



## (8) Solving novel problems

Some species are known to have advanced abilities to solve complex problems. For example, New Caledonian crows (*Corvus moneduloides*) can bend wire into hooks in order to extract a reward-containing basket from within a well (Weir, Chappell, & Kacelnik, 2002), and black rats (*R. rattus*) can develop new techniques for extracting pine seeds from cones when other food is not available (Zohar & Terkel, 1991). Recent studies indicate that reptiles can also learn novel foraging techniques.

### (a) Turtles and tortoises

Painted turtles (*C. picta*) learned to push response keys (Reiner & Powers, 1978, 1980, 1983; Cranney & Powers, 1983; Blau & Powers, 1989; Grisham & Powers, 1989, 1990; Yeh & Powers, 2005; Powers *et al.*, 2009) and Florida red-bellied cooters (*P. nelsoni*) and pond sliders (*T. scripta*) both exited water to climb a platform to tip bottles for food, all of which can be interpreted as novel foraging techniques (Davis & Burghardt, 2007, 2011, 2012).

### (b) Lizards

Eight different studies trained lizards to remove lids from wells for a reward; although training was involved, these are also examples of reptiles solving novel problems (Leal & Powell, 2012; Powell, 2012; Clark *et al.*, 2014; Noble *et al.*, 2014; Damas-Moreira *et al.*, 2018; Qi *et al.*, 2018; Riley *et al.*, 2018; Whiting *et al.*, 2018). Only two studies have tested a reptile using a puzzle box task. Black-throated monitors (*Varanus albigularis albigularis*) opened a plastic tube to retrieve a reward within 10 min of the first presentation and subsequently solved this novel task faster during a second and third trial (Manrod, Hartdegen, & Burghardt, 2008). Using a modified version of this tube task, Cooper *et al.* (2019) tested a roughneck monitor (*V. rudicollis*), two emerald tree monitors (*V. prasinus*), two Mertens' water monitors (*V. mertensi*), two Guatemalan beaded lizards (*Heloderma charlesbogerti*) and one Jamaican iguana (*Cyclura collei*). Of these five species, no result was obtained for the iguana because of low motivation (it did not approach the tube) and only two (*V. prasinus* and *V. mertensi*) of the remaining four species showed evidence of learning (decreased time needed to open the tube). Over 40 trials, individuals needed up to 30 min to retrieve the reward. Both the snout and claws were used to open the tube but to a differing degree depending on the species' natural foraging behaviour (Cooper *et al.*, 2019).

### (c) Snakes

Wild Burmese pythons (*Python bivittatus*) successfully learned to push a response key to open a door to gain access to a reward (Emer *et al.*, 2015). This trained behaviour was not used in further tests.

### (d) Summary

Reptiles can be trained to perform complex behaviours and some species are proficient in opening puzzle boxes. However, little research has examined complex problem solving in reptiles. Puzzle boxes used to date are simple tubes with hinged doors, so how reptiles perform at more complex tasks requiring several steps to solve remains unknown. Arguably, it may be hard to design problem-solving tasks suitable for reptiles because they do not use their front legs or mouths in the same way as mammals and birds. With ingenuity, however, tasks can be designed that could clarify the extent to which reptiles show problem-solving skills.

## (9) Social learning

Social learning refers to learning from other individuals (conspecifics or heterospecifics) as a shortcut to solving novel problems, while avoiding costly trial-and-error learning. Social learning is a summary term for several abilities from simple enhancement and social facilitation to imitation and emulation (Byrne, 1994; Heyes, 1994) and could be beneficial for both social and solitary species (Galef & Laland, 2005; Shettleworth, 2010), because even seemingly solitary animals can have a complex social life (Leyhausen, 1965). Nonetheless, research has focused mainly on social learning ability in group-living animals, and much less is known about social information use in less-social species (Galef & Laland, 2005). Recent work has shown that some less-social reptiles can learn from their conspecifics. Social learning has been studied in six lizard and two turtle species and is likely to be more common in reptiles than previously believed.

### (a) Turtles and tortoises

Florida red-bellied cooters (*P. nelsoni*) were the first reptile species to show social learning. Turtles matched the choice of a demonstrator during a brightness discrimination, demonstrating stimulus enhancement (Davis, 2009; Davis & Burghardt, 2011). Solitary-living red-footed tortoises (*C. carbonarius*) demonstrated social learning in a detour task (Wilkinson *et al.*, 2010). Tortoises that observed a demonstrator walking around a barrier learned to detour to obtain 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).

### (b) Lizards

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 (the door opening by itself) did not learn to open the door, indicating some involvement of socially facilitated enhancement (Kis, Huber, &

Wilkinson, 2015). Interestingly, ‘cold’-incubated hatchling bearded dragons were faster at opening the door after demonstration than ‘hot’-incubated lizards. There was, however, no significant difference between groups in the number of successful door openings (Siviter *et al.*, 2017). Wild Lilford’s wall lizards (*Podarcis lilfordi*) preferred locations with conspecifics present when given a choice between food with and without conspecifics (including static copper models). Lizards also preferred to associate with conspecifics (trapped in a glass jar) instead of an empty glass jar when no food was present. These lizards occur naturally at high densities, and are generalist foragers; conspecifics could thus be a reliable source of information regarding foraging opportunities (Perez-Cembranos & Perez-Mellado, 2015).

Age or sex can affect the probability with which animals use social information (Galef & Laland, 2005). In eastern water skinks (*E. quoyii*), age but not dominance status predicted whether lizards learned a two-choice discrimination from a conspecific. Lizards selected the correctly coloured lid out of two choices with and without a demonstration; young males, however, learned faster than controls while older lizards did not (Noble *et al.*, 2014). In a follow-up study on the same species, Kar *et al.* (2017) separated the effects of age and dominance by manipulating dominance status and presenting similar learning tasks. Dominant observers learned faster than subordinate observers during task acquisition but not during reversals suggesting that social learning is indeed age related rather than the result of age–dominance correlations (Kar *et al.*, 2017). Water skinks are often found at high densities around water bodies (Cogger, 2014) where social information will be readily available.

Social learning improves acquisition of information that is essential for naïve individuals (e.g. 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 of nine genera, with species that vary in their degree of social complexity from solitary to monogamous species living in multi-generational family groups (Chapple, 2003; Gardner *et al.*, 2008; While *et al.*, 2015). In monogamous White’s skinks (*L. whitii*), tests show that familiarity can improve social information use during reversal learning but not during acquisition. In a study by Munch *et al.* (2018b), White’s skinks were tested in three treatment groups: individuals observing their mating partner (demonstrator), an unfamiliar conspecific (demonstrator), or a non-demonstrator (control). Lizards observing their mate reversed faster than controls (Munch *et al.*, 2018b). Reversals are expected to be computationally challenging, and thus social information may be particularly valuable for reversal tasks. By contrast, juvenile tree skinks (*E. striolata*), which also live in family groups, 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 remain together for at least one season (Whiting & While, 2017) and juveniles have the opportunity to learn from parents, learning from any adult might have a cost

because juveniles experience a high risk of cannibalism from unrelated adult conspecifics (O’Connor & Shine, 2004; While *et al.*, 2015) and therefore may be less likely to use them as a source of social information. Adult females of this species do learn a two-choice discrimination readily 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 a demonstrator for juveniles might thus lead to different results.

Typically, animals are tested with conspecific demonstrators, but learning from heterospecifics 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 (CABI, 2018) including locations with other congeneric species. This creates a novel opportunity to test if *P. sicula* can exploit social information from congeneric lizards. When tested on a colour-discrimination task in which information was provided either from a conspecific or a heterospecific (*P. bocagae*) species, 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 could play a role during establishment in a novel habitat.

### (c) Summary

Reptiles are generally viewed as solitary, ‘asocial’ animals. However, despite the fact that most reptiles species do not form groups like mammals or birds, many species form territories and have territorial neighbours (e.g. Brattstrom, 1974; Pianka & Vitt, 2003). In some species, individuals form groups during the mating season (e.g. Brattstrom, 1974; Pianka & Vitt, 2003), in overwintering sites (e.g. Brown & Parker, 1976) or at basking spots [e.g. Amarello (2012) cited by Waters, Bowers, & Burghardt, 2017; Brattstrom, 1974; Pianka & Vitt, 2003] and sometimes juveniles group together (e.g. Burghardt, 1983). Adults of some species even protect their young for at least some period of time (e.g. Garrick, Lang, & Herzog, 1978; Butler, Hull, & Franz, 1995; Schuett *et al.*, 2016; Whiting & While, 2017), and some species form long-term family groups (e.g. Whiting & While, 2017). All these provide opportunities for social information transmission. Suboski (1992) regarded some reptile behaviours as simple forms of social learning (enhancement and social facilitation). Recent research has confirmed that reptiles can learn socially, and future work should investigate this in more detail (Laland, 2004).

## IV. FUTURE DIRECTIONS

Since the first detailed review by Burghardt (1977) on reptile learning, there has been a steady increase in reptile cognition research (Fig. 1). Especially in the last 10 years has seen a resurgence in cognition research as highlighted by Wilkinson & Huber (2012) and Burghardt (2013). We have gained

a better understanding of reptile learning abilities as new species have been tested and new methodologies have been developed. Interestingly, lizards are increasingly popular research subjects (Figs 1, 2, 3). Overall, the focus of the field has somewhat changed. While studies investigating habituation of behaviour remain rare, operant conditioning has become popular in zoos to improve reptile welfare but is less often used in research. Aversion learning is becoming a popular tool in conservation to train animals to avoid novel toxic invader species. Spatial learning remains a well-studied topic, but comparative approaches investigating why species or individuals differ in their abilities are rare. Research now focuses more on learning performance but how a discrimination is learned is still poorly understood. Behavioural flexibility tested using reversal-learning tasks is widely applied in turtles and lizards but is less popular in snakes. Additional tests of behavioural flexibility including problem-solving tasks should improve our understanding of the flexibility of reptiles in response to environmental change. Social learning and quantity discrimination in reptiles are new research areas that have emerged very recently while partial reinforcement studies, probability learning and classical conditioning are no longer studied. Some cognitive processes, such as executive functions, have yet to receive attention in reptiles. Below we present some key themes and questions that have emerged from our review as interesting topics for future research.

### (1) The fitness consequences of individual differences in cognition

The relationship between cognitive processes and fitness has received increasing attention during the past decade (e.g. Thornton *et al.*, 2014; Huebner *et al.*, 2018; Madden *et al.*, 2018) in order to understand how cognitive traits evolve. Research into reptile personality, defined as individual differences in behaviour that are consistent across time and/or context, has demonstrated low levels of heritable variation for many behavioural traits. Nonetheless, it has been shown that female behavioural type can affect offspring survival (see Waters *et al.*, 2017). Cognitive ability, similar to personality, might change an individual's fitness in many ways (e.g. foraging ability, learning resource distribution, location of safe refuges, etc.), although this is not widely supported by empirical data (e.g. Healy, 2012; Thornton *et al.*, 2014). In his original review, Burghardt (1977, p. 667) posed the question: "What are the selective pressures and cost–benefit relationships involved [in learning]?" We found only one study that tested how success in a learning task predicted survival: geckos that were better learners survived for longer, potentially leading to greater future reproductive success (Dayananda & Webb, 2017). While the precise mechanism(s) by which spatial learning improves survival in geckos is still not understood, we encourage more research into the links between cognition and fitness. For example, does cognitive ability influence survival and/or reproductive success directly or does cognitive ability instead correlate

with some other fitness-related trait? In relation to reptiles, learning the location of safe refuges in their environment, the location of thermally suitable refugia, the spatial variation of prey/food and information about social structure/dominance of individuals in their social neighbourhoods could all potentially influence fitness. With more research into individual differences in cognitive ability and better insights into how these differences relate to fitness (assuming that cognitive ability is heritable in reptiles as found in other taxa: e.g. Galsworthy *et al.*, 2005; Hopkins, Russell, & Schaeffer, 2014) we will be better able to understand the evolution of cognitive traits.

### (2) Cognition in ecologically relevant contexts

While the ability to learn is shared by most animals, the proficiency with which an individual can learn about certain stimuli depends on the degree to which selection has operated on a given cognitive process (Shettleworth, 2010). Few studies covered in our review attempted to test learning in the wild (e.g. Marcellini & Jenssen, 1991; Shafir & Roughgarden, 1994; Schall, 2000; Roth 2nd & Krochmal, 2015), or even in ecologically relevant contexts in captivity (e.g. Foa *et al.*, 2009; Price-Rees *et al.*, 2011; Somaweera *et al.*, 2011; Robbins *et al.*, 2013). Inadequate attention to a species' ecology can dramatically affect study results and any general inferences (Holtzman *et al.*, 1999; Stone *et al.*, 2000), an issue raised by Burghardt (1977) but still receiving too little attention.

