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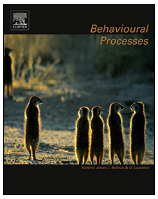

Sex-dependent discrimination learning in lizards: A meta-analysis

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ABSTRACT

We have a poor understanding of differences in learning performance between male and female non-avian reptiles compared to other vertebrates. Learning studies in non-avian reptiles have greatly increased in the last 10 years providing an opportunity to test for sex-based learning using a meta-analysis. Although, we initially considered all reptiles, only lizard studies (N = 11) provided sufficient data to calculate effect sizes. We found weak evidence for sex-dependent learning and moderate heterogeneity in effect sizes across studies. Although, our hypothesized moderator variables (stimulus or task type, species, genus and family) explained little variation. Indeed, our results show that only one species (*Egernia striolata*) exhibited a sex-dependent learning difference, with males learning faster than females. Together, our meta-analysis indicated a general lack of effective reporting on attributes of study methodology (i.e., animal sex, sample sizes). We propose that future research improve reporting by openly sharing their data for the use in similar analyses. The limited sample currently constrains our ability to effectively disentangle whether sex differences vary across different tasks and stimuli. We urge authors to incorporate both sexes in experimental designs and test them on ecologically relevant cognitive assays to improve our understanding of the degree of sex differences in non-avian reptile learning.

1. Introduction

Cognition is the mechanism by which information from the environment is obtained, processed, remembered and subsequently acted upon (Shettleworth, 2010). Through learning, animals use information to alter their behaviour and solve novel problems – making learning integral to fitness (Healy et al., 2009; Rowe and Healy, 2014). The skills to successfully complete learning tasks can vary greatly between individuals, which in part, can be explained by sex (Shettleworth, 2010). Sex differences are triggered during development through changes in gonadal steroid hormones that affect brain organisation and ultimately lead to differences in behaviour (Naeve, 2008). From an evolutionary perspective, males may experience stronger sexual selection compared to females (Janicke et al., 2016) and both sexual conflict (Cummings, 2018) and/ or differences in ecology can result in sex-dependent learning specialisations (Adaptive Specialisation Hypothesis; Alcock, 1998). For example, males of species that mate multiply have been shown to have better spatial learning ability compared to females, possibly as a result of greater spatial demands from searching for females and having bigger range sizes (Jones et al., 2003). However, in other systems, where there is less sexual conflict (i.e. monogamous mating systems), males and females tend to have more similar spatial cognitive ability (Gaulin and Fitzgerald, 1989; Perdue et al., 2011).

Given the preponderance of sex across the animal kingdom, we expect sex differences in cognitive ability to be associated with sex-specific differences in life history, reproduction or ecology (Molina-García and Barrios, 2018). Spatial memory, for example, differs between male and female mammals (e.g. Gaulin and Fitzgerald, 1989; Perdue et al., 2011), male birds learn more complex songs than females (e.g. Molina-García and Barrios, 2018; Yamaguchi, 2001), and in fish, attention and inhibition for colour signals and spatial learning ability differs between the sexes (Cummings, 2018; Lucon-Xiccato and Bisazza, 2014; 2017; Miletto Petrazzini et al., 2017). Nonetheless, the current body of knowledge on cognitive sex differences is taxonomically skewed (Healy et al., 2009) with only a few studies considering sex as a possible explanation for individual variation in task performance in non-avian reptiles although it can be a major driver of cognitive differences in other vertebrate groups (e.g. Molina-García and Barrios, 2018).

Similar selective pressures (i.e., natural and/ or sexual) between the sexes of different species are expected to produce repeated patterns of sex-dependent learning (Healy et al., 2009). Adaptations to resolve sexual conflict and cope with sex-specific ecological demands are similar in non-avian reptiles to those found in other vertebrates (e.g.

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Molina-García and Barrios, 2018), and so we might predict reptiles to exhibit similar sex-dependent learning as is seen in other vertebrates. For example, female guppies show rapid colour discrimination when choosing a mate (preferentially mating with novel males) and perform better on a colour and numerosity discrimination reversal than males (Eakley and Houde, 2004; Lucon-Xiccato and Bisazza, 2014; Miletto Petrazzini et al., 2017). These abilities have been linked to this species' polygamous mating system – females use colour and need greater flexibility during mate choice whereas males need greater persistence to overcome female resistance (Miletto Petrazzini et al., 2017). In reptiles, optimal mating rates differ between the sexes leading to increased sexual conflict (e.g. Fitze et al., 2005). Consequently, females choose males based on territory or male traits that improve fitness such as body colouration (linked to increased aggression), size or display behaviour (e.g. Berry and Shine, 1980; Olsson and Madsen, 1998; Sinervo et al., 2000; Tokarz, 1995), possibly selecting for similar learning patterns. Furthermore, scramble competition and range size have been linked to sex differences in spatial abilities in several species (e.g. great panda: Perdue et al., 2011; hummingbirds: Gonzalez-Gomez et al., 2014; túngara frog: Liu and Burmeister, 2017). Similarly, in many lizards range size differs between the sexes (Stamps, 1977), which could potentially lead to differences in spatial cognition. Importantly, studies in rats demonstrated how male and female spatial learning performance can be affected by manipulating the hormonal environment during development directly influencing brain organisation. Females experiencing high testosterone levels showed male-typical performance while castrated males exhibited more female-like spatial learning (Naeve, 2008). Likewise, differences in behaviour (and possibly cognition) between the sexes are based on different activity patterns in the reptilian brain (e.g. Godwin and Crews, 1997) implicating a possible relationship between hormones and cognition in non-avian reptiles.

Here we conduct a meta-analysis to gain insight into whether learning is impacted by sex in non-avian reptiles and how this varies across species and cognitive assays. In recent years, studies on non-avian reptile learning have surged, making this an opportune time to test the generality of sex related learning differences, and to begin to elucidate how such differences vary across cognitive domains, ecology and species. Furthermore, given the logistical constraints of cognitive learning assays, establishing the existence and generality of sex-differences for particular cognitive tasks will help: 1) inform on effective experimental design that properly accounts for sex differences and 2) expose current shortcomings in the existing empirical literature that can be improved upon in the future.

2. Methods

2.1. Literature search and study selection

We conducted a literature search using Web of Knowledge, Scopus and ProQuest Dissertation & Theses Global for publications up to 1st October 2018 (Fig. 1). In addition, we searched Papers Library, GoogleScholar, PubMed and ScienceDirect using the built-in search engine in Papers (reference management software by ReadCube) for publications up to 20th September 2017. We searched for any publication describing a learning task using the keywords 'learning', 'cognition', 'behaviour', 'choice' and 'discrimination' conducted in any non-avian reptile species (turtles, lizards, snakes, crocodilians) using the keyword 'reptile' (accounting for differences in spelling). To focus our search on relevant publications only, we excluded publications based on the keywords 'bird', 'mammal', 'fish', 'fossil', 'parasite', 'frog', 'insect', 'morph' and 'chemi' (Fig. 1).

We identified a total of 35,209 records of which 1741 were duplicates and 199 articles were selected based on title. To affirm completeness of the initial search, we conducted a backward literature search on all initially selected publications (N = 199) which produced an additional 85 records (75 original works, 10 reviews). Additionally, we conducted a forward search on the same dataset and identified a further 21 records, of which all were original studies (for a full overview of the search see Fig. 1 and electronic supplementary material). Of the 305 included records (199 initially found plus 85 from the backwards search and 21 from the forward search), 15% (N = 47) were books, book chapters or reviews and 21% (N = 64) were not available in a full text version and were excluded. Furthermore, we directly contacted researchers in the field for unpublished and/or raw data. We included Publications in Chinese, German, Japanese, Russian, Polish and French as well as 9 doctorial or master theses.

We then screened the abstracts of the 305 papers initially identified as being relevant and identified 164 papers for full-text screening. Full text publications were then screened and studies were included if: (1) animals were tested on a repeated (more than one trial per individual) choice task between at least two alternative choices to a predetermined learning criterion; (2) males and females were tested with a minimum sample size of two animals per sex and (3) a measure of learning (e.g. trials to criterion or number of errors to criterion) was reported. We only included studies that reported a predetermined learning criterion. Some studies tested animals to a set number of trials which might greatly underestimate the number of trials that individuals need to learn a certain task. With no comparison between methods (learning scores based on a certain number of trials and set learning criteria) available, we decided to only include one method (trials to criterion) to reduce variation between studies. Furthermore, studies reporting latencies were excluded because a reduction in latency to approach can be caused by habituation to the setup, changes in motivation, and in reptiles, latency is likely correlated with ambient temperature and these factors are difficult to disentangle from how learning affects latency. We excluded studies that did not report a choice task or learning criterion (N = 93), only tested one sex (N = 12) or did not determine/ mention the sex of the subjects (N = 35) and studies providing insufficient data or sample sizes (N = 17) leaving us with a total of 11 studies (Carazo et al., 2014; Clark et al., 2014; Damas-Moreira, unpublished data; Leal and Powell, 2012; Paulissen, 2008; Riley, Noble et al., 2016; Riley et al., 2018; Szabo et al., 2018; 2019a; [Szabo et al.,2019b], 2019b; Szabo & Whiting, unpublished data) that were appropriate for our meta-analysis (nine published and two unpublished). For more details see electronic supplementary material (Table S1 and S2).