Taking a species' ecology and life history into account will enhance the validity of the results generated by cognitive studies. Testing cognition in the wild will make results more biologically relevant, although this can be challenging with reptiles (see also Whiting & Noble, 2018). For questions that are only testable within a controlled laboratory setting, using wild-caught individuals (accounting for negative effects of captivity, e.g. Mohammed *et al.*, 2002) could be the best alternative although individuals need to be properly acclimated to laboratory conditions because the stress of captivity and testing could alter their behaviour and affect results (Langkilde & Shine, 2006; Bailey, 2018). Nonetheless, using wild-caught individuals could circumvent issues associated with decreased cognitive ability arising from breeding in captivity (du Toit *et al.*, 2012). Adequate reporting on the origin of animals is high in studies involving squamates (lizards and snakes) while more than half of studies on turtles did not report the origin of the test animals (Table S1). Furthermore, information on the duration that animals were maintained in captivity is scarce. We encourage researchers to improve reporting of critical study details and to select study species considering carefully their ecology and life history. For example, nocturnal species should be tested in the dark under red/blue light, and all reptiles (which are ectotherms) should be tested at environmental temperatures that allow them to reach optimal physiological function, which can impact response time and motivation (Burghardt, 1977; Whiting & Noble, 2018). For active foragers that rely on prey odour

during foraging, task design needs to control for olfactory cues, while this may be less important for sit-and-wait foragers that rely more heavily on vision (Cooper, 1995). These and other variables need to be considered when designing laboratory studies on reptiles (see Whiting & Noble, 2018).

### (3) Cognition and behaviour in invasive species

Introduced species can have detrimental effects on local communities (e.g. Reaser *et al.*, 2007). For example, introduction of the brown tree snake (*Boiga irregularis*), native to parts of Australasia, to Guam led to a major decrease in, and extinction of, some native bird populations within a few decades (Lowe *et al.*, 2000). Similarly, the red-eared slider (*T. scripta elegans*) has spread from its natural range in North America to many regions of the world including Europe and Australia, threatening native turtle species by competition for resources (Burger, 2019). The mechanisms favouring successful invasion of a species into a new habitat are of major interest but are often species and habitat specific, with no general factor increasing invasion success across species yet emerging (Kolar & Lodge, 2001; Hayes & Barry, 2008). Success and failure during invasion have been linked to behaviour and personality (Amiel, Tingley, & Shine, 2011; Chapple, Simmonds, & Wong, 2012) but how learning benefits individuals has received little attention (Averages-Weber, Dawson, & Chittka, 2013). Social learning and behavioural flexibility might play an important role during the early stages of establishment when animals face novel predators or prey. Using social information from congeneric species or behavioural flexibility could be key to survival (Sol, Timmermans, & Lefebvre, 2002; Wright *et al.*, 2010). It has been demonstrated that invasive lizards are able effectively to use information provided by heterospecifics (Damas-Moreira *et al.*, 2018) and that they are more plastic compared to sympatric, non-invasive congeneric species (Damas-Moreira *et al.*, 2019). Past experience with competition (e.g. Yeager & Burghardt, 1991), prey (e.g. Arnold, 1978; Stimac, Radcliffe, & Chiszar, 1982; Mori, 1996; Shafir & Roughgarden, 1998; Burghardt & Krause, 1999; Clark, 2004) and predation (e.g. Herzog, 1990; Desfilis, Font, & Guillen-Salazar, 2003) all affect how individuals react in future situations. These studies, however, are only a first step in understanding which cognitive abilities might be beneficial for invasive species facing novel challenges. Future research could compare performance at different tasks (foraging, social and spatial learning) among species known to be successful and unsuccessful invaders.

### (4) Social learning in social reptiles

Social learning is usually studied in group-living animals (Galef & Laland, 2005) because the demands of group living are likely to act as a selective pressure to improve cognition (and thus increase brain size) (Jolly, 1966; Humphrey, 1976; Reader & Laland, 2002). Reptiles, however, are also capable of social learning (e.g. Wilkinson *et al.*, 2010; Noble

*et al.*, 2014), and we encourage researchers to test both social and less-social reptiles (Whiting & While, 2017). Although some reptiles have a demonstrated ability to learn from conspecifics under controlled laboratory settings, it is less clear if this social information use occurs in the wild. It would be interesting to investigate how wild reptiles respond to seeing a conspecific with an unusual prey item or using a novel technique to gain access to a previously inaccessible food source. By using video recordings (e.g. Kis *et al.*, 2015; Siviter *et al.*, 2017), researchers can exert control over task variables and gain insight into information transfer. Comparing results between social and less-social species might then reveal if the degree of sociality has an effect on the type or degree of social information use, a previously unexplored research area in reptiles.

### (5) 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, 2013; Somaweera *et al.*, 2011; Ward-Fear *et al.*, 2016, 2017) that otherwise have detrimental effects on naïve native species (e.g. Indigo *et al.*, 2018). Crocodiles (*C. johnstoni*), blue-tongue skinks (*T. scincoides*) and monitor lizards (*V. panoptes*, *V. rudicollis* and *V. varius*) can be trained to avoid toxic novel prey. Future experiments could investigate whether 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 behaviour-centred approach by incorporating species-specific cognitive abilities (avoidance learning and social information use). Previous work has demonstrated that social learning is widespread among reptiles (see Section III.9). Training a subset of individuals to spread valuable information (genetically or through social transmission) might prove a rapid and effective approach to conservation.

### (6) Executive functions

Core executive functions comprise inhibitory skills, working memory, and flexibility in cognition. These processes prevent automatic responses, allowing individuals to make informed decisions. Tests for executive functions include reversal learning, set-shifting, or detour tasks; these are well studied in mammals (Diamond, 2013; Brown & Tait, 2015) but less understood in other vertebrates. In reptiles, behavioural flexibility has been investigated using reversal learning, however, how inhibition is exerted during reversals has received little attention. One lizard species demonstrated motor response inhibition in a detour task (Szabo *et al.*, 2019b) and one turtle (Cranney & Powers, 1983) and two lizard species (Szabo *et al.*, 2018, 2019a) were able to perform an extradimensional shift in a set-shifting task, but formation of an attentional set

was not determined. Importantly, working memory has been unexplored in reptiles. Executive functions comprise layers of processing forming the basis of higher order abilities such as planning, reasoning and self-regulation (Diamond, 2013). To understand, for example, if reptiles plan their actions we first need to establish if they possess basic executive functions underlying these complex, higher-order abilities.

### (7) 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, the sexes differ in spatial memory ability in promiscuous mammals while not in monogamous species likely due to different selection resulting from different spatial demands between males and females (Gaulin & Fitzgerald, 1989; Perdue *et al.*, 2011). Most studies on spatial learning, especially in lizards, have used only males (e.g. Day *et al.*, 1999, 2001; Foa *et al.*, 2009; LaDage *et al.*, 2012; Mueller-Paul *et al.*, 2012) and studies using 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 (Carazo *et al.*, 2014). Sex-dependent spatial learning could be 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 interesting to compare male and female spatial learning performance between species with high and low levels of sexual selection such as polygamous *versus* monogamous (respectively) lizards. This unexplored research field will likely produce novel insights into reptile spatial navigation and how sexual selection shapes spatial learning.

## V. CONCLUSIONS

- (1) Our knowledge of reptile learning has greatly advanced, especially in the last decade. Most studies included in this review were conducted on lizards and turtles, while comparatively little is known about learning abilities in snakes, the tuatara and crocodylians, a bias that has persisted since the emergence of this field. Although the range of species tested has expanded, our review still emphasises the need for broader taxonomic coverage within reptiles.
- (2) We provide an up-to-date overview of current knowledge on reptile learning and summarise the results of 118 studies showing how reptiles habituate their behaviour, how they can be trained to perform new behaviour, how they avoid aversive stimuli including

flavour-aversion learning and escaping predators, which cues they use during spatial learning and during foraging, their numerical abilities, their ability to solve novel problems, how they cope with change, and what we know about their social learning ability.

- (3) We highlight seven contemporary research themes and avenues which we believe will be of special interest in the near future.
- (4) Our review emphasises that differences in cognitive ability between distantly related taxa are of degree rather than kind. Reptiles are not driven simply by instinct, but their abilities are certainly not those of higher primates. The field of reptile cognition should now move from descriptive studies testing if a species can learn a task towards more experimental approaches to elucidate the drivers of cognitive variation within and among species. A more ecologically focused approach will produce data that are easier to interpret in relation to fitness. We encourage researchers in this young and promising field to be bolder in applying complex methodologies, taking inspiration from other fields such as experimental and comparative psychology.

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## VII. REFERENCES

- ABRAMSON, C. I. & CHICAS-MOSIER, A. M. (2016). Lessons from *Mimosa pudica*. *Frontiers in Psychology* **7**, 417.
- ABRAMSON, J. Z., HERNÁNDEZ-LLOREDA, V., CALL, J. & COLMENARES, F. (2011). Relative quantity judgments in south American sea lions (*Otaria flavescens*). *Animal Cognition* **14**, 695–706.
- AGRILLO, C. (2015). Numerical and arithmetic abilities in non-primate species. In *The Oxford Handbook of Numerical Cognition* (eds R. KADOSH and A. DOWKER), pp. 214–236. Oxford University Press, Oxford.
- AGRILLO, C. & BISAZZA, A. (2014). Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* **234**, 82–91.
- AGRILLO, C. & BISAZZA, A. (2018). Understanding the origin of number sense: a review of fish studies. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20160511.
- ALCOCK, J. (1998). *Animal Behavior: An Evolutionary Approach*, 6th Edition (0). Sinauer Associates, Sunderland.
- ALFÖLDI, J., DI PALMA, F., GRABHERR, M., WILLIAMS, C., KONG, L., MAUCELLI, E., RUSSELL, P., LOWE, C. B., GLOR, R. E., JAFFE, J. D., RAY, D. A., BOISSINOT, S., SHEDLOCK, A. M., BOTKA, C., CASTOE, T. A., *et al.* (2011). The genome of the green anole lizard and a comparative analysis with birds and mammals. *Nature* **477**, 587–591.
- ALMLI, L. M. & BURGHARDT, G. M. (2006). Environmental enrichment alters the behavioral profile of ratsnakes (Elaphe). *Journal of Applied Animal Welfare Science* **9**, 85–109.

- AMARELLO, M. (2012). Social snakes? Non-random association patterns detected in a population of Arizona black rattlesnakes (*Crotalus cerebrus*). Unpublished thesis. Arizona State University, Tempe.
- AMIEL, J. J. & SHINE, R. (2012). Hotter nests produce smarter young lizards. *Biology Letters* **8**, 372–374.
- AMIEL, J. J., TINGLEY, R. & SHINE, R. (2011). Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. *PLoS One* **6**, e18277.
- AMIEL, J. J., LINDSTRÖM, T. & SHINE, R. (2014). Egg incubation effects generate positive correlations between size, speed and learning ability in young lizards. *Animal Cognition* **17**, 337–347.
- AMIEL, J. J., BAO, S. & SHINE, R. (2016). The effects of incubation temperature on the development of the cortical forebrain in a lizard. *Animal Cognition* **20**, 117–125.
- ARNOLD, S. J. (1978). Some effects of early experience on feeding responses in the common garter snake, *Thamnophis sirtalis*. *Animal Behaviour* **26**, 455–462.
- AUERSPERG, A. M. I., GAJDON, G. K. & VON BAYERN, A. M. P. (2014). A new approach to comparing problem solving, flexibility and innovation. *Communicative & Integrative Biology* **5**, 140–145.
- AUGUSTINE, L. & BAUMER, M. (2012). Training a Nile crocodile to allow for collection of blood at the Wildlife Conservation Society's Bronx zoo. *Herpetological Review* **43**, 432–435.
- AVARGUES-WEBER, A., DAWSON, E. H. & CHITTKA, L. (2013). Mechanisms of social learning across species boundaries. *Journal of Zoology* **290**, 1–11.
- AVIGAN, M. R. & POWERS, A. S. (1995). The effects of MK-801 injections and dorsal cortex lesions on maze-learning in turtles (*Chrysemys picta*). *Psychobiology* **23**, 63–68.
- BAILEY, J. (2018). Does the stress of laboratory life and experimentation on animals adversely affect research data? A critical review. *Alternatives to Laboratory Animals* **46**, 291–305.
- BATABYAL, A. & THAKER, M. (2019). Lizards from suburban areas learn faster to stay safe. *Biology Letters* **15**, 20190009.
- BEGUN, D., KUBIE, J. L., O'KEEFE, P. M. & HALPERN, M. (1988). Conditioned discrimination of airborne odors by garter snakes (*Thamnophis radix* and *T. sirtalis sirtalis*). *Journal of Comparative Psychology* **102**, 35–43.
- BENSON-AMRAM, S., GILFILLAN, G. & MCCOMB, K. (2018). Numerical assessment in the wild: insights from social carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20160508.
- BERNSTEIN, I. L. (1999). Taste aversion learning: a contemporary perspective. *Nutrition* **15**, 229–234.
- BEZZINA, C. N., AMIEL, J. J. & SHINE, R. (2014). Does invasion success reflect superior cognitive ability? A case study of two congeneric lizard species (*Lampropholis*, Scincidae). *PLoS One* **9**, e86271.
- BIRO, P. A. (2013). Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. *Oecologia* **171**, 339–345.
- BITTERMAN, M. E. (1975). The comparative analysis of learning. *Science* **188**, 699–709.
- BLAU, A. & POWERS, A. S. (1989). Discrimination-learning in turtles after lesions of the dorsal cortex or basal forebrain. *Psychobiology* **17**, 445–449.
- BOGALE, B. A., AOYAMA, M. & SUGITA, S. (2014). Spontaneous discrimination of food quantities in the jungle crow, *Corvus macrorhynchos*. *Animal Behaviour* **94**, 73–78.
- BOOGERT, N. J., MADDEN, J. R., MORAND-FERRON, J. & THORNTON, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **373**, 20170280.
- BOOTH, D. T. (2006). Influence of incubation temperature on hatchling phenotype in reptiles. *Physiological and Biochemical Zoology* **79**, 274–281.
- BRATTSTROM, B. H. (1974). The evolution of reptilian social behavior. *American Zoologist* **14**, 35–49.
- BRIDGEMAN, J. M. & TATTERSALL, G. J. (2019). Tortoises develop and overcome position biases in a reversal learning task. *Animal Cognition* **22**, 265–275.
- BROWN, W. S. & PARKER, W. S. (1976). Movement ecology of *Coluber constrictor* near communal hibernacula. *Copeia* **1976**, 225–242.
- BROWN, V. J. & TAIT, D. S. (2015). Behavioral flexibility: attentional shifting, rule switching and response reversal. In *Encyclopedia of Psychopharmacology* (eds I. P. Stolerman and L. H. Price), pp. 264–269. Springer-Verlag, New York.
- BRYANT, Z., HARDING, L., GRANT, S. & RENDLE, M. (2016). A method for blood sampling the Galápagos tortoise, *Chelonoidis nigra* using operant conditioning for voluntary blood draws. *The Herpetological Bulletin* **135**, 7–10.
- BUCKINGHAM, J. N., WONG, B. B. M. & ROSENTHAL, G. G. (2007). Shoaling decisions in female swordtails: how do fish gauge group size. *Behaviour* **144**, 1333–1346.
- BULL, J. J. (1980). Sex determination in reptiles. *The Quarterly Review of Biology* **55**, 3–21.
- BURGER, J. (2019). Red-eared slider. <http://www.invasivespeciesinitiative.com/redeared-slider>
- BURGHARDT, G. M. (1977). Learning processes in reptiles. In *Biology of the Reptilia. Ecology and Behaviour A* (Volume 7, eds C. Gans and D. W. Tinkle), pp. 555–681. Academic Press, Cambridge.
- BURGHARDT, G. M. (1983). Aggregation and species discrimination in newborn snakes. *Zeitschrift für Tierpsychologie* **61**, 89–101.
- BURGHARDT, G. M. (2013). Environmental enrichment and cognitive complexity in reptiles and amphibians: concepts, review, and implications for captive populations. *Applied Animal Behaviour Science* **147**, 286–298.
- BURGHARDT, G. M. & KRAUSE, M. A. (1999). Plasticity of foraging behavior in garter snakes (*Thamnophis sirtalis*) reared on different diets. *Journal of Comparative Psychology* **113**, 277–285.
- BURGHARDT, G. M., BARTMESS-LEVASSEUR, J. N., BROWNING, S. A., MORRISON, K. E., STEG, C. L., ZACHAU, C. E. & FREEBERG, T. M. (2012). Perspectives - minimizing observer bias in behavioral studies: a review and recommendations. *Ethology* **118**, 511–517.
- BUTLER, J. A., HULL, T. W. & FRANZ, R. (1995). Neonate aggregations and maternal attendance of Young in the eastern diamondback rattlesnake, *Crotalus adamanteus*. *Copeia* **1995**, 196–198.
- BYRNE, R. W. (1994). The evolution of intelligence. In *Behaviour and Evolution* (eds P. J. B. Slater and T. R. Halliday), pp. 223–265. Cambridge University Press, Cambridge.
- CABI (2018). *Podarcis sicula* [original text by Silva-Rocha, I.]. In *Invasive Species Compendium*. CAB International, Wallingford, UK. [www.cabi.org/isc](http://www.cabi.org/isc).
- CAMPBELL, J. D. (1981). The metabolic cost of behavioral thermoregulation of body temperature in the Northern alligator lizard (*Gerrhonotus coeruleus*), and how it affects the classical concept of eurythermality. Unpublished Master thesis. Portland State University.
- CARAZO, P., NOBLE, D. W. A., CHANDRASOMA, D. & WHITING, M. J. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133275.
- CAREW, T. J., PINSKER, H. M. & KANDEL, E. R. (1972). Long-term habituation of a defensive withdrawal reflex in *Aplysia*. *Science* **175**, 451–454.
- CARTER, A. J., HEINSOHN, R., GOLDIZEN, A. W. & BIRO, P. A. (2012). Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour* **83**, 1051–1058. <https://doi.org/10.1016/j.anbehav.2012.01.033>.
- CHAPPLE, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**, 145–180.
- CHAPPLE, D. G., SIMMONDS, S. M. & WONG, B. B. M. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution* **27**, 57–64.
- CHARVET, C. J. & STRIEDTER, G. F. (2011). Developmental modes and developmental mechanisms can channel brain evolution. *Frontiers in Neuroanatomy* **5**, 1–5.
- CHUNG, M., GOULET, C. T., MICHELANGELO, M., MELKI-WEGNER, B., WONG, B. B. M. & CHAPPLE, D. G. (2017). Does personality influence learning? A case study in an invasive lizard. *Oecologia* **185**, 641–651.
- CLARK, R. W. (2004). Feeding experience modifies the assessment of ambush sites by the timber rattlesnake, a sit-and-wait predator. *Ethology* **110**, 471–483.
- CLARK, B. F., AMIEL, J. J., SHINE, R., NOBLE, D. W. A. & WHITING, M. J. (2014). Colour discrimination and associative learning in hatchling lizards incubated at 'hot' and 'cold' temperatures. *Behavioral Ecology and Sociobiology* **68**, 239–247.
- COGGER, H. G. (2014). *Reptiles and Amphibians of Australia*, 7th Edition (). CSIRO Publishing, Collingwood.
- COOPER, W. E. (1995). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behaviour* **50**, 973–985.
- COOPER, T., LIEW, A., ANDRLE, G., CAFRITZ, E., DALLAS, H., NIESEN, T., SLATER, E., STOCKERT, J., VOLD, T., YOUNG, M. & MENDELSON, J. (2019). Latency in problem solving as evidence for learning in Varanid and Helodermatid lizards, with comments on foraging techniques. *Copeia* **107**, 78–84.
- CRANNEY, J. & POWERS, A. S. (1983). The effects of core nucleus and cortical lesions in turtles on reversal and dimensional shifting. *Physiological Psychology* **11**, 103–111.
- CUMMINGS, M. E. (2018). Sexual conflict and sexually dimorphic cognition—reviewing their relationship in poeciliid fishes. *Behavioral Ecology and Sociobiology* **72**, 73.
- DAMAS-MOREIRA, I., OLIVEIRA, D., SANTOS, J. L., RILEY, J. L., HARRIS, D. J. & WHITING, M. J. (2018). Learning from others: an invasive lizard uses social information from both conspecifics and heterospecifics. *Biology Letters* **14**, 20180532.
- DAMAS-MOREIRA, I., RILEY, J. L., HARRIS, D. J. & WHITING, M. J. (2019). Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. *Animal Behaviour* **115**, 195–202.
- DAVIS, K. M. (2009). *Sociality, cognition and social learning in turtles (Emydidae)*. Unpublished doctoral dissertation, University of Tennessee, Knoxville Tennessee.
- DAVIS, K. & BURGHARDT, G. M. (2007). Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). *Behavioral Processes* **75**, 225–230.
- DAVIS, K. M. & BURGHARDT, G. M. (2011). Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. *Journal of Comparative Psychology* **125**, 404–410.
- DAVIS, K. M. & BURGHARDT, G. M. (2012). Long-term retention of visual tasks by two species of emydid turtles, *Pseudemys nelsoni* and *Trachemys scripta*. *Journal of Comparative Psychology* **126**, 213–223.