2.2. Data collection and effect size calculation

We extracted the number of individuals that learnt the task and the mean number of trials to criterion/ errors to criterion and their standard deviation (SD) for each sex. We used the log response ratio (lnRR) as a standardised effect size to test for differences in learning performance between males and females for trials and errors to criterion. We corrected lnRR and its sampling variance (s^2_{lnRR}) for bias due to small study sample size (Lajeunesse, 2015) as follows:

$$\text{lnRR}^* = \ln\left(\frac{\bar{x}_F}{\bar{x}_M}\right) + 0.5\left(\frac{s_F^2}{n_F\bar{x}_F^2} - \frac{s_M^2}{n_M\bar{x}_M^2}\right)$$

$$s^2_{\text{lnRR}^*} = \frac{s_M^2}{n_M\bar{x}_M^2} + \frac{s_F^2}{n_F\bar{x}_F^2} + 0.5\left(\frac{s_F^4}{n_F^2\bar{x}_F^4} - \frac{s_M^4}{n_M^2\bar{x}_M^4}\right)$$

Where $\bar{x}_F$ denotes the mean number of trials/ errors to criterion for females, $\bar{x}_M$ the mean number of trials/ errors to criterion for males, s_F the standard deviation of trials/ errors to criterion for females, s_M the standard deviation of trials/ errors to criterion for males, n_F the sample size of females and n_M the sample size of males tested. Positive lnRR* values indicate a higher mean performance in males whereas negative lnRR* values indicate higher mean performance in females.

We also collected data on the proportion of individuals learning a task (i.e. the proportion reaching the learning criterion) for both males and females. Using these data, we used the log-odds ratio (lnOR) as a

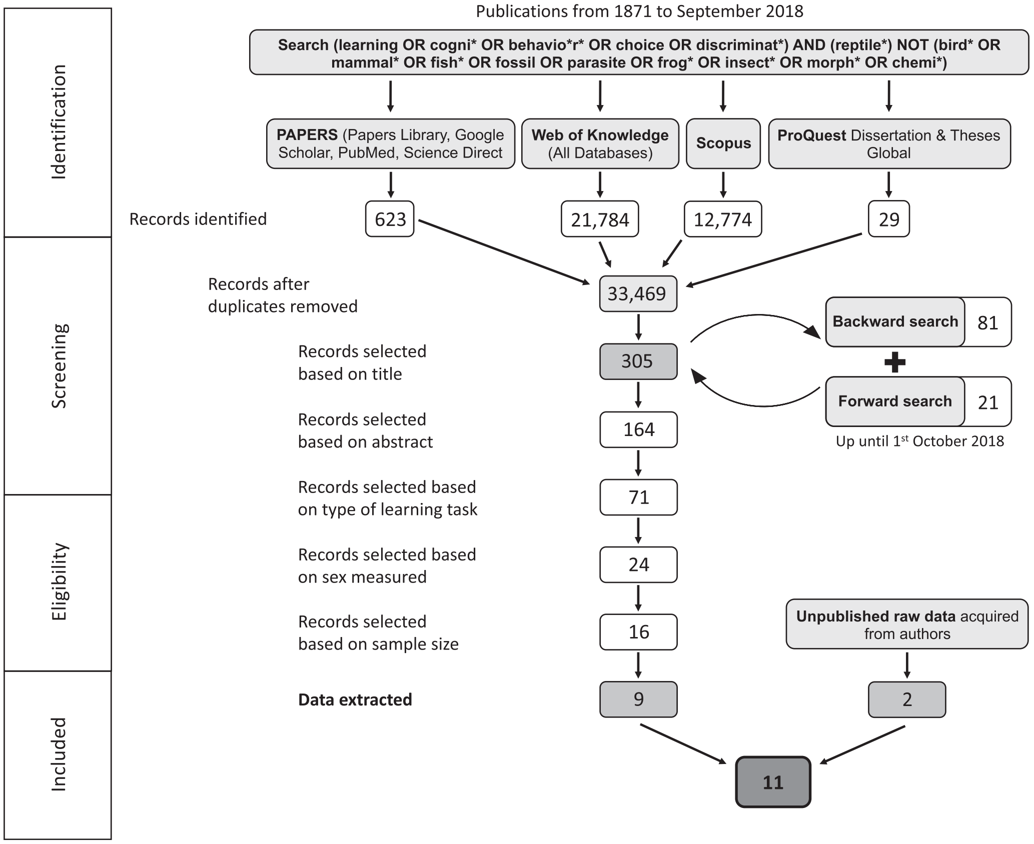

Fig. 1. PRISMA diagram showing the systematic search for literature on learning in non-avian reptiles. Included are the search terms, which datasets were searched and when, how many entries were identified and a step-by-step description of the selection of data for the meta-analysis.

standardised effect size to compare whether the proportion of animals learning differed between males and females. We calculated lnOR and its sampling variance (s^2_{lnRO}) following Borenstein et al. (2009):

$$\text{lnRO}=\ln\left(\frac{n_{M_s} * n_{F_f}}{n_{F_s} * n_{M_f}}\right)$$

$$s^2_{\text{lnRO}} = \frac{1}{n_{M_s}} + \frac{1}{n_{F_s}} + \frac{1}{n_{M_f}} + \frac{1}{n_{F_f}}$$

Where n_{M_s} denotes the number of males that successfully learnt, n_{F_s} the number of females that learnt, n_{M_f} the number of males that did not learn (failed) and n_{F_f} the number of females that failed to learn. Positive lnOR values indicate a higher proportion of males learning whereas negative lnOR indicated a higher proportion of females learning.

2.3. Moderator variables

A number of study-specific attributes are expected to impact whether sex-dependent learning exists or not and so we collected a number of moderator variables that we, *a priori*, expected to vary with effect size. More specifically, we expected an effect with stimulus type (colour, shape, position or pattern) because males and females might use different cues to learn (e.g. Jones et al., 2003). We also expected an effect of task type (acquisition or reversal), as studies in fish show differences between the sexes in reversal learning but not during acquisition (e.g. Lucon-Xiccato and Bisazza, 2014 2017). Lastly, we may expect an effect of phylogeny because species might be specifically adapted to their ecological niche (convergent evolution) or more closely related species might show more similar abilities. Furthermore, data on the age class (adult or juvenile) and the predetermined learning criterion were included in the raw dataset. Measurements (mean and SD) were calculated based on raw data. From the 11 studies appropriate for our analyses, we extracted between one to eight effect sizes each resulting in between 29 and 33 effect sizes in total per measure of learning. Effect sizes from the same study were non-independent repeated measures of the same individuals. The data extraction and calculation was conducted by the same person (BS). Raw data tables are available in the electronic supplementary material (Table S3, S4 and S5).

2.4. Meta-analyses

All statistical analyses were performed with R version 3.4.2 (R Development Core Team, 2008) using the *metafor* package (Viechtbauer, 2010). Raw datasets and R code are available on Zenodo (https://doi.org/doi:10.5281/zenodo.2558567). We ran both multi-level meta-analytic (i.e., intercept-only models; MLM) and multi-level meta-regression (MLMR) models. In all models we included a study and observation-level random effect (estimating the residual variance). Given that species and study were confounded, and we were interested in estimating species-level moderators (see below), we did not include a species-level random effect in our models. From our MLM models, we estimated an overall meta-analytic mean (i.e., intercept) for each effect size, which describes the overall support for sex-dependent learning across the studies and taxa included in our analysis. Our MLMR models investigated the influence of our moderator variables (described above) and included: (1) the specific stimulus used (colour, position, colour/shape and colour/position), (2) the learning task presented (discrimination or reversal) and (3) three taxonomic moderators (species, genus and family). Due to the limited sample size of effects after screening we ran three (for trials to criterion, errors to criterion and the proportion that learnt) univariate MLMR models for each of the moderators separately to explore support for these moderators. Unfortunately, given the small number of studies, it was not possible to fit