- DAY, L. B., CREWS, D. & WILCZYNSKI, W. (1999). Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour* **57**, 393–407.
- DAY, L. B., CREWS, D. & WILCZYNSKI, W. (2001). Effects of medial and dorsal cortex lesions on spatial memory in lizards. *Behavioural Brain Research* **118**, 27–42.
- DAY, L. B., ISMAIL, N. & WILCZYNSKI, W. (2003). Use of position and feature cues in discrimination learning by the whiptail lizard (*Cnemidophorus inornatus*). *Journal of Comparative Psychology* **117**, 440–448.
- DAYANANDA, B. & WEBB, J. K. (2017). Incubation under climate warming affects learning ability and survival in hatchling lizards. *Biology Letters* **13**, 20170002.
- DESFILIS, E., FONT, E. & GUILLEN-SALAZAR, F. (2003). Stimulus control of predatory behavior by the Iberian wall lizard (*Podarcis hispanica*, Sauria, Lacertidae): effects of familiarity with prey. *Journal of Comparative Psychology* **117**, 309–316.
- DIAMOND, A. (2013). Executive functions. *Annual Reviews in Psychology* **64**, 135–168.
- DOUGHERTY, L. R. & GUILLETTE, L. M. (2018). Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **373**, 20170282.
- EMER, S. A., MORA, C. V., HARVEY, M. T. & GRACE, M. S. (2015). Predators in training: operant conditioning of novel behavior in wild Burmese pythons (*Python molurus bivittatus*). *Animal Cognition* **18**, 269–278.
- FOA, A., BASAGLIA, F., BELTRAMI, G., CARNACINA, M., MORETTO, E. & BERTOLUCCI, C. (2009). Orientation of lizards in a Morris water-maze: roles of the sun compass and the parietal eye. *Journal of Experimental Biology* **212**, 2918–2924.
- FOX, S. F., MCCOY, J. K. & BAIRD, A. (2003). *Lizard Social Behavior*. Johns Hopkins University Press, Baltimore.
- FRIESE, R. R. (2017). *Spatial learning of shelter locations and associative learning of a foraging task in the cottonmouth (Agkistrodon piscivorus)*. (MSc). Missouri State University, 3175.
- GAALEMA, D. E. (2007). *Food choice, reinforcer preference, and visual discrimination in monitor lizards (Varanus spp.)*. (MSc). Georgia Institute of Technology, Georgia.
- GAALEMA, D. E. (2011). Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). *Journal of Comparative Psychology* **125**, 246–249.
- GAALEMA, D. E. & BENBOE, D. (2008). Positive reinforcement training of Aldabra tortoises (*Geochelone gigantea*) at zoo Atlanta. *Herpetological Review* **39**, 331–334.
- GALEF, B. G. J. & LALAND, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience* **55**, 489–499.
- GALSWORTHY, M. J., PAYA-CANO, J. L., LIU, L., MONLEON, S., GREGORYAN, G., FERNANDES, C., SCHALKWYK, L. C. & PLOMIN, R. (2005). Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behavior Genetics* **35**, 675–692.
- GARDNER, M. G., HUGALL, A. F., DONNELLAN, S. C., HUTCHINSON, M. N. & FOSTER, R. (2008). Molecular systematics of social skinks- phylogeny and taxonomy of the *Egernia* group (Reptilia- Scincidae). *Zoological Journal of the Linnean Society* **154**, 781–794.
- GARLAND, A., LOW, J. & BURNS, K. C. (2012). Large quantity discrimination by North Island robins (*Petroica longipes*). *Animal Cognition* **15**, 1129–1140.
- GARRICK, L. D., LANG, J. W. & HERZOG, H. A. (1978). Social signals of adult American alligators. *Bulletin of the American Museum of Natural History* **160**, 155–192.
- GAULIN, S. J. C. & FITZGERALD, R. W. (1989). Sexual selection for spatial-learning ability. *Animal Behaviour* **37**, 322–331.
- GAVISH, L. (1979). Conditioned-response of snakes (*Malpolon monspessulanum*) to light (Reptilia, Serpentes, Colubridae). *Journal of Herpetology* **13**, 357–359.
- GAZZOLA, A., VALLORTIGARA, G. & PELLITTERI-ROSA, D. (2018). Continuous and discrete quantity discrimination in tortoises. *Biology Letters* **14**, 20180649.
- GLAUDAS, X. (2004). Do cottonmouths (*Agkistrodon piscivorus*) habituate to human confrontations? *Southeastern Naturalist* **3**, 129–138.
- GLAUDAS, X., WINNE, C. T. & FEDEWA, L. A. (2006). Ontogeny of anti-predator behavioral habituation in cottonmouths (*Agkistrodon piscivorus*). *Ethology* **112**, 608–615.
- GONZALEZ-GOMEZ, P. L., MADRID-LOPEZ, N., SALAZAR, J. E., SUAREZ, R., RAZETO-BARRY, P., MPODOZIS, J., BOZINOVIC, F. & VASQUEZ, R. A. (2014). Cognitive ecology in hummingbirds: the role of sexual dimorphism and its anatomical correlates on memory. *PLoS One* **9**, e90165.
- GOULET, C. T., MICHELANGELO, M., CHUNG, M., RILEY, J. L., WONG, B. B. M., THOMPSON, M. B. & CHAPPLE, D. G. (2018). Evaluating cognition and thermal physiology as components of the pace-of-life syndrome. *Evolutionary Ecology* **32**, 469–488.
- GRAND, T. I. (1992). Altricial and precocial mammals - a model of neural and muscular development. *Zoo Biology* **11**, 3–15.
- GRISHAM, W. & POWERS, A. S. (1989). Function of the dorsal and medial cortex of turtles in learning. *Behavioral Neuroscience* **103**, 991–997.
- GRISHAM, W. & POWERS, A. S. (1990). Effects of dorsal and medial cortex lesions on reversals in turtles. *Physiology & Behavior* **47**, 43–49.
- GÜNTÜRKÜN, O., STACHO, M. & STRÖCKENS, F. (2017). The brains of reptiles and birds. In *Evolution of Nervous Systems*, 2nd Edition (Volume 1, ed. J. KAAS), pp. 171–221. Elsevier, Oxford.
- HAMPTON, R. E. & GILLINGHAM, J. C. (1989). Habituation of the alarm reaction in neonatal eastern garter snakes, *Thamnophis sirtalis*. *Journal of Herpetology* **23**, 433–435.
- HANUS, D. & CALL, J. (2007). Discrete quantity judgments in the great apes: the effect of presenting whole sets vs. item-by-item. *Journal of Comparative Psychology* **121**, 241–249.
- HARRISON, F. E., REISERER, R. S., TOMARKEN, A. J. & McDONALD, M. P. (2006). Spatial and non-spatial escape strategies in the Barnes maze. *Learning & Memory* **13**, 809–819.
- HAYES, K. R. & BARRY, S. C. (2008). Are there any consistent predictors of invasion success? *Biological Invasions* **10**, 483–506.
- HEALY, S. D. (2012). Animal cognition: the trade-off to being smart. *Current Biology* **22**, R840–R841.
- HELLMUTH, H., AUGUSTINE, L., WATKINS, B. & HOPE, K. (2012). Using operant conditioning and desensitization to facilitate veterinary care with captive reptiles. *Veterinary Clinics of North America - Exotic Animal Practice* **15**, 425–443.
- HERR, M. W., ROBBINS, T. R., CENTI, A., THAWLEY, C. J. & LANGKILDE, T. (2016). Irresistible ants: exposure to novel toxic prey increases consumption over multiple temporal scales. *Oecologia* **181**, 749–756.
- HERZOG, H. A. (1990). Experimental modification of defensive behaviors in garter snakes (*Thamnophis sirtalis*). *Journal of Comparative Psychology* **104**, 334–339.
- HERZOG, H. A. J., BOWERS, B. B. & BURGHARDT, G. M. (1989). Development of antipredator responses in snakes: IV. Interspecific and intraspecific differences in habituation of defensive behavior. *Developmental Psychobiology* **22**, 489–508.
- HEYES, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews* **69**, 207–231.
- HIGGINS, J. P. T. & GREEN, S. (2011). *Cochrane Handbook for Systematic Reviews of Interventions* Version 5.1.0. The Cochrane Collaboration. <http://handbook.cochrane.org>.
- HOLTZMAN, D. A. (1998). From slither to hither- orientation and spatial learning in snakes. *Integrative Biology: Issues, News and Reviews* **1**, 81–89.
- HOLTZMAN, D. A., HARRIS, T. W., ARANGUREN, G. & BOSTOCK, E. (1999). Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Animal Behaviour* **57**, 51–60.
- HOPKINS, W. D., RUSSELL, J. L. & SCHAEFFER, J. (2014). Chimpanzee intelligence is heritable. *Current Biology* **24**, 1649–1652.
- HUEBNER, F., FICHEL, C. & KAPPELER, P. M. (2018). Linking cognition with fitness in a wild primate: fitness correlates of problem-solving performance and spatial learning ability. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **373**, 20170295.
- HUMPHREY, N. (1976). The social function of intellect. In *Growing Points in Ethology* (eds P. P. G. BATESON and R. A. HINDE), pp. 303–317. Cambridge University Press, Cambridge.
- INDIGO, N., SMITH, J., WEBB, J. K. & PHILLIPS, B. (2018). Not such silly sausages: evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. *Australian Ecology* **43**, 592–601.
- ISHIDA, M. & PAPINI, M. R. (1997). Massed-trial overtraining effects on extinction and reversal performance in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology* **50**, 1–16.
- IVAZOV, N. I. (1983). Role of the hippocampal cortex and dorsal ventricular ridge in conditioned reflex activity of the anguid lizard Scheltopusik (*Ophisaurus apodus*). *Neuroscience and Behavioral Physiology* **13**, 397–403.
- JOLLY, A. (1966). Lemur social behavior and primate intelligence. *American Association for the Advancement of Science* **153**, 501–506.
- JOLLY, C. J., SHINE, R. & GREENLEES, M. J. (2016). The impacts of a toxic invasive prey species (the cane toad, *Rhinella marina*) on a vulnerable predator (the lace monitor, *Varanus varius*). *Biological Invasions* **18**, 1499–1509.
- JONES, C. M., BRAITHWAITE, V. A. & HEALY, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience* **117**, 403–411.
- KANG, F., GOULET, C. T. & CHAPPLE, D. G. (2018). The impact of urbanization on learning ability in an invasive lizard. *Biological Journal of the Linnean Society* **123**, 55–62.
- KAR, F., WHITING, M. J. & NOBLE, D. W. A. (2017). Dominance and social information use in a lizard. *Animal Cognition* **20**, 805–812.
- KELLY, E. & PHILLIPS, B. (2017). Get smart: native mammal develops toad-smart behavior in response to a toxic invader. *Behavioral Ecology* **28**, 854–858.
- KELLY, E. & PHILLIPS, B. L. (2018). Targeted gene flow and rapid adaptation in an endangered marsupial. *Conservation Biology* **33**, 112–121.
- KIRKISH, P. M., FOBES, J. L. & RICHARDSON, A. M. (1979). Spatial reversal learning in the lizard *Coleonyx variegatus*. *Bulletin of Psychonomic Science* **13**, 265–267.
- KIS, A., HUBER, L. & WILKINSON, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal Cognition* **18**, 325–331.
- KOLAR, C. S. & LODGE, D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**, 199–204.
- KOOPMANS, G., BLOKLAND, A., VANNIEUWENHUIJZEN, P. & PRICKAERTS, J. (2003). Assessment of spatial learning abilities of mice in a new circular maze. *Physiology & Behavior* **79**, 683–693.
- KUMAR, S., STECHER, G., SULESKI, M. & HEDGES, S. B. (2017). TimeTree: a resource for timelines, timetrees, and divergence times. *Molecular Biology and Evolution* **34**, 1812–1819.
- LADAGE, L. D., RIGGS, B. J., SINERVO, B. & PRAVOSUDOV, V. V. (2009). Dorsal cortex volume in male side-blotched lizards, *Uta stansburiana*, is associated with different space use strategies. *Animal Behaviour* **78**, 91–96.

- LA DAGE, L. D., ROTH, T. C., CERJANIC, A. M., SINERVO, B. & PRAVOSUDOV, V. V. (2012). Spatial memory: are lizards really deficient? *Biology Letters* **8**, 939–941.
- LALAND, K. N. (2004). Social learning strategies. *Learning & Behavior* **32**, 4–14.
- LANGKILDE, T. & SHINE, R. (2006). How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *Journal of Experimental Biology* **209**, 1035–1043.
- LEAL, M. & POWELL, B. J. (2012). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters* **8**, 28–30.
- LEFEBVRE, L., READER, S. M. & SOL, D. (2004). Brains, innovations and evolution in birds and primates. *Brain Behavior and Evolution* **63**, 233–246.
- LEIGHTY, K. A., GRAND, A. P., COURTE, V. L. P., MALONEY, M. A. & BETTINGER, T. L. (2013). Relational responding by eastern box turtles (*Terrapene carolina*) in a series of color discrimination tasks. *Journal of Comparative Psychology* **127**, 256–264.
- LEYHAUSEN, P. (1965). The communal organization of solitary mammals. *Symposia of the Zoological Society of London* **14**, 249–263.
- LIU, Y. & BURMEISTER, S. S. (2017). Sex differences during place learning in the túngara frog. *Animal Behaviour* **128**, 61–67.
- LLEWELYN, J., SCHWARZKOPF, L., PHILLIPS, B. L. & SHINE, R. (2014). After the crash: how do predators adjust following the invasion of a novel toxic prey type? *Australian Ecology* **39**, 190–197.
- LOPEZ, J. C., RODRIGUEZ, F., GOMEZ, Y., VARGAS, J. P., BROGLIO, C. & SALAS, C. (2000). Place and cue learning in turtles. *Animal Learning & Behavior* **28**, 360–372.
- LOPEZ, J. C., GOMEZ, Y., RODRIGUEZ, F., BROGLIO, C., VARAGAS, J. P. & SALAS, C. (2001). Spatial learning in turtles. *Animal Cognition* **4**, 49–59.
- LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. (2000). 100 of the World's worst invasive alien species: a selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG), Species Survival Commission (SSC), World Conservation Union (IUCN)*.
- MADDEN, J. R., LANGLEY, E. J. G., WHITESIDE, M. A., BEARDSWORTH, C. E. & VAN HORIK, J. O. (2018). The quick are the dead: pheasants that are slow to reverse a learned association survive for longer in the wild. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **373**, 20170297.
- MANROD, J. D., HARTDEGEN, R. & BURGHARDT, G. M. (2008). Rapid solving of a problem apparatus by juvenile black-throated monitor lizards (*Varanus albigularis albigularis*). *Animal Cognition* **11**, 267–273.
- MARCELLINI, D. L. & JENSSEN, T. A. (1991). Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersii*: implication for anti-predator behavior. *Journal of Herpetology* **25**, 238–241.
- MATSUBARA, S., DEEMING, D. C. & WILKINSON, A. (2017). Cold-blooded cognition - new directions in reptile cognition. *Current Opinion in Behavioural Sciences* **16**, 126–130.
- MCGOWAN, J. & SAMPSON, M. (2005). Systematic reviews need systematic searchers. *Journal of the Medical Library Association* **93**, 74–80.
- MOHAMMED, A. H., ZHU, S. W., DARMOPIL, S., HJERLING-LEFFLER, J., ERNFORS, P., WINBLAD, B., DIAMOND, M. C., ERIKSSON, P. S. & BOGDANOVIC, N. (2002). Environmental enrichment and the brain. *Progress in Brain Research* **138**, 109–133.
- MORI, A. (1996). A comparative study of the development of prey handling behavior in young rat snakes, *Elaphe quadrivirgata* and *E. climacophora*. *Herpetologica* **52**, 313–322.
- MUELLER-PAUL, J., WILKINSON, A., HALL, G. & HUBER, L. (2012). Response-stereotypy in the jewelled lizard (*Timon lepidus*) in a radial-arm maze. *Herpetology Notes* **5**, 243–246.
- MUELLER-PAUL, J., WILKINSON, A., AUST, U., STEURER, M., HALL, G. & HUBER, L. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (*Chelonioidis carbonaria*). *Behavioural Processes* **106**, 187–192.
- MUNCH, K. L., NOBLE, D. W. A., BOTTERILL-JAMES, T., KOOLHOF, I. S., HALLIWELL, B., WAPSTRA, E. & WHILE, G. M. (2018a). Maternal effects impact decision-making in a viviparous lizard. *Biology Letters* **14**, 20170556.
- MUNCH, K. L., NOBLE, D. W. A., WAPSTRA, E. & WHILE, G. M. (2018b). Mate familiarity and social learning in a monogamous lizard. *Oecologia* **188**, 1–10.
- MUSTAFAR, F., HARVEY, M. A., KHANI, A., ARATO, J. & RAINER, G. (2018). Divergent solution to visual problem solving across mammalian species. *eNeur* **5**, ENEURO.0167-18.2018.
- NOBLE, D. W. A., CARAZO, P. & WHITING, M. J. (2012). Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions. *Biology Letters* **8**, 946–948.
- NOBLE, D. W. A., BYRNE, R. W. & WHITING, M. J. (2014). Age-dependent social learning in a lizard. *Biology Letters* **10**, 20140430.
- NOBLE, D. W. A., STENHOUSE, V. & SCHWANZ, L. E. (2018). Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biological Reviews* **93**, 72–97.
- O'CONNOR, D. & SHINE, R. (2004). Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour* **68**, 1361–1369.
- PAHL, M., SI, A. & ZHANG, S. (2013). Numerical cognition in bees and other insects. *Frontiers in Psychology* **4**, 162.
- PAPINI, M. R. & ISHIDA, M. (1994). Role of magnitude of reinforcement in spaced-trial instrumental learning in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology Section B - Comparative and Physiological Psychology* **47**, 1–13.
- PARADIS, S. & CABANAC, M. (2004). Flavour aversion learning induced by lithium chloride in reptiles but not in amphibians. *Behavioural Processes* **67**, 11–18.
- PAULISSEN, M. A. (2008). Spatial learning in the little brown skink, *Scincella lateralis*: the importance of experience. *Animal Behaviour* **76**, 135–141.
- PAULISSEN, M. A. (2014). The role of visual cues in learning escape behaviour in the little brown skink (*Scincella lateralis*). *Behaviour* **151**, 2015–2028.
- PEEKE, H. V. S. & HERZ, M. J. (1973). *Habituation. Volume 1: Behavioral studies*. Academic Press, Cambridge.
- PERDUE, B. M., SNYDER, R. J., ZHIHE, Z., MARR, M. J. & MAPLE, T. L. (2011). Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora. *Biology Letters* **7**, 380–383.
- PEREZ-CEMBRANOS, A. & PEREZ-MELLADO, V. (2015). Local enhancement and social foraging in a non-social insular lizard. *Animal Cognition* **18**, 629–637.
- PETRAZZINI, M. E. M., FRACCAROLI, I., GARIBOLDI, F., AGRILLO, C., BISAZZA, A., BERTOLUCCI, C. & FOA, A. (2017). Quantitative abilities in a reptile (*Podarcis sicula*). *Biology Letters* **13**, 20160899.
- PETRAZZINI, M. E. M., BERTOLUCCI, C. & FOA, A. (2018). Quantity discrimination in trained lizards (*Podarcis sicula*). *Frontiers in Psychology* **9**, 1–6.
- PETRILLO, M., RITTER, C. A. & POWERS, A. S. (1994). A role for acetylcholine in spatial memory in turtles. *Physiology & Behavior* **56**, 135–141.
- PIANKA, E. P. & VITT, L. J. (2003). *Lizards: Windows into the Evolution of Diversity*. University of California Press, Berkeley.
- PLACE, A. J. (2005). *Role of Learning in the Expression of Rattling Behavior in Western Diamondback Rattlesnakes, Crotalus atrox*. (PhD), Oklahoma State University, 9503.
- PLACE, A. J. & ABRAMSON, C. I. (2008). Habituation of the rattle response in western diamondback rattlesnakes, *Crotalus atrox*. *Copeia* **2008**, 835–843.
- POWELL, B. J. (2012). *A Comparative Study of Habitat Complexity, Neuroanatomy, and Cognitive Behavior in Anolis Lizards*. (PhD), Duke University.
- POWERS, A. S., HOGUE, P., LYNCH, C., GATTUSO, B., LISSEK, S. & NAYAL, C. (2009). Role of acetylcholine in negative patterning in turtles (*Chrysemys picta*). *Behavioral Neuroscience* **123**, 804–809.
- PRICE-REES, S. J., WEBB, J. K. & SHINE, R. (2011). School for skinks: can conditioned taste aversion enable bluetongue lizards (*Tiliqua scincoides*) to avoid toxic cane toads (*Rhinella marina*) as prey? *Ethology* **117**, 749–757.
- PRICE-REES, S. J., WEBB, J. K. & SHINE, R. (2013). Reducing the impact of a toxic invader by inducing taste aversion in an imperiled native reptile predator. *Animal Conservation* **16**, 386–394.
- PUNZO, F. (1985). Neurochemical correlates of learning and role of the basal forebrain in the brown anole, *Anolis sagrei* (Lacertilia: Iguanidae). *Copeia* **1985**, 409–414.
- PUNZO, F. (2002). Spatial associative learning in the crevice spiny lizard, *Sceloporus poinsettii* (Sauria: Iguanidae). *Texas Journal of Science* **54**, 45–50.
- PYKE, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* **15**, 523–575.
- QI, Y., NOBLE, D. W. A., FU, J. & WHITING, M. J. (2018). Testing domain general learning in an Australian lizard. *Animal Cognition* **21**, 595–602.
- RANKIN, C. H., ABRAMS, T., BARRY, R. J., BHATNAGAR, S., CLAYTON, D. F., COLOMBO, J., COPPOLA, G., GEYER, M. A., GLANZMAN, D. L., MARSLAND, S., MCSWEENEY, F. K., WILSON, D. A., WU, C.-F. & THOMPSON, R. F. (2009). Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory* **92**, 135–138.
- READER, S. M. & LALAND, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 4436–4441.
- REASER, J. K., MEYERSON, L. A., CRONK, Q., DE POORTER, M. A. J., ELDRIDGE, L. G., GREEN, E., KAIRO, M., LATASI, P., MACK, R. N., MAUREMOTOO, J., O'DOWD, D., ORAPA, W., SASTROUTOMO, S., SAUNDERS, A., SHINE, C., et al. (2007). Ecological and socioeconomic impacts of invasive alien species in Island ecosystems. *Environmental Conservation* **34**, 98–111.
- REILLY, S. M., MCBRAYER, L. B. & MILES, D. B. (2009). *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge University Press, Cambridge.
- REINER, A. J. & POWERS, A. S. (1978). Intensity and pattern discrimination in turtles after lesions of nucleus rotundus. *Journal of Comparative and Physiological Psychology* **92**, 1156–1168.
- REINER, A. & POWERS, A. S. (1980). The effects of extensive fore brain lesions of visual discriminative performance in turtles *Chrysemys picta picta*. *Brain Research* **192**, 327–338.
- REINER, A. & POWERS, A. S. (1983). The effects of lesions of telencephalic visual structures on visual discriminative performance in turtles (*Chrysemys picta picta*). *Journal of Comparative Neurology* **218**, 1–24.
- RILEY, J. L., NOBLE, D. W., BYRNE, R. W. & WHITING, M. J. (2016). Does social environment influence learning ability in a family-living lizard? *Animal Cognition* **20**, 449–458.



- RILEY, J. L., KÜCHLER, A., DAMASIO, T., NOBLE, D. W. A., BYRNE, R. W. & WHITING, M. J. (2018). Learning ability is unaffected by isolation rearing in a family-living lizard. *Behavioral Ecology and Sociobiology* **72**, 20.
- ROBBINS, T. R., FREIDENFELDS, N. A. & LANGKILDE, T. (2013). Native predator eats invasive toxic prey: evidence for increased incidence of consumption rather than aversion-learning. *Biological Invasions* **15**, 407–415.
- ROBERTS, A. C., ROBBINS, T. W. & EVERITT, B. J. (1988). The effects of intradimensional and extradimensional shifts on visual discrimination learning in humans and non-human primates. *The Quarterly Journal of Experimental Psychology Section B* **40**, 321–341.
- RODRIGUEZ-PRieto, I., MARTIN, J. & FERNANDEZ-JURICIC, E. (2011). Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences* **278**, 266–273.
- ROTH, T. C. 2ND & KROCHMAL, A. R. (2015). The role of age-specific learning and experience for turtles navigating a changing landscape. *Current Biology* **25**, 333–337.
- ROTH, T. C. 2ND, KROCHMAL, A. R. & LADAGE, L. D. (2019). Reptilian cognition: a more complex picture via integration of neurological mechanisms, behavioral constraints, and evolutionary context. *BioEssays* **41**, e1900033.
- ROTHBLUM, L. M., WATKINS, J. W. & JENSSEN, T. A. (1979). A learning paradigm and the behavioural demonstration of audition for the lizard *Anolis graham*. *Copeia* **1979**, 490–494.
- RUGANI, R., REGOLIN, L. & VALLORTIGARA, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology Animal Behavior Processes* **34**, 388–399.
- SCHALL, J. J. (2000). Learning in free-ranging populations of the whiptail lizard *Cnemidophorus murinus*. *Herpetologica* **56**, 38–45.
- SCHUETT, G. W., CLARK, R. W., REPP, R. A., AMARELLO, M., SMITH, C. F. & GREENE, H. W. (2016). Social behavior in rattlesnakes: a shifting paradigm. In *Rattlesnakes of Arizona. Conservation, Behavior, Venom, and Evolution* (Volume 2, eds G. W. SCHUETT, M. J. FELDNER, C. F. SMITH and R. S. REISERER), pp. 161–244. Rodeo, New Mexico, USA: ECO Publishing.
- SHAFIR, S. & ROUGHGARDEN, J. (1994). Instrumental discrimination conditioning of *Anolis cristellus* in the field with food as a reward. *Caribbean Journal of Science* **30**, 228–233.
- SHAFIR, S. & ROUGHGARDEN, J. (1998). Testing predictions of foraging theory for a sit-and-wait forager. *Anolis gingivinus*. *Behavioral Ecology* **9**, 74–84.
- SHANBHAG, B. A., AMMANNA, V. H. F. & SAIDAPUR, S. K. (2010). Associative learning in hatchlings of the lizard *Calotes versicolor*: taste and colour discrimination. *Amphibia-Reptilia* **31**, 475–481.
- SHETTLEWORTH, S. J. (2010). *Cognition, Evolution and Behavior*. Oxford University Press, Oxford.
- SIH, A. & DEL GIUDICE, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **367**, 2762–2772.
- SIVITER, H., DEEMING, D. C., VAN GIEZEN, M. F. T. & WILKINSON, A. (2017). Incubation environment impacts the social cognition of adult lizards. *Royal Society Open Science* **4**, 9.
- SLOTNICK, B. (2001). Animal cognition and the rat olfactory system. *Trends in Cognitive Sciences* **5**, 216–222.
- SOL, D., TIMMERMANS, S. & LEFEBVRE, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**, 495–502.
- SOLDATI, F., BURMAN, O. H., JOHN, E. A., PIKE, T. W. & WILKINSON, A. (2017). Long-term memory of relative reward values. *Biology Letters* **13**, 20160853.
- SOMAWEERA, R., WEBB, J. K., BROWN, G. P. & SHINE, R. (2011). Hatchling Australian freshwater crocodiles rapidly learn to avoid toxic invasive cane toads. *Behaviour* **148**, 501–517.
- STAMPS, J. A. (1977). Social behaviour and spacing patterns in lizards. In *Biology of the Reptilia. Ecology and Behavior A* (Volume 7, eds C. GANS and D. W. TINKLE), pp. 149–171. Academic Press, Cambridge.
- STAMPS, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. In *Lizard Ecology: Studies of a Model Organism* (eds R. B. HUEY, E. R. PIANKA and T. W. SCHOENER), pp. 162–204. Harvard University Press, Cambridge.
- STANCHER, G., RUGANI, R., REGOLIN, L. & VALLORTIGARA, G. (2015). Numerical discrimination by frogs (*Bombina orientalis*). *Animal Cognition* **18**, 219–229.
- STANGER-HALL, K. F., ZELMER, D. A., BERGREN, C. & BURNS, S. A. (2001). Taste discrimination in a lizard (*Anolis carolinensis*, Polychrotidae). *Copeia* **2001**, 490–498.
- STEVENS, K. R. (2001). Systematic reviews: the heart of evidence-based practice. *AACN Clinical Issues* **12**, 529–538.
- STIMAC, K., RADCLIFFE, C. W. & CHISZAR, D. (1982). Prey recognition learning by red spitting cobras, *Naja mossambica pallida*. *Bulletin of the Psychonomic Society* **19**, 187–188.
- STONE, A., FORD, N. B. & HOLTZMAN, D. A. (2000). Spatial learning and shelter selection by juvenile spotted pythons, *Antaresia maculosa*. *Journal of Herpetology* **34**, 575–587.
- SUBOSKI, M. D. (1992). Releaser-induced recognition learning by amphibians and reptiles. *Animal Learning & Behavior* **20**, 63–82.
- SUN, B.-J., WANG, T.-T., PIKE, D. A., LIANG, L. & DU, W.-G. (2014). Embryonic oxygen enhances learning ability in hatchling lizards. *Frontiers in Zoology* **11**, 21–29.
- SZABO, B., NOBLE, D. W. A., BYRNE, R. W., TAIT, D. S. & WHITING, M. J. (2018). Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility? *Animal Behaviour* **144**, 17–26.
- SZABO, B., NOBLE, D. W. A., BYRNE, R. W., TAIT, D. S. & WHITING, M. J. (2019a). Precocious juvenile lizards show adult-level learning and behavioural flexibility. *Animal Behaviour* **154**, 75–84.
- SZABO, B., NOBLE, D. W. A. & WHITING, M. J. (2019b). Context-specific response inhibition and differential impact of a learning bias in a lizard. *Animal Cognition* **22**, 317–329.
- SZABO, B., WHITING, M. J. & NOBLE, D. W. A. (2019c). Sex-dependent discrimination learning in lizards: a meta-analysis. *Behavioural Processes* **164**, 10–16.
- TERRICK, T. D., MUMME, R. L. & BURGHARDT, G. M. (1995). Aposematic coloration enhances chemosensory recognition of noxious prey in the garter snake *Thamnophis radix*. *Animal Behaviour* **49**, 857–866.
- THAKER, M., VANAK, A. T., LIMA, S. L. & HEWS, D. K. (2010). Stress and aversive learning in a wild vertebrate: the role of corticosterone in mediating escape from a novel stressor. *American Naturalist* **175**, 50–60.
- THORNTON, A., ISDEN, J. & MADDEN, J. R. (2014). Toward wild psychometrics: linking individual cognitive differences to fitness. *Behavioral Ecology* **25**, 1299–1301.
- THORPE, W. H. (1963). *Learning and Instinct in Animals*. Harvard University Press, Cambridge.
- DU TOIT, L., BENNETT, N. C., NICKLESS, A. & WHITING, M. J. (2012). Influence of spatial environment on maze learning in an African mole-rat. *Animal Cognition* **15**, 797–806.
- UETZ, P., FREED, P. & HOŠEK, J. (2019). The Reptile Database. <http://www.reptile-database.org>.
- ULLER, C. & LEWIS, J. (2009). Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Animal Cognition* **12**, 733–738.
- ULLER, T. & OLSSON, M. (2008). Multiple paternity in reptiles: patterns and processes. *Molecular Ecology* **17**, 2566–2580.
- ULLER, C., JAEGER, R., GUIDRY, G. & MARTIN, C. (2003). Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian. *Animal Cognition* **6**, 105–112.
- VENABLE, C. P., ADAMS, T. S. & LANGKILDE, T. (2019). Aversion learning in response to an invasive venomous prey depends on stimulus strength. *Biological Invasions* **22**, 1973–1980.
- VOLTER, C. J., TINKLENBERG, B., CALL, J. & SEED, A. M. (2018). Comparative psychometrics: establishing what differs is central to understanding what evolves. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **373**, 20170283.
- VORHEES, C. V. & WILLIAMS, M. T. (2006). Morris water maze: procedures for assessing spatial and related forms of learning and memory. *Nature Protocols* **1**, 848–858.
- WARD-FEAR, G., PEARSON, D. J., BROWN, G. P., RANGERS, B. & SHINE, R. (2016). Ecological immunization: in situ training of free-ranging predatory lizards reduces their vulnerability to invasive toxic prey. *Biology Letters* **12**, 20150863.
- WARD-FEAR, G., THOMAS, J., WEBB, J. K., PEARSON, D. J. & SHINE, R. (2017). Eliciting conditioned taste aversion in lizards: live toxic prey are more effective than scent and taste cues alone. *Integrative Zoology* **12**, 112–120.
- WARNER, D. A. (2010). Sex determination in reptiles. In *Hormones and Reproduction of Vertebrates* (Volume 3, eds D. NORRIS and K. H. LOPEZ), pp. 1–38. Academic Press, Cambridge.
- WATERS, R. M., BOWERS, B. B. & BURGHARDT, G. M. (2017). Personality and individuality in reptile behavior. In *Personality in Nonhuman Animals* (eds J. VONK, A. WEISS and S. A. KUCZAJ), pp. 153–184. Springer International Publishing, New York.
- WEIR, A. A. S., CHAPPELL, J. & KACELNIK, A. (2002). Shaping of hooks in new Caledonian crows. *Science* **297**, 981.
- WEISS, E. & WILSON, S. (2003). The use of classical and operant conditioning in training Aldabra tortoises (*Geochelone gigantea*) for venipuncture and other husbandry issues. *Journal of Applied Animal Welfare Science* **6**, 33–38.
- WHILE, G. M., CHAPPLE, D. G., GARDNER, M. G., ULLER, T. & WHITING, M. J. (2015). *Egernia* lizards. *Current Biology* **25**, R593–R595.
- WHILE, G. M., NOBLE, D. W. A., ULLER, T., WARNER, D. A., RILEY, J. L., DU, W.-G. & SCHWANZ, L. E. (2018). Patterns of developmental plasticity in response to incubation temperature in reptiles. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* **329**, 162–176.
- WHITING, M. J. & NOBLE, D. W. A. (2018). Lizards - measuring cognition: practical challenges and the influence of ecology and social behaviour. In *Field and Laboratory Methods in Animal Cognition* (eds N. BUENO-GUERRA and F. AMICI), pp. 266–285. Cambridge University Press, Cambridge.
- WHITING, M. J. & WHILE, G. M. (2017). Sociality in lizards. In *Comparative Social Evolution* (eds D. R. RUBENSTEIN and P. ABBOT), pp. 390–426. Cambridge University Press, Cambridge.
- WHITING, M. J., XU, F., KAR, F., RILEY, J. L., BYRNE, R. W. & NOBLE, D. W. A. (2018). Evidence for social learning in a family living lizard. *Frontiers in Ecology and Evolution* **6**, 70.