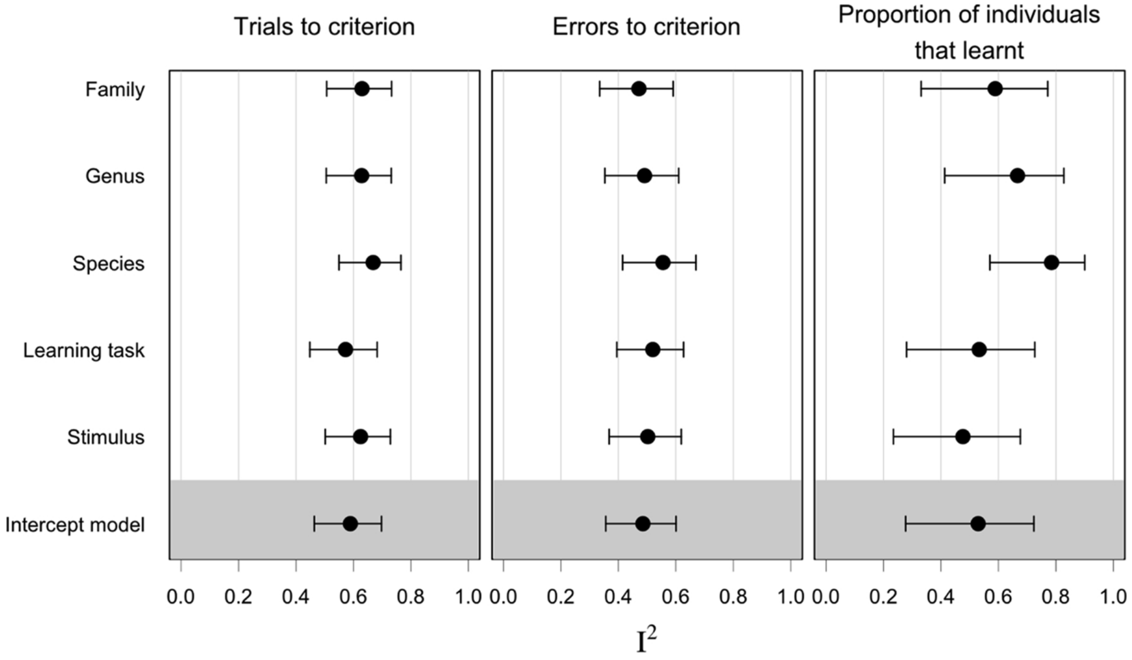

Fig. 2. Total heterogeneity (I^2) with 95% confidence interval for trials to criterion, errors to criterion and the proportion of individuals that learnt. Rows indicate the different models (MLMR) run for each of the five moderators. The MLM model is highlighted in grey. For raw values see electronic supplementary material Table S6.

more complex models with interactions between moderators even though differences between the sexes may depend on multiple moderator variables. For example, the specific stimulus and type of task may interact – one sex may use particular stimuli more in some cognitive assays compared with others (e.g. Jonasson, 2005; Kimura, 1992; Lucon-Xiccato and Bisazza, 2017). From our models we also estimated heterogeneity (i.e., variance) in effect sizes using I^2 (i.e., the proportion of variance for each variance component divided by total variance). Given that total heterogeneity will be conditioned on moderators in these models, we were interested in also understanding how total heterogeneity changed as this can provide insight into how much variation may be explained by them. To do this, we qualitatively compared changes in I^2 from our MLMR models to I^2 from our MLM models.

2.5. Publication bias

To quantify publication bias that might be present in our sample we visually inspected funnel plot asymmetry and performed Egger's tests. Because our sample sizes are low, however, apparent publication bias can be difficult to detect and results from Egger's tests are of low power and should be interpreted with caution (Sterne et al., 2011).

3. Results

Of the 24 studies that reported the sex of subjects only 10 included sex as a possible variable in their analysis. Most strikingly, only studies on lizards provided sufficiently high-quality data to conduct our meta-analysis (see electronic supplementary material Table S1). In total, we found 11 studies, and from these studies, we collected between 29 and 33 effect sizes (depending on the measure of learning) from lizards on various tasks. Stimuli used to test for discrimination learning ranged from simple colours ($N = 8$), to shapes ($N = 4$), striped patterns ($N = 1$) and spatial left/ right discriminations ($N = 3$) or combinations forming more than one dimension ($N = 6$). Our sample included mostly two-choice task ($N = 9$), only one study (Riley et al., 2016) tested lizards on a three-choice task. To detect learning, all studies used pre-determined learning criteria; these were, however, very diverse from 5/5, 5/6, 6/6, 7/7, 7/8, 8/8 and 8/9 correct trials in a row. No consensus seems to exist on what is an appropriate criterion to quantify the point of learning. Most included studies tested only one species, except for one study (Damas-Moreira et al., unpublished) comparing learning performance between three closely related *Podarcis* species. Only one species, *Egernia striolata*, was tested in three separate studies (testing spatial learning, visual discrimination learning and discrimination learning with spatial and visual cues present), and a second species, *Eulamprus quoyii*, in two unrelated studies (testing spatial learning and visual discrimination learning). Three out of the 11 studies tested juveniles, all other experiments were conducted on adult individuals. In our dataset, the mean (+/- standard deviation) sample size for males was 12.4 (+/- 7.5 standard deviation) and for females 12.6 (+/- 6.6 standard deviation). All studies provided data on the proportion of individuals that learnt while only 10 provided data on trials or errors to criterion (electronic supplementary material Table S3, S4 and S5).

Across lizards there was a weak overall sex difference in learning that was biased towards males (MLM, Trials to criterion = 0.066, Z-value = 1.038, CI_{low} = -0.058, CI_{up} = 0.190, P = 0.299; Errors to criterion = 0.115, Z-value = 1.148, CI_{low} = -0.081, CI_{up} = 0.311, P = 0.251) except for the proportion that learnt in which it was biased towards females (MLM, Proportion that learnt = -0.319, Z-value = -0.800, CI_{low} = -1.099, CI_{up} = 0.462, P = 0.424). Males were 6.8% more likely than females to make a correct choice and 12.2% less likely to make an error, whereas males were only 27% as likely to be classified as a learner at a given task compared to females. Between-study heterogeneity varied depending on the measure of learning (Trials to criterion: $I^2_{study} = 0$; Errors to criterion: $I^2_{study} = 0.021$; Proportion that learnt: $I^2_{study} = 0.529$) and we found moderate total heterogeneity for each measure (Trials to criterion: $I^2_{total} = 0.589$; Errors to criterion: $I^2_{total} = 0.485$; Proportion that learnt: $I^2_{total} = 0.\ 529$), suggesting that effects could not simply be explained by sampling variance alone (electronic supplementary material Table S7).

Unsurprisingly – given our limited sample size – stimulus, learning task, genus and family did not predict variation in effect sizes; this was also apparent when looking at the change in total heterogeneity (Fig. 2 and electronic supplementary material Table S6). A significant difference between males and females appeared in one species when considering trials to criterion and errors to criterion but not in the proportion of individuals that learnt (electronic supplementary material Table S8). Males of *Egernia striolata* learnt 40.8% faster (MLMR, mean

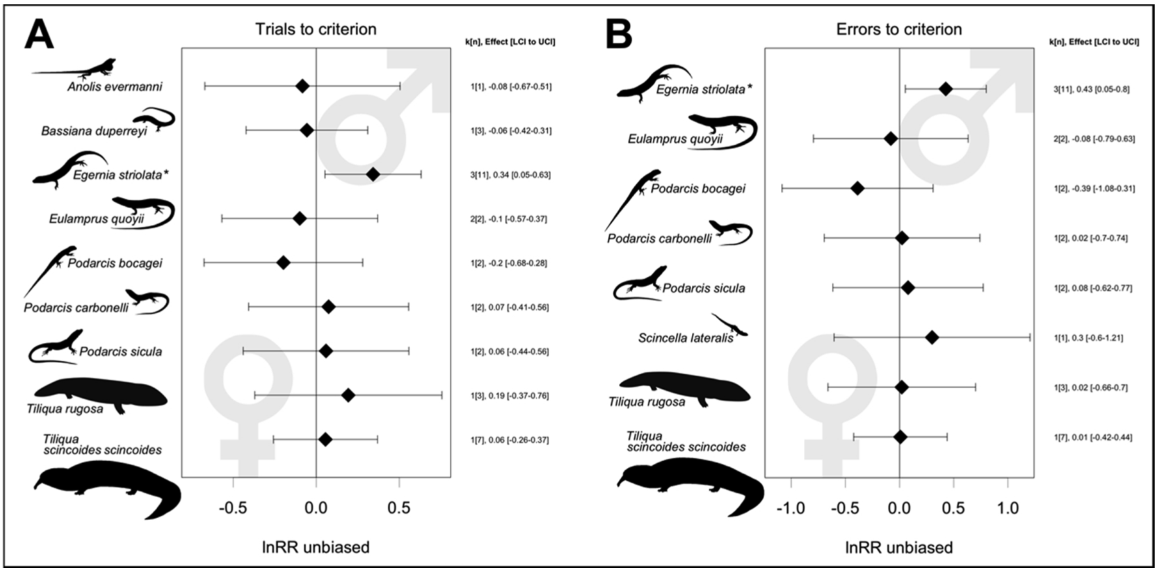

Fig. 3. Summary effect sizes (+/- 95% confidence interval) representing the difference between males and females (unbiased lnRR) for each of the species with data on trials to criterion (A) and errors to criterion (B). A negative effect size indicates female superiority, a positive effect size indicates male superiority. k – number of studies, n – number of effect sizes, Effect – summary effect size, LCI – lower 95% confidence interval, UCI – upper 95% confidence interval. * significant difference of $P < 0.05$.

lnRR = 0.334, Z-value = 2.314, $CI_{low} = 0.052$, $CI_{up} = 0.632$, $P = 0.021$) and made 53.2% less errors (MLMR, mean lnRR = 0.427, Z-value = 2.240, $CI_{low} = -0.053$, $CI_{up} = 0.801$, $P = 0.025$) than females (Fig. 3).

3.1. Publication bias

Visual inspection of the funnel plots indicated some asymmetry and suggests the possibility of missing studies (Fig. 4). However, Egger's tests revealed no significant asymmetry (Trials to criterion: estimate = 0.054, t-value = 0.69, $CI_{low} = -0.105$, $CI_{up} = 0.212$, $P = 0.495$; Errors to criterion: estimate = 0.022, t-value = 0.203, $CI_{low} = -0.202$, $CI_{up} = 0.246$, $P = 0.841$; Proportion that learnt: estimate = -0.094, t-value = -0.512, $CI_{low} = -0.471$, $CI_{up} = 0.283$, $P = 0.613$).

4. Discussion

Since Burghardt's (1978) pivotal review, studies on non-avian reptile cognition have more than doubled and after Wilkinson and Huber's (2012) update they increased by about 40%. Surprisingly, only a few studies report on sex differences although learning is frequently assessed in both sexes. After selecting studies based on the types of tasks, 24 studies reported using both sexes, but only 10 accounted for it in either study design (balancing sex between groups, N = 3) or including sex as a variable in the analysis (N = 7). Of these 10 studies, seven were included in our meta-analysis. The other three studies did not use a predetermined learning criterion to quantify the point of task acquisition. Similar trends were found in social learning (Choleris and Kavaliers, 1999). This low reporting frequency resulted in only a few studies (11 in total) providing sufficient data to conduct our meta-analysis, all investigating lizard learning.

The lack of studies outside of lizards is a significant dearth in knowledge with respect to how the sexes of non-avian reptiles might differ in cognitive abilities, despite strong empirical evidence in other vertebrates (e.g. Cummings, 2018; Gaulin and Fitzgerald, 1989; Jones et al., 2003; Molina-García and Barrios, 2018). Indeed, many studies on

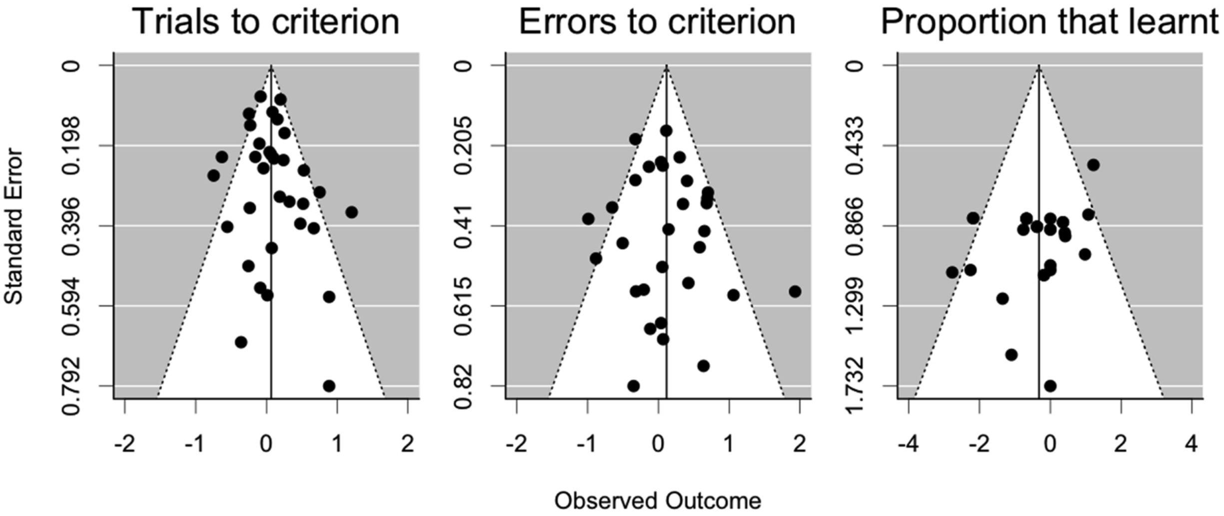

Fig. 4. Funnel plots generated from residuals from our MLM model based on trials to criterion, errors to criterion and the proportion that learnt. Effect size residuals are plotted against their standard error (precision). The dashed line indicates the 95% pseudo confidence interval.

turtles were excluded due to our inability to link individual performance to sex due to insufficient methodological details and/or a difficulty in sexing animals. Our meta-analysis revealed little evidence for sex-based learning differences with results pointing towards males performing better in only one species, the tree skink (*Egernia striolata*). Male and female *E. striolata* differ in their mating system: females tend to mate monogamously (pairing up with their partner for at least one breeding season; Duckett et al., 2012) while males mate multiply (Riley, unpublished data) and this may explain differences in learning in this species because males need to locate possible mating partners outside their seasonally monogamous pair and outwit possible competitors (males paired with unfamiliar females). Nonetheless, we still know little about how male and female tree skinks differ in their ecological niche which might similarly underlie the difference in learning. Therefore, results may change after more empirical studies testing sex differences become available, improving our understanding of the drivers of learning variability among the sexes.

Across lizard species, we found weak evidence of a sex difference in all three measures of learning (trials or errors to criterion and the proportion of individuals that learnt) and, for the most part, our predictors (stimulus, learning task, species, genus, family) did not explain differences. While the lack of learning difference may suggest that selection or developmental experience does not impact cognitive processes differently in males and females across the taxa included, we have to consider other explanations. Of the nine published studies included in our analyses, only one targeted sex as a possible predictor for individual differences in task performance (Carazo et al., 2014), five of the nine did account for sex in their analysis (Clark et al., 2014; Paulissen, 2008; Riley et al., 2016; Szabo et al., 2018; 2019a) and the last three provided sex of subjects in raw datasets (Leal and Powell, 2012; Riley et al., 2018; Szabo et al., 2019b). Task type was, therefore, not selected to test sex-based learning. Many of the tasks presented were foraging-based tasks. It is possible that selective pressures for the sexes are the same in a foraging context and we might not expect them to vary in their ability to find food. Furthermore, sex differences may depend on multiple factors combined. In some species, males and females differ in some cognitive tasks but not others (e.g. Lucon-Xiccato and Bisazza, 2014; 2017; Miletto Petrazzini et al., 2017; Naeve, 2008) and this is expected to vary across species given they occupy different ecological niches (Molina-García and Barrios, 2018). Our sample size was limited, preventing us from estimating interactions which may exist between moderators. A particularly important interaction not captured by our models includes sex-dependent learning that depends on the type of task within a species. Estimating overall effects for a species without considering different sex-based patterns of learning across tasks may result in a net effect size of zero, possibly explaining why there was weak evidence across species for the existence of sex-dependent learning strategies. Finally, sample sizes in primary studies were small. If individual variation is high within a sex, samples of less than 10 individuals might be too small to detect differences. In the future, as more empirical estimates across sexes and different tasks accumulate for a species, we will be able to test how sex affects learning more rigorously.

Studies in mammals, including humans, have revealed distinct sex related spatial learning abilities that have been linked to different spatial demands (e.g. Jonasson, 2005; Jones et al., 2003; Kimura, 1992) and similar patterns have begun to emerge in birds and fishes (e.g. Gonzalez-Gomez et al., 2014; Lucon-Xiccato and Bisazza, 2017). The sex experiencing bigger range sizes is predicted to show enhanced spatial cognitive abilities (e.g. Jones et al., 2003; Molina-García and Barrios, 2018) and these range size differences are also present in lizards (e.g. Stamps, 1977). The few studies in our sample looking at spatial learning tested simple left/ right discrimination. The lack of a sex difference might again be task related and differences might only occur in more complex spatial tasks such as maze or route learning for which presently no data are available. This deficiency is partly related to single sex studies testing males only (e.g. Day et al., 1999, 2001; Foa et al., 2009; LaDage et al., 2012; Mueller-Paul et al., 2012) leaving a gap in knowledge in dire need of being filled. Nevertheless, the single study examining sex as a possible explanatory variable for individual differences in learning in eastern water skinks (*Eulapmrus quoyii*) found that males were more likely to find a 'safe' refuge than females in the first trials of task acquisition, however, this difference disappeared in later trials (Carazo et al., 2014). Given that male *E. quoyii* either defend territories or adopt a floater strategy, there may be greater spatial demands for males than for females (Noble et al., 2013), possibly explaining sex-based difference in spatial learning. Our meta-analysis, however, did not reflect this result. As discussed in the preceding section our analysis was limited and existing differences might be masked. Therefore, targeting sex-based learning in lizards, and relating results to differing ecological demands or levels of sexual conflict, will be a rewarding future research endeavour especially in the context of spatial cognition, where clear predictions on differences between the sexes can be established.