- WILKINSON, A. & HUBER, L. (2012). Cold-blooded cognition: reptilian cognitive abilities. In *The Oxford Handbook of Comparative Evolutionary Psychology* (eds J. VONK and T. K. SHACKELFORD), pp. 129–141. Oxford University Press, Oxford.
- WILKINSON, A., CHAN, H.-M. & HALL, G. (2007). Spatial learning and memory in the tortoise (*Geochelone carbonaria*). *Journal of Comparative Psychology* **121**, 412–418.
- WILKINSON, A., COWARD, S. & HALL, G. (2009). Visual and response-based navigation in the tortoise (*Geochelone carbonaria*). *Animal Cognition* **12**, 779–787.
- WILKINSON, A., KUENSTNER, K., MUELLER, J. & HUBER, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters* **6**, 614–616.
- WILKINSON, A., MUELLER-PAUL, J. & HUBER, L. (2013). Picture-object recognition in the tortoise *Chelonoidis carbonaria*. *Animal Cognition* **16**, 99–107.
- WOO, K. L., HUNT, M., HARPER, D., NELSON, N. J., DAUGHERTY, C. H. & BELL, B. D. (2009). Discrimination of flicker frequency rates in the reptile tuatara (*Sphenodon*). *Naturwissenschaften* **96**, 415–419.
- WRIGHT, T. F., EBERHARD, J. R., HOBSON, E. A., AVERY, M. L. & RUSSELLO, M. A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution* **22**, 393–404.
- YEAGER, C. P. & BURGHARDT, G. M. (1991). Effect of food competition on aggregation: evidence for social recognition in the plains garter snake (*Thamnophis radix*). *Journal of Comparative Psychology* **105**, 380–386.
- YEH, C. I. & POWERS, A. S. (2005). Effects of blocking nitric oxide on learning in turtles (*Chrysemys picta*). *Behavioral Neuroscience* **119**, 1656–1661.
- YORI, J. G. (1978). Active one-way avoidance to a heat aversive stimulus in tegu lizards (*Tupinambus teguixen*). *Behavioral Biology* **23**, 100–106.
- ZOHAR, O. & TERKEL, J. (1991). Acquisition of pine cone stripping behaviour in black rats (*Rattus rattus*). *International Journal of Comparative Psychology* **5**, 1–6.
- ZURI, I. & BULL, C. M. (2000). The use of visual cues for spatial orientation in the sleepy lizard (*Tiliqua rugosa*). *Canadian Journal of Zoology* **78**, 515–520.

### VIII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article. **Table S1.** Summary table of studies included in our review, with additional information not discussed in the main text.

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1 **Table S1.** Summary table of studies included in our review with additional information not discussed in the main text. #, study number; learning  
 2 task, details of the tested task (e.g. spatial learning task with eight choices in an arena); stimulus and reward used; and learning criterion applied.  
 3 The table also includes the species tested (common and scientific name), family, age class, animal origin and reference. Data are sorted by order,  
 4 then alphabetically by species scientific name and date of publication. If more than one species was tested within the same study, species are  
 5 presented together and not in alphabetical order. Multiple rows for a single study indicate the number of tests applied. n-choice, number of  
 6 choices not specified; ED, extradimensional; UV, ultraviolet

SAURIA											
#	Learning task			Stimulus	Reward	Criterion	Species	Family	Age class	Origin	Reference
1	Spatial	8-choice	Arena	Distal cues Local cue Light	Heat	No criterion, latency measured	Bosk's fringe- fingered lizard ( <i>Acanthodactylus</i> <i>boskianus</i> )	Lacertidae	Adult	Wild	Day <i>et al.</i> (1999)
	Discrimination	2-choice	Fork	Multiple	Food	10/12					
	Spatial	8-choice	Arena	Distal cues Local cue Light	Heat	No criterion, latency measured	Nidua fringe- fingered lizard ( <i>Acanthodactylus</i> <i>scutellatus</i> )				
	Discrimination	2-choice	Fork	Multiple	Food	10/12					
2	Spatial	2-choice	Arena	Location	Shelter	No criterion	Lesueur's velvet gecko ( <i>Amalosa</i> <i>lesueurii</i> )	Diplodactylidae	Hatchling	Captive	Dayananda & Webb (2017)
3	Taste aversion	1-choice	Arena	Taste	Food	No criterion, eaten or not	Green anole ( <i>Anolis</i> <i>carolinensis</i> )	Dactyloidae	Adult	Captive	Stanger-Hall <i>et al.</i> (2001)
4	Conditioning	1-choice	Runway	Colour	Food	No criterion, proportion correct	Crested anole ( <i>Anolis cristatellus</i> )	Dactyloidae	Adult/ sub-adult	Wild	Shafir & Roughgarden (1994)
	Discrimination	2-choice	T-maze								
5	Motor task	1-choice	Wells	Multiple	Food	6/6	Crested anole ( <i>Anolis cristatellus</i> )	Dactyloidae	Adult	Wild	Powell (2012)
	Discrimination	2-choice	Wells	Colour							
	Reversal	2-choice	Wells								

	Motor task	1-choice	Wells	Multiple	Food	6/6	Emerald anole ( <i>Anolis evermanni</i> )				
	Discrimination	2-choice	Wells	Colour							
	Reversal	2-choice	Wells	Colour							
	Motor task	1-choice	Wells	Multiple							
	Discrimination	2-choice	Wells	Colour							
6	Reversal	2-choice	Wells	Colour	Food	6/6	Puerto Rican anole ( <i>Anolis pulchellus</i> )				
	Discrimination	2-choice	Wells	Colour	Food	6/6	Emerald anole ( <i>Anolis evermanni</i> )	Dactyloidae	Adult	Wild	Leal & Powell (2012)
7	Conditioning	1-choice	Arena	Sound	Escape	No criterion, 80 trials	Graham's anole ( <i>Anolis grahami</i> )	Dactyloidae	Adult	Not given	Rothblum <i>et al.</i> (1979)
8	Avoidance	1-choice	Box	Shock	Relief	No criterion, number of shocks	Brown anole ( <i>Anolis sagrei</i> )	Dactyloidae	Adult	Captive	Punzo (1985)
9	Spatial	4-choice	Arena	Local cues	Heat	No criterion, latency measured	Little striped whiptail ( <i>Aspidoscelis inornatus</i> )	Teiidae	Adult	Wild	Day <i>et al.</i> (2001)
10	Spatial	2-choice	Arena	Multiple	Shelter	2 × 6/8	Little striped whiptail ( <i>Aspidoscelis inornatus</i> )	Teiidae	Adult	Wild	Day <i>et al.</i> (2003)
11	Taste aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Brown basilisk ( <i>Basiliscus vittatus</i> )	Corytophanidae	Sub-adult	Not given	Paradis & Cabanac (2004)
	Taste aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Common basilisk ( <i>Basiliscus basiliscus</i> )				
	Taste aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Schneider's skink ( <i>Eumeces schneideri</i> )	Scincidae			

	Taste aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Common sun skink ( <i>Eutropis multifasciata</i> )				
12	Spatial	2-choice	Arena	Location	Shelter	No criterion, 16 trials	Three-lined skink ( <i>Bassiana duperreyi</i> )	Scincidae	Hatchling	Captive	Amiel & Shine (2012)
13	Discrimination	2-choice	Y-maze	Multiple	Food	No criterion, 15 trials	Three-lined skink ( <i>Bassiana duperreyi</i> )	Scincidae	Hatchling	Captive	Amiel <i>et al.</i> (2014)
14	Motor task	1-choice	Wells	Multiple	Food	5/6	Three-lined skink ( <i>Bassiana duperreyi</i> )	Scincidae	Hatchling	Captive	Clark <i>et al.</i> (2014)
	Discrimination	3-choice	Wells								
	Discrimination	3-choice	Wells	Colour							
	Reversal	3-choice	Wells								
15	Discrimination	2-choice	Arena	Colour	Food	No criterion, number consumed	Oriental garden lizard ( <i>Calotes versicolor</i> )	Agamidae	Hatchling	Captive	Shanbhag <i>et al.</i> (2010)
16	Discrimination	n-choice	Natural habitat	Colour	Food	No criterion, volume and damage recorded	Laurent's whiptail ( <i>Cnemidophorus murinus</i> )	Teiidae	Adult	Wild	Schall (2000)
	Discrimination	n-choice	Natural habitat	Location							
17	Spatial	2-choice	Y-maze	Position	Food	16/20	Western banded gecko ( <i>Coleonyx variegatus</i> )	Eublepharidae	Adult	Not given	Kirkish <i>et al.</i> (1979)
	Reversal	2-choice	Y-maze								
18	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, latency measured	Jamaican iguana ( <i>Cyclura collei</i> )	Iguanidae	Adult	Captive	Cooper <i>et al.</i> (2019)
	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, latency measured	Beaded lizard ( <i>Heloderma charlesbogerti</i> )	Helodermatidae	Adult/sub-adult		
	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, latency measured	Mertens's water monitor ( <i>Varanus mertensi</i> )	Varanidae	Adult		