In summary, only Carazo et al. (2014) specifically predicted sex to be a possible explanation for individual learning differences as part of their experimental design, possibly because such experiments require larger sample sizes and more complex designs and analyses that may be more logistically challenging to execute. Despite this, many other studies were designed appropriately, but did not report critical information necessary to assess sex-differences in our meta-analysis. The paucity of available data greatly limited our analyses and general conclusions about the factors that are involved in producing sex related learning differences in non-avian reptiles. Recently, there has been a push to provide and share data to improve transparency of research (e.g. Ihle et al., 2017; Powers and Hampton, 2019; Garamszegi, 2016). We would encourage cognitive biologists to provide as much detail as possible in their raw datasets to make analysis such as the one presented here more frequent in the future. Gaining a more detailed insight into how sex influences learning in non-avian reptiles can help elucidate the ecological and selective pressures shaping cognitive differences among the sexes. We hope that, in the future, research in non-avian reptile learning will continue to grow by including tests of sex-based learning.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.04.002.

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Electronic Supplementary material

“Sex-dependent discrimination learning in lizards: a meta-analysis” by Birgit Szabo, Martin J. Whiting, Daniel W. A. Noble

Search and search criteria

A comprehensive online search was conducted using the following search terms:

(learning OR cogni OR behavio*r* OR choice OR discriminat*)* ***AND***
(reptile)* ***NOT***
(bird OR mammal* OR fish* OR fossil OR parasite OR frog* OR insect* OR morph* OR chemi*)*

The search was conducted on the 30th of September 2017 and again 10th October 2018 (to include publications published after 30th of September 2017).

We searched

- **PAPERS**, resulting in 623 records
- **Web of Knowledge**, resulting in 21,621 records (2017) and 162 records (2018)
- **Scopus**, resulting in 12,609 records (2017) and 165 records (2018)
- **ProQuest Dissertation & Theses Global**, resulting in 28 records (2017) and 1 record (2018)

Search parameters for each database:

- **PAPERS:** all Databases **(**Papers Library, GoogleScholar, PubMed, ScienceDirect)
- **Web of knowledge**: all Databases (Web of Science Core Collection, BIOSIS Citation index, Current Contents Connect, Inspec, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index, SciELO Citation Index, Zoological Records), 1864-

now

- **Scopus:** 1960-now, subject areas: Life sciences, Health sciences, Physical sciences, Social sciences & Humanities (all for second search), All document types, search in Title, Abstract and Keywords
- **ProQuest Dissertation & Theses Global:** Anywhere except full text, all dates, all manuscript type (dissertation & master's thesis), all languages

Summary:

- Number of publication found (first search): 34,881
- Number of publication found (second search): 329
- All publication: 35,210
- Number of duplicates (first search): 1629
- Number of duplicates (second search): 112
- All duplicates: 1,741
- Final count (first search): 33,252
- Final count (second search): 217
- Final number of publication: 33,469

Detailed selection criteria:

Selection by title

- Must include words (including forms of) and/or expressions indicating a learning experiment was conducted.

  For example:

  Learning, discrimination, choice, reinforcement, selection, behaviour, avoidance, conditioning, instrumental, cue, stimulus, performance, ability, recognition, task, cognition, training, shift, memory or retention, orientation, smart, intelligent, refuge use, aversive, response, detour, problem apparatus or box, maze, habituation, social facilitation, local/stimulus enhancement, strategy, etc.

- Might mention being conducted on a reptile species or using a more general term describing a reptile such as turtle, crocodilian or lizard
- 305 publications were selected by title

Selection by abstract:

- Must describe a learning experiment such as any form of general associative learning such as (but not just) spatial learning, discrimination learning, avoidance learning, reinforcement learning, social learning or motor learning and taste aversion, conditioning, habituation or maze learning
- The study must be conducted on a species defined as part of the class reptilia (no aves)
- If the full text was not available and the online entry was found, the abstract was saved in the library and treated as described above
- If the full text was not available and the online entry was not found the publication was excluded
- If the abstract was not available within the publication, the main text was searched for a description of the procedure
- Any book chapter or review article was excluded at this stage
- 164 publications were selected by abstract

Selection by learning task:

- Describing a learning task = “The acquisition of a novel behaviour, novel behaviour-sequence or novel application of existing behaviour.”
- With repeated testing (NO one trial learning)
- Applying a learning criterion (trials, errors, learning score)
- Confronting animals with at least two simultaneously presented choices

(**discrimination task** -> no aversion learning, social learning, etc.)

- If no full text version was available the study was excluded
- 71 publications were selected

Selection based on if sex was measured and sample size was big enough:

- Studies in which the sex of subjects was measured but N for each sex was not specified were searched for sex based analysis. If present, these studies were included
- If sex was measured but not reported authors were contacted by email
- Studies testing only one sex were excluded
- If no sex was reported the study was excluded
- 16 publications were selected

Selection based on presented data:

- Studies providing either raw data or mean and some variance measure (SD, SE) per sex were included
- 7** studies were selected

** one unpublished study was recently published, its status as unpublished was not changed in the dataset (see U3, Szabo et al., 2019)s

Table S1. Summary table containing publications (empirical studies only) selected based on a systematic selection process implemented to identify appropriate publications to include in the meta-analysis. Given are the label assigned to each publication, during which search it was found (initial search, backward search or forward search), based on which criterion it was selected (by title, by abstract or search criteria (1), (2) or (3), see main manuscript), the reason for exclusion, the family and species tested (divided into Crocodilia, Rhynchocephalia, Squamata - Serpentes separate and Testudines) and the reference. * next to the label indicated that no full text was available, - no data on taxon available.

Label	Search	Selection by		Selection criteria			Reason for exclusion	Taxon	Reference
		Title	Abstract	(1)	(2)	(3)			
CROCODILIA									
A023	Initial	✓	✓				Conference Abstract	Alligatoridae, *Alligator mississippiensis*	Araneo-Yowell et al (2011)
A220	Backward	✓	✓				No choice task tested	Alligatoridae, *Alligator mississippiensis*	Davidson (1964)
A053	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Alligator mississippiensis*	Davidson (1966a)
A054	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, Alligator mississippiensis	Davidson (1966b)
A152	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Caiman crocodilus*	Northcutt & Heath (1971)
A142	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Caiman crocodilus*	Williams (1967)
A143	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Caiman crocodilus*	Williams (1968a)
A208	Backward	✓	✓	✓			Sex not mentioned	Alligatoridae, *Caiman crocodilus*	Williams (1968b)
A141	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Caiman crocodilus*	Williams & Robertson (1970)
A074	Initial	✓	✓	✓			Sex not mentioned	Alligatoridae, *Alligator mississippiensis* Crocodylidae, *Crocodilus americanus*	Gossette & Hombach (1969)
A122	Initial	✓	✓				No choice task tested	Crocodylidae, *Crocodylus johnstoni*	Somaweera et al (2011)
A026*	Initial	✓					Full text unavailable	Crocodylidae, *Crocodylus niloticus*	Augustine et al (2013)
A046	Initial	✓	✓				No choice task tested	Crocodylidae, *Crocodylus porosus*	Bustard (1968)
RHYNCHOCEPHALIA									
A101	Initial	✓	✓	✓			N too small	Sphenodontidae, *Sphenodon punctatus*	Northcutt & Heath (1973)
A147	Initial	✓	✓				No criterion	Sphenodontidae, *Sphenodon punctatus*	Woo et al (2009)
SQUAMATA									
A132	Initial	✓					Not a learning study	Agamidae, *Amphibolurus muricatus*	Van Dyk & Evans (2007)
A121	Initial	✓	✓				No choice task tested	Agamidae, *Calotes versicolor*	Shanbhag et al (2010)
A036	Initial	✓					Not a learning study	Agamidae, *Ctenophorus ornatus*	Beazley et al (2003)
A086	Initial	✓	✓				No choice task tested	Agamidae, *Pogona vitticeps*	Kis et al (2015)
A267	Initial	✓	✓				No choice task tested	Agamidae, *Pogona vitticeps*	Siviter et al (2017)
A231	Backward	✓	✓	✓			Sex not mentioned	Anguidae, *Pseudopus apodus*	Ivazov (1983)
A032	Initial	✓					Not a learning study	Chamaeleonidae, Cha*maeleo calyptratus*	Ballen et al (2014)

A095	Initial	✓	✓				No choice task tested	Chamaeleonidae, *Chamaeleo chameleon*	Lustig et al (2013)
A137	Initial	✓					Not a learning study	Cordylidae, *Platysaurus intermedius*	Whiting et al (2003)
A104	Initial	✓	✓				No repetitions	Corytophanidae, *Basiliscus vitattus* Corytophanidae, *Basiliscus basiliscus* Scincidae, *Eumeces schneideri* Scincidae, *Eutropis mutifasciata*	Paradis & Cabanac (2004)
A161	Backward	✓	✓				No choice task tested	Crotaphytidae, *Crotaphytus collaris*	Davidson & Richardson (1970)
A133	Initial	✓	✓	✓	✓		Raw data unavailable	Crotaphytidae, *Crotaphytus collaris*	Vance et al (1965)
A155*	Backward	✓	✓				Full text unavailable	Crotaphytidae, *Crotaphytus collaris* Iguanidae, *Dipsosaurus dorsalis*	Bicknell & Richardson (1973)
A040	Initial	✓					Not a learning study	Dactyloidae, *Anolis carolinensis*	Borgmans & Van Damme (2016)
A196*	Backward	✓					Full text unavailable	Dactyloidae, *Anolis carolinensis*	Norton et al (1976)
A126	Initial	✓	✓				No choice task tested	Dactyloidae, *Anolis carolinensis*	Stanger-Hall et al (2001)
A119	Initial	✓	✓				No criterion	Dactyloidae, *Anolis cristatellus*	Shafir (1995)
A120*	Initial	✓					Full text unavailable	Dactyloidae, *Anolis cristatellus*	Shafir & Roughgarden (1994)
A089	Initial	✓	✓	✓	✓	✓	**INCLUDED**	Dactyloidae, *Anolis evermanni*	Leal & Powell (2012)
A250	Forward	✓	✓				No choice task tested	Dactyloidae, *Anolis grahami*	Rothblum et al (1979)
A245	Forward	✓	✓				No choice task tested	Dactyloidae, *Anolis humilis*	Baruch et al (2016)
A227	Initial	✓	✓	✓			Sex not mentioned	Dactyloidae, *Anolis pulchellus* Dactyloidae, *Anolis evermanni* Dactyloidae, *Anolis cristatellus*	Powell (2012)
A166*	Backward	✓	✓				Full text unavailable	Dactyloidae, *Anolis sagrei*	Powell (1968)
A167*	Backward	✓	✓				Full text unavailable	Dactyloidae, *Anolis sagrei*	Powell & Mantor (1969)
A219	Backward	✓	✓				No choice task tested	Dactyloidae, *Anolis sagrei*	Punzo (1985)
A057	Initial	✓	✓				Conference Abstract	Dactyloidae, *Anolis carolinensis* Dactyloidae, *Anolis sagrei* Eublepharidae, *Coleonyx brevis* Gekkonidae, *Hemidactylus turcicus*	Davis et al (2015)
A235	Forward	✓	✓				No criterion	Diplodactylidae, *Amalosia lesueurii*	Dayananda & Webb (2017)
A223*	Backward	✓					Full text unavailable	Eublepharidae, *Coleonyx spp.*	Baird (1970)
A178	Backward	✓	✓	✓	✓		Raw data unavailable	Eublepharidae, *Coleonyx variegatus*	Kirkish et al (1979)
A204*	Backward	✓					Full text unavailable	Eublepharidae, *Coleonyx variegatus*	Richardson & Kirkish (1976)
A033	Initial	✓					Not a learning study	Gekkonidae, *Chondrodactylus turneri*	Barabanov et al (2015)
A090*	Initial	✓	✓				Full text unavailable	Gekkonidae, *Gecko gecko*	Liu et al (2008)
A065*	Initial	✓					Not a learning study	Gekkonidae, *Hemidactylus frenatus*	Duelli (1975)
A234	Forward	✓					Not a learning study	Gekkonidae, *Hemidactylus mabouia* Phyllodactylidae, *Phyllodactylus pulcher*	Williams et al (2016)

A030	Initial	✓	✓				No repetitions	Helodermatidae, *Heloderma horridum*	Baldepas-Valdivia & Ramirez-Bautista (2005)
A187	Backward	✓	✓	✓			Sex not mentioned	Iguanidae, *Dipsosaurus dorsalis*	Garzanit & Richardson (1974)
A191*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Julian & Richardson (1968)
A233	Forward	✓	✓				No choice task tested	Iguanidae, *Dipsosaurus dorsalis*	Kemp (1969)
A194	Backward	✓	✓				No choice task tested	Iguanidae, *Dipsosaurus dorsalis*	Krekorian et al (1968)
A195*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Mautner et al (1971)
A198*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Peterson (1974)
A199*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Peterson (1976)
A170*	Backward	✓	✓				Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Richardson & Iuuan (1974)
A202*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Richardson et al (1974)
A203*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Richardson et al (1979)
A207*	Backward	✓					Full text unavailable	Iguanidae, *Dipsosaurus dorsalis*	Vance & Richardson (1966)
A179	Backward	✓					Not a learning study	Iguanidae, *Iguana iguana*	Alkov (1965)
A009	Initial	✓	✓				No choice task tested	Iguanidae, *Iguana Iguana*	Alkov & Crawford (1965)
A058	Initial	✓	✓	✓			Males only	Lacertidae, *Acanthodactylus boskianus* Lacertidae, *Acanthodactylus scutellatus*	Day et al (1999)
A229	Backward	✓					Not a learning study	Lacertidae, *Acanthodactylus erythrurus*	Martin & Lopez (2003)
A128	Initial	✓	✓	✓	✓		Raw data unavailable	Lacertidae, *Eremias argus*	Sun et al (2014)
A171*	Backward	✓					Full text unavailable	Lacertidae, *Lacerta agilis*	Swiezawska (1949)
A022	Initial	✓					Not a learning study	Lacertidae, *Lacerta cyreni*	Amo et al (2007)
A228	Backward	✓					Not a learning study	Lacertidae, *Lacerta monticola*	Martin & Lopez (2004)
A063	Initial	✓					Not a learning study	Lacertidae, *Podarcis hispanica*	Desfilis et al (2003)
A107	Initial	✓	✓				No choice task tested	Lacertidae, *Podarcis lilfordi*	Perez-Cembranos & Perez-Mellado (2015)
A014	Initial	✓	✓				No repetitions	Lacertidae, *Podarcis muralis*	Amo et al (2004a)
A015	Initial	✓					Not a learning study	Lacertidae, *Podarcis muralis*	Amo et al (2004b)
A016	Initial	✓					Not a learning study	Lacertidae, *Podarcis muralis*	Amo et al (2004c)
A017	Initial	✓	✓				No repetitions	Lacertidae, *Podarcis muralis*	Amo et al (2004d)
A018	Initial	✓					Not a learning study	Lacertidae, *Podarcis muralis*	Amo et al (2004e)
A019	Initial	✓					Not a learning study	Lacertidae, *Podarcis muralis*	Amo et al (2005a)
A020	Initial	✓	✓				No repetitions	Lacertidae, *Podarcis muralis*	Amo et al (2005b)
A021	Initial	✓	✓				No repetitions	Lacertidae, *Podarcis muralis*	Amo et al (2006)
A039	Initial	✓					Not a learning study	Lacertidae, *Podarcis muralis*	Bonati et al (2010)
A052	Initial	✓	✓				No choice task tested	Lacertidae, *Podarcis muralis*	Csermely et al (2010)
A257	Backward	✓	✓				No choice task tested	Lacertidae, *Podarcis sicula*	Foa et al (2009)
A264	Initial	✓					Not a learning study	Lacertidae, *Podarcis sicula*	Petrazzini et al (2017)
A263	Initial	✓	✓	✓			Sex not mentioned	Lacertidae, *Podarcis sicula*	Petrazzini et al (2018)