	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, latency measured	Roughneck monitor ( <i>Varanus rudicollis</i> )		Adult		
	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, latency measured	Emerald monitor ( <i>Varanus prasinus</i> )		Adult		
19	Conditioning	–	Arena	Clicker	Food	Not given	Caiman lizard ( <i>Dracaena guianensis</i> )	Teiidae	Sub-adult/adult	Captive	Hellmuth <i>et al.</i> (2012)
	Conditioning	1-choice	Arena	Target							
20	Spatial	3-choice	Vertical maze	Multiple	Food	5/6	Tree skink ( <i>Egernia striolata</i> )	Scincidae	Juvenile	Captive	Riley <i>et al.</i> (2016)
21	Motor task	1-choice	Wells	Multiple	Food	5/6	Tree skink ( <i>Egernia striolata</i> )	Scincidae	Juvenile	Captive	Riley <i>et al.</i> (2018)
	Social	Discrimination	Wells	Multiple	Food	7/8					
	Social	Reversal	Wells								
22	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Tree skink ( <i>Egernia striolata</i> )	Scincidae	Adult	Wild	Szabo <i>et al.</i> (2018)
	Reversal	2-choice	Wells								
23	Discrimination	2-choice	Wells	Colour	Food	7/8	Tree skink ( <i>Egernia striolata</i> )	Scincidae	Adult	Wild	Whiting <i>et al.</i> (2018)
24	Spatial	2-choice	Arena	Location	Shelter	No criterion, 16 trials	Mongolia racerunner ( <i>Eremias argus</i> )	Lacertidae	Hatchling	Captive	Sun <i>et al.</i> (2014)
25	Spatial	3-choice	Arena	Location	Shelter	5/5	Eastern water skink ( <i>Eulamprus quoyii</i> )	Scincidae	Adult	Wild	Noble <i>et al.</i> (2012)
	Reversal	3-choice	Arena								
26	Spatial	2-choice	Arena	Location	Shelter	Significant performance	Eastern water skink ( <i>Eulamprus quoyii</i> )	Scincidae	Adult	Wild	Carazo <i>et al.</i> (2014)
27	Motor task	1-choice	Wells	Multiple	Food	5/6	Eastern water skink ( <i>Eulamprus quoyii</i> )	Scincidae	Adult	Wild	Noble <i>et al.</i> (2014)
	Discrimination	2-choice	Wells								
	Social	2-choice	Wells								
28	Social	Discrimination	Wells	Multiple	Food	5/6	Eastern water skink ( <i>Eulamprus quoyii</i> )	Scincidae	Adult	Wild	Kar <i>et al.</i> (2017)
	Social	Reversal	Wells								
29	Motor task	1-choice	Wells	Multiple	Food	5/6	Eastern water skink	Scincidae	Adult	Wild	Qi <i>et al.</i> (2018)

	Discrimination	3-choice	Wells	Multiple			( <i>Eulamprus quoyii</i> )				
	Discrimination	3-choice	Wells	Colour							
30	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Eastern water skink ( <i>Eulamprus quoyii</i> )	Scincidae	Adult	Wild	Szabo <i>et al.</i> (2019b)
	Detour	1-choice	Cylinder	Multiple	Food	4/5					
	Detour	1-choice	Cylinder	Multiple	Food	Correct out of 10					
31	Discrimination	2-choice	Y-maze	Multiple	Food	No criterion, 15 trials	Delicate skink ( <i>Lampropholis delicata</i> )	Scincidae	Adult	Wild	Bezzina <i>et al.</i> (2014)
	Discrimination	2-choice	Y-maze	Multiple	Food	No criterion, 15 trials	Common garden skinks ( <i>Lampropholis guichenoti</i> )				
32	Spatial	2-choice	Arena	Location	Shelter	5/6	Delicate skink ( <i>Lampropholis delicata</i> )	Scincidae	Adult	Wild	Chung <i>et al.</i> (2017)
33	Discrimination	2-choice	Y-maze	Multiple	Shelter	5/6	Delicate skink ( <i>Lampropholis delicata</i> )	Scincidae	Adult	Wild	Kang <i>et al.</i> (2018)
	Discrimination	2-choice	Y-maze	Colour							
34	Discrimination	2-choice	Y-maze	Multiple	Shelter	5/6	Delicate skink ( <i>Lampropholis delicata</i> )	Scincidae	Adult	Wild	Goulet <i>et al.</i> (2018)
	Discrimination	2-choice	Y-maze	Colour							
35	Avoidance	n-choice	Natural habitat	Threat	Shelter	Defence reaction	Red-sided curlytail ( <i>Leiocephalus schreibersii</i> )	Leiocephalidae	Adult	Wild	Marcellini & Jenssen (1991)
36	Social	Discrimination	Wells	Multiple	Food	7/8	White's skink ( <i>Liopholis whitii</i> )	Scincidae	Adult	Wild	Munch <i>et al.</i> (2018b)
	Social	Reversal	Wells								
37	Discrimination	2-choice	Wells	Multiple	Food	No criterion, 20 trials	White's skink ( <i>Liopholis whitii</i> )	Scincidae	Juvenile	Captive	Munch <i>et al.</i> (2018a)
	Spatial	2-choice	Arena	Location	Shelter						
38	Habituation	–	Arena	Threat	Shelter	No criterion, 6 test days	Iberian wall lizard ( <i>Podarcis hispanicus</i> )	Lacertidae	Adult	Wild	Rodriguez-Prieto <i>et al.</i> (2011)

39	Social	Enhancement	Arena	Multiple	Food	No criterion, number of individuals	Lilford's wall lizard ( <i>Podarcis lilfordi</i> )	Lacertidae	Adult	Wild	Perez-Cembranos & Perez-Mellado (2015)
	Social	Enhancement	Arena	Multiple	Conspicuous						
	Social	Enhancement	Arena	Multiple	Models						
40	Spatial	1-choice	Water maze	Location	Escape	>6 for two sessions	Italian wall lizard ( <i>Podarcis sicula</i> )	Lacertidae	Adult	Wild	Foa <i>et al.</i> (2009)
41	Discrimination	2-choice	Y-maze	Quantity	Food	75% correct 2 days, >chance 120 trials	Italian wall lizard ( <i>Podarcis sicula</i> )	Lacertidae	Adult	Wild	Petrazzini <i>et al.</i> (2018)
	Discrimination	2-choice	Y-maze	Size							
42	Motor task	1-choice	Wells	Multiple	Food	7/7 or 7/8	Italian wall lizard ( <i>Podarcis sicula</i> )	Lacertidae	Adult	Wild	Damas-Moreira <i>et al.</i> (2018)
	Discrimination	3-choice	Wells	Colour							
	Social	3-choice	Wells								
43	Discrimination	2-choice	Y-maze	Quantity	Food	No criterion, 64 trials	Italian wall lizard ( <i>Podarcis sicula</i> )	Lacertidae	Adult	Wild	Petrazzini <i>et al.</i> (2017)
	Discrimination	2-choice	Y-maze	Size							
44	Social	Bidirectional	Door	Direction	Food	No criterion, 10 trials	Central bearded dragon ( <i>Pogona vitticeps</i> )	Agamidae	Adult	Captive	Kis <i>et al.</i> (2015)
45	Social	Bidirectional	Door	Direction	Food	No criterion, 10 trials	Central bearded dragon ( <i>Pogona vitticeps</i> )	Agamidae	Adult	Captive	Siviter <i>et al.</i> (2017)
46	Discrimination	2-choice	Arena	Location	Shelter	5/5	South Indian rock agama ( <i>Psammophilus dorsalis</i> )	Agamidae	Adult	Wild	Batabyal & Thaker (2019)
	Reversal	2-choice	Arena								
47	Discrimination	2-choice	Arena	Shape	Food	Minimum 5/6	European glass lizard ( <i>Pseudopus apodus</i> )	Anguidae	Adult	Wild	Ivazov (1983)
48	Spatial	4-choice	Arena	Location	Food	No criterion	Crevice spiny lizard ( <i>Sceloporus poinsettii</i> )	Phrynosomatidae	Adult	Captive	Punzo (2002)
49	Avoidance	n-choice	Natural	Threat	Shelter	No criterion,	Fence lizard	Phrynosomatidae	Adult	Wild	Thaker <i>et al.</i> (2010)



			habitat			hiding time and FID	<i>(Sceloporus undulatus)</i>				
50	Taste aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard <i>(Sceloporus undulatus)</i>	Phrynosomatidae	Juvenile	Wild	Robbins <i>et al.</i> (2013)
51	Taste aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard <i>(Sceloporus undulatus)</i>	Phrynosomatidae	Sub-adult	Wild	Herr <i>et al.</i> (2016)
52	Taste aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard <i>(Sceloporus undulatus)</i>	Phrynosomatidae	Hatchling	Captive	Venable <i>et al.</i> (2019)
53	Spatial	2-choice	Arena	Location	Shelter	No criterion, latency measured	Little brown skink <i>(Scincella lateralis)</i>	Scincidae	Adult	Wild	Paulissen (2008)
	Spatial	2-choice	Arena	Location + experience							
54	Discrimination	2-choice	Arena	Pattern	Shelter	5/5	Little brown skink <i>(Scincella lateralis)</i>	Scincidae	Adult	Wild	Paulissen (2014)
55	Discrimination	2-choice	Arena	Multiple	Shelter	No criterion, time at location	Sleepy lizard <i>(Tiliqua rugosa)</i>	Scincidae	Adult	Wild	Zuri & Bull (2000)
56	Taste aversion	1-choice	Arena	Taste	Food	No criterion, remaining food	Eastern blue-tongue skink <i>(Tiliqua scincoides)</i>	Scincidae	Adult/ sub-adult	Mixed	Price-Rees <i>et al.</i> (2011)
57	Taste aversion	1-choice	Arena	Taste	Food	No criterion, vomiting	Eastern blue-tongue skink <i>(Tiliqua scincoides)</i>	Scincidae	Adult	Wild	Price-Rees <i>et al.</i> (2013)
58	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Eastern blue-tongue skink <i>(Tiliqua scincoides)</i>	Scincidae	Adult/ juvenile	Wild	Szabo <i>et al.</i> (2019a)
	Reversal	2-choice	Wells								
59	Spatial	8-choice	Radial arm maze	Location	Food	40 trial 6/18 correct in last 20 trials	Jewelled lizard <i>(Timon lepidus)</i>	Lacertidae	Adult/ sub-adult	Captive	Mueller-Paul <i>et al.</i> (2012)
60	Avoidance	1-choice	Shuttle	Light	Relief	Mean %	Common golden	Teiidae	Juvenile	Not given	Yori (1978)

			box			avoidance	tegu ( <i>Tupinambis teguixin</i> )				
61	Spatial	10-choice	Barnes maze	Location	Shelter	3/3	Side-blotched lizard ( <i>Uta stansburiana</i> )	Phrynosoma-tidae	Sub-adult	Captive	LaDage <i>et al.</i> (2012)
62	Problem solving	1-choice	Puzzle box	Visual	Food	No criterion, 3 trials	White-throated monitor ( <i>Varanus albigularis</i> )	Varanidae	Juvenile	Captive	Manrod <i>et al.</i> (2008)
63	Discrimination	2-choice	Target	Brightness	Food	2 × 8/10	Komodo dragon ( <i>Varanus komodoensis</i> )	Varanidae	Adult	Captive	Gaalema (2007)
	Reversal	2-choice	Target								
	Reversal	2-choice	Target								
64	Taste aversion	1-choice	Natural habitat	Taste	Food	No criterion, biting of toad	Yellow-spotted monitor ( <i>Varanus panoptes</i> )	Varanidae	Adult	Wild	Ward-Fear <i>et al.</i> (2016)
65	Taste aversion	1-choice	Arena	Taste	Food	No criterion, interest levels	Yellow-spotted monitor ( <i>Varanus panoptes</i> )	Varanidae	Adult	Wild	Ward-Fear <i>et al.</i> (2017)
66	Taste aversion	2-choice	Natural habitat	Taste	Food	No criterion, eaten or not	Yellow-spotted monitor ( <i>Varanus panoptes</i> )	Varanidae	Mixed	Wild	Llewelyn <i>et al.</i> (2014)
	Taste aversion	2-choice	Natural habitat	Taste	Food	No criterion, eaten or not		Varanidae	Adult		
67	Discrimination	2-choice	Target	Brightness	Food	2 × 8/10	Roughneck monitor ( <i>Varanus rudicollis</i> )	Varanidae	Adult	Not given	Gaalema (2011)
	Reversal	2-choice	Target								
	Reversal	2-choice	Target								
68	Taste aversion	3-choice	Natural habitat	Taste	Food	No criterion, eaten or not	Lace monitor ( <i>Varanus varius</i> )	Varanidae	Mixed	Wild	Jolly <i>et al.</i> (2016)
	Taste aversion	3-choice	Natural habitat	Taste	Food	No criterion, eaten or not					
	Taste aversion	3-choice	Natural habitat	Taste	Food	No criterion, eaten or not					
<b>SERPENTES</b>											
<b>#</b>	<b>Learning task</b>			<b>Stimuli</b>	<b>Reward</b>	<b>Criterion</b>	<b>Species</b>	<b>Family</b>	<b>Age class</b>	<b>Origin</b>	<b>Reference</b>
69	Habituation	–	Arena	Artificial	None	No criterion, 5	Cottonmouth	Viperidae	Adult	Wild	Glaudas (2004)