A064	Initial	✓					Not a learning study	Lacertidae, *Podarcis sicula* Lacertidae, *Podarcis melisellensis*	Downes & Bauwens (2002)
A083*	Initial	✓	✓				Full text unavailable	Lacertidae, *Takydromus spp.*	Johki & Hidaka (1982)
A097	Initial	✓	✓	✓			Males only	Lacertidae, *Timon lepidus*	Mueller-Paul et al (2012)
A218	Backward	✓	✓				No choice task tested	Leiocephalidae, *Leiocephalus schreibersii*	Marcellini & Jenssen (1991)
A116	Initial	✓	✓				Conference Abstract	Phrynosomatidae, *Sceloporus occidentalis*	Rosas et al (2016)
A111	Initial	✓	✓				No repetitions	Phrynosomatidae, *Sceloporus poinsettii*	Punzo (2002)
A115	Initial	✓	✓				No choice task tested	Phrynosomatidae, *Sceloporus undulatus*	Robbins et al (2013)
A130	Initial	✓	✓				No choice task tested	Phrynosomatidae, *Sceloporus undulatus*	Thaker et al (2010)
A261	Initial	✓					Not a learning study	Phrynosomatidae, *Sceloporus woodi*	McBrayer & Parker (2018)
A243	Forward	✓	✓	✓			Males only	Phrynosomatidae, *Uta stansburiana*	LaDage et al (2012)
A242	Forward	✓	✓				Duplicate of A243	Phrynosomatidae, *Uta stansburiana*	LaDage et al (2017)
A062	Initial	✓					Not a learning study	Phrynosomatidae, *Holbrookia maculata* Phrynosomatidae, *Sceloporus undulatus* Teiidae, *Aspidoscelis inornatus*	Des Roches et al (2014)
A012	Initial	✓	✓	✓	✓		Raw data unavailable	Scincidae, *Bassiana duperreyi*	Amiel & Shine (2012)
A011	Initial	✓	✓	✓	✓		Raw data unavailable	Scincidae, *Bassiana duperreyi*	Amiel et al (2014)
A050	Initial	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Bassiana duperreyi*	Clark et al (2014)
A217*	Backward	✓					Full text unavailable	Scincidae, *Ctenotus spp.*	Punzo & Madragon (2002)
A254	Backward	✓					Not a learning study	Scincidae, *Egernia striolata*	Bull et al (2001)
A265	Initial	✓					Not a learning study	Scincidae, *Egernia striolata*	Riley et al (2018a)
A266	Backward	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Egernia striolata*	Riley et al (2018b)
A225	Initial	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Egernia striolata*	Riley, et al (2016)
A270	other	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Egernia striolata*	Szabo et al (2018)
A047	Initial	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Eulamprus quoyii*	Carazo et al (2014)
A260	Initial	✓	✓	✓			Males only	Scincidae, *Eulamprus quoyii*	Kar et al (2017)
A237	Forward	✓					Not a learning study	Scincidae, *Eulamprus quoyii*	Langkilde & Shine (2005)
A100	Initial	✓	✓	✓			Males only	Scincidae, *Eulamprus quoyii*	Noble et al (2012)
A099	Initial	✓	✓	✓			Males only	Scincidae, *Eulamprus quoyii*	Noble et al (2014)
A168	Backward	✓	✓				No choice task tested	Scincidae, *Eumeces inexpectatus*	Powell & Peck (1970)
A271	Initial	✓	✓	✓			Males only	Scincidae, *Lampropholis delicata*	Chung et al (2017)
A259	Initial	✓	✓	✓			Males only	Scincidae, *Lampropholis delicata*	Kang et al (2018)
A037	Initial	✓	✓				No choice task tested	Scincidae, *Lampropholis delicata* Scincidae, *Lampropholis guichenoti*	Bezzina et al (2014)
A262	Initial	✓	✓	✓			Females only	Scincidae, *Liopholis whitii*	Munch et al (2018a)
A269	Forward	✓	✓	✓			Sex undetermined	Scincidae, *Liopholis whitii*	Munch et al (2018b)
A078	Initial	✓	✓				No repetitions	Scincidae, *Plestiodon latiscutatus*	Hasegawa & Taniguchi (1993)

A105	Initial	✓	✓				No choice task tested	Scincidae, *Scincella lateralis*	Paulissen (2008)
A226	Initial	✓	✓	✓	✓	✓	**INCLUDED**	Scincidae, *Scincella lateralis*	Paulissen (2014)
A150	Initial	✓					Not a learning study	Scincidae, *Sphenomorphus indicus*	Zhu et al (2015)
A232	Backward	✓	✓				No criterion	Scincidae, *Tiliqua rugosa*	Zuri & Bull (2000)
A110	Initial	✓	✓				No repetitions	Scincidae, *Tiliqua sincoides scincoides* Scincidae, *Tiliqua scincoides intermedia*	Price-Rees et al (2011)
A082	Initial	✓					Not a learning study	Shinisauridae, *Shinisaurus crocodilurus*	Jiang et al (2009)
A010	Initial	✓	✓				No choice task tested	Sphaerodactylidae, *Sphaerodactylus notatus*	Allen et al (2015)
A059	Initial	✓	✓				No choice task tested	Teiidae*, Aspidoscelis inornatus*	Day et al (2001)
A060	Initial	✓	✓	✓			Males only	Teiidae, *Aspidoscelis inornatus*	Day et al (2003)
A154	Backward	✓	✓	✓			Sex not mentioned	Teiidae, *Aspidoscelis tigris*	Benes (1969)
A118	Initial	✓	✓				No criterion	Teiidae, *Cnemidophorus murinus*	Schall (2000)
A149	Initial	✓	✓				No choice task tested	Teiidae, *Tupinambis teguixin*	Yori (1978)
A096	Initial	✓	✓				No choice task tested	Varanidae, *Varanus albigularis*	Manrod et al (2008)
A025	Initial	✓					Not a learning study	Varanidae, *Varanus bengalensis*	Auffenberg (1979)
A091	Initial	✓	✓	✓			Sex not mentioned	Varanidae, *Varanus bengalensis*	Loop (1976)
A177	Backward	✓	✓	✓			Sex not mentioned	Varanidae, *Varanus komodoensis*	Gaalema (2007)
A268	Initial	✓					Not a learning study	Varanidae, *Varanus panoptes*	Ward-Fear et al (2018)
A072	Initial	✓	✓	✓			Males only	Varanidae, *Varanus rudicollis*	Gaalema (2011)
SQUAMATA - SERPENTES									
A044	Initial	✓					Not a learning study	Colubridae, *Coluber constrictor* Colubridae, *Lampropeltis getula*	Burger (1990)
A214	Backward	✓	✓				No choice task tested	Colubridae, *Drymarchon corais*	Kleinginna (1970)
A129	Initial	✓					Not a learning study	Colubridae, *Elaphe quadrivirgata*	Tanaka et al (2001)
A209	Backward	✓	✓				No choice task tested	Colubridae, *Nerodia rhombifer*	Wolfle & Brown (1940)
A192	Backward	✓	✓				No choice task tested	Colubridae, *Nerodia sipedon*	Kellogg & Pomeroy (1936)
A080	Initial	✓	✓				No choice task tested	Colubridae, *Pantherophis guttatus*	Holtzman et al (1999)
A258	Backward	✓	✓				No choice task tested	Colubridae, *Pantherophis spiloides*	Crawford & Bartlett (1966)
A045	Initial	✓					Not a learning study	Colubridae, *Pituophis melanoleucus*	Burger (1991)
A186	Backward	✓	✓	✓			Sex not mentioned	Colubridae, *Thamnophis radix*	Fuenzalida & Ulrich (1975)
A159	Backward	✓	✓				No choice task tested	Colubridae, *Thamnophis sirtalis*	Burghardt et al (1973)
A087*	Initial	✓					Full text unavailable	Colubridae, *Thamnophis sirtalis*	Lawson (1989)
A109	Initial	✓					Not a learning study	Colubridae, *Thamnophis sirtalis*	Porter & Czaplicki (1974)
A088	Initial	✓					Not a learning study	Colubridae, *Thamnophis sirtalis* Colubridae, *Thamnophis ordinoides*	Lawson (1994)
A197	Backward	✓	✓	✓			Sex not mentioned	Colubridae, *Thamnophis sirtalis*	Peretti & Carberry (1973)