				human hand		days	( <i>Agkistrodon piscivorus</i> )				
70	Habituation	–	Arena	Artificial human hand	None	No criterion, 5 days	Cottonmouth ( <i>Agkistrodon piscivorus</i> )	Viperidae	Adult	Wild	Glaudas <i>et al.</i> (2006)
									Neonate	Captive	
71	Spatial	4-choice	Arena	White card	Shelter	No criterion, 16 trials	Cottonmouth ( <i>Agkistrodon piscivorus</i> )	Viperidae	Juvenile	Captive	Friesen (2017)
	Discrimination	2-choice	Arena	Red card	Food	No criterion, 11–14 days					
72	Spatial	8-choice	Arena	Multiple	Shelter	8/10	Spotted python ( <i>Antaresia maculosa</i> )	Pythonidae	Juvenile	Captive	Stone <i>et al.</i> (2000)
73	Habituation	–	Box	Lid opening	None	No response in 10/10 or 120 trials max	Diamondback rattlesnake ( <i>Crotalus atrox</i> )	Viperidae	Adult	Wild	Place (2005), Place & Abramson (2008)
74	Conditioning	1-choice	Arena	Target	Food	Not given	False water cobra ( <i>Hydrodynastes gigas</i> )	Colubridae	Juvenile	Not given	see Hellmuth <i>et al.</i> (2012)
75	Conditioning	1-choice	Key	Light	Food	No criterion, 20 trials	Montpellier snake ( <i>Malpolon monspessulanus</i> )	Psammophiidae	Not Given	Not given	Gavish (1979)
76	Spatial	4-choice	Arena	Location	Shelter	No criterion, latency measured	Red cornsnake ( <i>Pantherophis guttatus</i> )	Colubridae	Adult	Not given	Holtzman (1998)
77	Spatial	8-choice	Arena	Location	Shelter	No criterion, latency measured	Red cornsnake ( <i>Pantherophis guttatus</i> )	Colubridae	Juvenile	Captive	Holtzman <i>et al.</i> (1999)
78	Spatial	12-choice	Arena	Location	Shelter	No criterion, latency measured	Rat snake ( <i>Pantherophis obsoletus</i> )	Colubridae	Juvenile	Captive	Almli & Burghardt (2006)
79	Conditioning	1-choice	Key	Light	Food	No criterion, latency measured	Indian rock python ( <i>Python molurus</i> )	Pythonidae	Neonate	Mixed	Emer <i>et al.</i> (2015)

80	Habituation	–	Arena	Human hand	None	No criterion, one 60 s presentation	Butler's garter snake ( <i>Thamnophis butleri</i> )	Colubridae	Neonatal	Captive	Herzog <i>et al.</i> (1989)
	Habituation	–	Arena	Human hand	None	No criterion, one 60 s presentation, repeated	Mexican garter snake ( <i>Thamnophis melanogaster</i> )				
	Habituation	–	Arena	Human hand	None	No criterion, 10 presentations in 30 s	Mexican garter snake ( <i>Thamnophis melanogaster</i> )	Colubridae	Juvenile		
81	Discrimination	2-choice	Arena	Lemon odour	Food	No criterion, 100 trials	Plains garter snake ( <i>Thamnophis radix</i> )	Colubridae	Juvenile/adult	Captive	Begun <i>et al.</i> (1988)
	Reversal	2-choice	Arena	Pine odour	Food	No criterion, 50 trials			Adult		
	Discrimination	2-choice	Y-maze	Amyl acetate	Food	Cumulative correct above chance in 2 sessions					
82	Taste aversion	1-choice	Arena	Multiple	Food	No criterion, attack latency	Plains garter snake ( <i>Thamnophis radix</i> )	Colubridae	Adult	Captive	Terrick <i>et al.</i> (1995)
	Taste aversion	2-choice	Arena								
	Taste aversion	2-choice	Arena								
83	Habituation	–	Arena	Grey card	None	No response in 4/4	Common garter snake ( <i>Thamnophis sirtalis</i> )	Colubridae	Neonate	Captive	Hampton & Gillingham (1989)
	Habituation	–	Arena	Grey card	None	No response in 4/4, for 5 days					
<b>RHYNCHOCEPHALIA</b>											
<b>#</b>	<b>Learning task</b>			<b>Stimuli</b>	<b>Reward</b>	<b>Criterion</b>	<b>Species</b>	<b>Family</b>	<b>Age class</b>	<b>Origin</b>	<b>Reference</b>
84	Discrimination	2-choice	Arena	Frequency	Food	No criterion	Tuatara ( <i>Sphenodon punctatus</i> )	Sphenodontidae	Juvenile	Captive	Woo <i>et al.</i> (2009)
<b>CHELONIA</b>											
<b>#</b>	<b>Learning task</b>			<b>Stimuli</b>	<b>Reward</b>	<b>Criterion</b>	<b>Species</b>	<b>Family</b>	<b>Age class</b>	<b>Origin</b>	<b>Reference</b>

85	Conditioning	–	Arena	Whistle	Food	Food search after sound	Aldabra tortoise ( <i>Aldabrachelys gigantea</i> )	Testudinidae	Adult	Captive	Weiss & Wilson (2003)
	Conditioning	1-choice	Arena	Red target	Food	Reliably touching target					
86	Conditioning	1-choice	Arena	Blue-and-white target	Food	4 × 30 s holding	Aldabra tortoise ( <i>Aldabrachelys gigantea</i> )	Testudinidae	Adult	Captive	Gaalema & Benboe (2008)
87	Spatial	8-choice	Radial arm maze	Location	Food	No criterion, number correct	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Adult	Captive	Wilkinson <i>et al.</i> (2007)
88	Spatial	8-choice	Radial arm maze	Location	Food	No criterion, number correct	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Adult	Captive	Wilkinson <i>et al.</i> (2009)
89	Social	Detour	Arena	Multiple	Food	No criterion, goal reached	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Juvenile/sub-adult	Not given	Wilkinson <i>et al.</i> (2010)
90	Social	Detour	Arena	Multiple	Food	No criterion, goal reached	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Juvenile/sub-adult	Not given	Wilkinson & Huber (2012)
91	Discrimination	2-choice	Arena	Visual	Food	No criterion, number correct	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Sub-adult	Captive	Wilkinson <i>et al.</i> (2013)
92	Discrimination	2-choice	Touch screen	Position	Food	Last 3 blocks above chance	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Juvenile	Captive	Mueller-Paul <i>et al.</i> (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					
93	Discrimination	2-choice	Arena	Quantity	Food	No criterion	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Sub-adult	Captive	Soldati <i>et al.</i> (2017)

94	Discrimination	2-choice	Y-maze	Multiple	Food	80% across 2 sessions	Red-footed tortoise ( <i>Chelonoidis carbonaria</i> )	Testudinidae	Adult	Captive	Bridgeman & Tattersall (2019)
	Reversal	2-choice	Y-maze								
95	Conditioning	1-choice	Arena	Neck touch	Food	No criterion	Galápagos tortoise ( <i>Chelonoidis nigra</i> )	Testudinidae	Adult	Captive	Bryant <i>et al.</i> (2016)
96	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Reiner & Powers (1978)
	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
97	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Not given	Not given	Reiner & Powers (1980)
	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
98	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Cranney & Powers (1983)
	Discrimination	2-choice	Keys	Multiple	Food	17/20					
	Reversal	2-choice	Keys								
	ED shifts	2-choice	Keys								
99	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Reiner & Powers (1983)
	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
100	Conditioning	1-choice	Key	Red light	Food	Short latencies for 3 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Grisham & Powers (1989)
	Discrimination	2-choice	Keys	Pattern	Food	Mean latency difference of 48 s for 4 days					
101	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Blau & Powers (1989)

						of sessions					
	Discrimination	2-choice	Keys	Pattern	Food	17/20					
102	Conditioning	1-choice	Key	Red light	Food	Short latencies for 3 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Grisham & Powers (1990)
	Discrimination	2-choice	Keys	Position	Food	2 × 17/20					
	Reversal	2-choice	Keys								
103	Spatial	3-choice	X-maze	Location	Water	67% 2 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Petrillo <i>et al.</i> (1994)
104	Discrimination	2-choice	T-maze	Position	Food	2/3 for 2 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Avigan & Powers (1995)
	Discrimination	2-choice	X-maze								
105	Conditioning	1-choice	Keys	Red/white stripes	Food	No criterion, 18 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult	Not given	Yeh & Powers (2005)
	Discrimination	3-choice	Keys	Multiple	Food	Probability of response					
106	Conditioning	1-choice	Keys	Red/white stripes	Food	No criterion, 18 days	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Sub-adult	Not given	Powers <i>et al.</i> (2009)
	Discrimination	2-choice	Keys	Multiple	Food	No criterion, responses per day					
	Negative patterning	3-choice	Keys								
107	Spatial	n-choice	Natural habitat	Multiple	None	No criterion	Painted turtle ( <i>Chrysemys picta</i> )	Emydidae	Adult/ juvenile	Mixed	Roth & Krochmal (2015)
	Discrimination	2-choice	Y-maze	UV Odour	None	No criterion, proportion correct					
108	Conditioning	1-choice	Runway	Quantity	Food	No criterion, latency measured	Reeves' turtle ( <i>Mauremys reevesii</i> )	Geoemydidae	Adult	Not given	Papini & Ishida (1994)
109	Conditioning	1-choice	Runway	Location	Food	No criterion, latency measured	Reeves' turtle ( <i>Mauremys reevesii</i> )	Geoemydidae	Adult	Not given	Ishida & Papini (1997)
110	Discrimination	2-choice	Bottles	Visual	Food	No criterion, latency	Florida red-bellied cooter ( <i>Pseudemys</i> )	Emydidae	Adult	Captive	Davis & Burghardt (2007)

						measured	<i>nelsoni</i> )				
111	Social	Discrimination	Bottles	Brightness	Food	6/6	Florida red-bellied cooter ( <i>Pseudemys nelsoni</i> )	Emyridae	Adult	Captive	Davis (2009), Davis & Burghardt, (2011)
112	Discrimination	2-choice	Bottles	Food pellet	Food	6/6	Florida red-bellied cooter ( <i>Pseudemys nelsoni</i> )	Emyridae	Adult	Captive	Davis & Burghardt (2012)
	Discrimination	2-choice	Bottles	Brightness							
	Discrimination	2-choice	Bottles	Brightness							
113	Discrimination	2-choice	Target	Brightness	Food	9/10 for 5 sessions	Box turtle ( <i>Terrapene carolina</i> )	Emyridae	Adult	Captive	Leighty <i>et al.</i> (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					
114	Discrimination	2-choice	Y-maze	Quantity	Food	No criterion, 60 trials	Hermann's tortoise ( <i>Testudo hermanni</i> )	Testudinidae	Adult	Wild	Gazzola <i>et al.</i> (2018)
	Discrimination	2-choice	Y-maze	Size							
115	Spatial	4-choice	4-arm maze	Distal cues Local cue	Food	13/15	Pond slider ( <i>Trachemys scripta</i> )	Emyridae	Juvenile	Not given	Lopez <i>et al.</i> (2000)
116	Spatial	4-choice	Water maze	Distal cues Local cue	Food	9/18	Pond slider ( <i>Trachemys scripta</i> )	Emyridae	Sub-adult	Not given	Lopez <i>et al.</i> (2001)
<b>CROCODYLIA</b>											
#	Learning task			Stimuli	Reward	Criterion	Species	Family	Age class	Origin	Reference
117	Conditioning	–	Arena	Clicker	Food	Food search after sound	Nile crocodile ( <i>Crocodylus niloticus</i> )	Crocodylidae	Sub-adult	Not given	Augustine & Baumer (2012)
	Conditioning	1-choice	Arena	Black target	Food	Reliably touching target					
118	Taste aversion	1-choice	Arena	Taste	Food	No criterion, eaten or not	Freshwater crocodile ( <i>Crocodylus johnstoni</i> )	Crocodylidae	Juvenile	Wild	Somaweera <i>et al.</i> (2011)