A084	Initial	✓	✓				No repetitions	Elapidae, *Laticauda semifasciata* Elapidae, *Laticauda laticaudata* Elapidae, *Laticauda colubrina*	Kidera et al (2013)
A127	Initial	✓					Not a learning study	Elapidae, *Naja pallida*	Stimac et al (1982)
TESTUDINES									
A253	Forward	✓	✓				No choice task tested	Lamprophiidae, *Malpolon monspessulanus*	Gavish (1979)
A213	Backward	✓	✓	✓	✓		Raw data unavailable	Pythonidae, *Antaresia maculosa*	Stone et al (2000)
A145	Initial	✓					Not a learning study	Pythonidae, *Morelia viridis*	Wilson et al (2006)
A066	Initial	✓	✓				No choice task tested	Pythonidae, *Python bivittatus*	Emer et al (2015)
A244	Forward	✓					Not a learning study	Viperidae, *Agkistrodon piscivorus*	Roth et al (2006)
A027	Initial	✓					Not a learning study	Cheloniidae, *Caretta caretta*	Avens & Lohmann (2003)
A028	Initial	✓					Not a learning study	Cheloniidae, *Caretta caretta*	Avens et al (2003)
A031*	Initial	✓					Full text unavailable	Cheloniidae, *Caretta caretta*	Baldwin (1971)
A185	Backward	✓	✓	✓			Sex not mentioned	Cheloniidae, *Caretta caretta*	Fehring (1972)
A069	Initial	✓					Not a learning study	Cheloniidae, *Caretta caretta*	Fisher et al (2014)
A160	Backward	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys marginata*	Casteel (1911)
A029	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Avigan & Powers (1995)
A157	Backward	✓	✓				No choice task tested	Emydidae, *Chrysemys picta*	Bitterman (1964)
A038	Initial	✓	✓	✓	✓		Sample size unavailable	Emydidae, *Chrysemys picta*	Blau & Powers (1989)
A041	Initial	✓					Not a learning study	Emydidae, *Chrysemys picta*	Bowne & White (2004)
A051	Initial	✓	✓	✓			Sample size unavailable	Emydidae, *Chrysemys picta*	Cranney & Powers (1983)
A256	Backward	✓	✓				No choice task tested	Emydidae, *Chrysemys picta*	Gonzalez & Bitterman (1962)
A188	Backward	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Graf & Tighe (1971)
A076	Initial	✓	✓	✓			Sample size unavailable	Emydidae, *Chrysemys picta*	Grisham & Powers (1989)
A077	Initial	✓	✓	✓			Sample size unavailable	Emydidae, *Chrysemys picta*	Grisham & Powers (1990)
A190	Backward	✓	✓				No choice task tested	Emydidae, *Chrysemys picta*	Heidt & Burbidge (1966)
A079	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Holmes & Bitterman (1966)
A193	Backward	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Kirk & Bitterman (1963)
A085	Initial	✓	✓				No criterion	Emydidae, *Chrysemys picta*	Kirk & Bitterman (1965)
A236	Forward	✓					Not a learning study	Emydidae, *Chrysemys picta*	Manshack et al (2016)
A238	Forward	✓	✓				No choice task tested	Emydidae, *Chrysemys picta*	Moran et al (1998)
A153	Initial	✓	✓				No choice task tested	Emydidae, *Chrysemys picta*	Pert & Bitterman (1970)
A211*	Backward	✓					Fulltext unavailable	Emydidae, *Chrysemys picta*	Petrillo & Powers (1987)
A108	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Petrillo et al (1994)
A114	Initial	✓	✓	✓			Sample size unavailable	Emydidae, *Chrysemys picta*	Reiner & Powers (1978)
A112	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Chrysemys picta*	Reiner & Powers (1980)
A113	Initial	✓	✓	✓			Sample size unavailable	Emydidae, *Chrysemys picta*	Reiner & Powers (1983)

A117	Initial	✓	✓				No criterion	Emydidae, *Chrysemys picta*	Roth et al (2015)
A148	Initial	✓	✓				No criterion	Emydidae, *Chrysemys picta*	Yeh & Powers (2005)
A123	Initial	✓	✓	✓	✓		Raw data unavailable	Emydidae, *Chrysemys picta marginata*	Spigel (1963)
A189*	Backward	✓	✓				Full text unavailable	Emydidae, *Chrysemys spp.*	Hart et al (1969)
A124	Initial	✓	✓				No choice task tested	Emydidae, *Chrysemys spp.*	Spigel (1964)
A205	Backward	✓	✓				No choice task tested	Emydidae, *Chrysemys spp.*	Spigel (1964b)
A125	Initial	✓	✓				No choice task tested	Emydidae, *Chrysemys spp.*	Spigel (1966)
A172	Backward	✓	✓				No choice task tested	Emydidae, *Glyptemys insculpta*	Tinklepaugh (1932)
A071	Initial	✓					Not a learning study	Emydidae, *Graptemys ouachitensis* Emydidae, *Trachemys scripta elegans*	Freedberg et al (2004)
A175	Backward	✓	✓				A055/056/176 duplicate	Emydidae, *Pseudemys nelsoni*	Davis (2009)
A176	Backward	✓	✓				No criterion	Emydidae, *Pseudemys nelsoni*	Davis & Burghardt (2007)
A055	Initial	✓	✓	✓	✓		N too small	Emydidae, *Pseudemys nelsoni*	Davis & Burghardt (2011)
A056	Initial	✓	✓	✓	✓		Duplicate of A055	Emydidae, *Pseudemys nelsoni*	Davis & Burghardt (2012)
A247*	Forward	✓					Full text unavailable	Emydidae, *Pseudemys nelsoni* Emydidae, *Pseudemys floridana*	Kramer (1989)
A239	Forward	✓	✓	✓			Males only	Emydidae, *Terrapene carolina*	Leighty et al (2013)
A042	Initial	✓	✓	✓			Males only	Emydidae, *Terrapene spp.*	Brosgole (1976)
A151*	Initial	✓					Full text unavailable	Emydidae, *Terrapene spp.*	Overmann (1970)
A093	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Trachemys scripta*	Lopez et al (2000)
A212	Backward	✓	✓	✓			Sex not mentioned	Emydidae, *Trachemys scripta*	Lopez et al (2001)
A092	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Trachemys scripta*	Lopez et al (2003a)
A094	Initial	✓	✓	✓			Sex not mentioned	Emydidae, *Trachemys scripta*	Lopez et al (2003b)
A210	Backward	✓					Not a learning study	Emydidae, *Trachemys scripta elegans*	Arnold & Neumeyer (1987)
A158	Backward	✓	✓				No choice task tested	Emydidae, *Trachemys scripta elegans*	Boycott & Guillery (1962)
A255	Backward	✓	✓				No choice task tested	Emydidae, *Trachemys scripta elegans*	Eskin & Bitterman (1961)
A162*	Backward	✓	✓				Full text unavailable	Emydidae, *Trachemys scripta elegans*	Farris & Breuning (1977)
A221	Backward	✓	✓	✓			Sex not mentioned	Emydidae, *Trachemys scripta elegans*	Seidman (1949)
A164	Backward	✓	✓				No choice task tested	Emydidae, *Trachemys scripta troostii*	Murillo et al (1961)
A146	Initial	✓	✓				No criterion	Emydidae, *Trachemys scripta troostii*	Wise & Gallagher (1964)
A163*	Backward	✓					Full text unavailable	Geoemydidae, *Mauremys japonica*	Kuroda (1933)
A081	Initial	✓	✓				No choice task tested	Geoemydidae, *Mauremys reevesii*	Ishida & Papini (1997)
A248	Forward	✓	✓	✓			Sex undetermined	Geoemydidae, *Mauremys reevesii*	Mueller-Paul et al (2014)
A103	Initial	✓	✓				No choice task tested	Geoemydidae, *Mauremys reevesii*	Papini & Ishida (1994)
A035	Initial	✓	✓				No choice task tested	Podocnemididae, *Podocnemis unifilis*	Bass (1977)
A252	Forward	✓	✓	✓			Sex not mentioned	Podocnemididae, *Podocnemis unifilis*	Bass et al (1973)
A169	Backward	✓	✓	✓			Sex not mentioned	Podocnemididae, *Podocnemis unifilis*	Pritz et al (1973)

A073*	Initial	✓					Full text unavailable	Testudinidae, *Aldabrachelys gigantea*	Gaalema & Benboe (2008)
A249	Forward	✓	✓				No criterion	Testudinidae, *Chelonoidis carbonarius*	Powers et al (2009)
A240	Forward	✓	✓				No choice task tested	Testudinidae, *Chelonoidis carbonarius*	Soldati et al (2017)
A138	Initial	✓	✓				No choice task tested	Testudinidae, *Chelonoidis carbonarius*	Wilkinson et al (2007)
A139	Initial	✓	✓				No choice task tested	Testudinidae, *Chelonoidis carbonarius*	Wilkinson et al (2009)
A140	Initial	✓	✓				No choice task tested	Testudinidae, *Chelonoidis carbonarius*	Wilkinson et al (2010)
A241	Forward	✓	✓	✓			Sex undetermined	Testudinidae, *Chelonoidis carbonarius*	Wilkinson et al (2013)
A200*	Backward	✓					Full text unavailable	Testudinidae, *Chelonoidis vicina*	Quaranta & Evans (1949)
A061	Initial	✓					Not a learning study	Testudinidae, *Gopherus polyphemus*	Demuth (2001)
A106	Initial	✓					Not a learning study	Testudinidae, *Testudo hermanni*	Pellitteri-Rosa et al (2010)
A024	Initial	✓					Not a learning study	Testudinidae, *Testudo kleinmanni*	Attum et al (2010)
NONE REPTILE OR NO DATA AVAILABLE									
A075	Initial	✓					Conference Abstract	-	Greenberg & Crews (1977)
A007*	Initial	✓					Full text unavailable	-	Abstracts, winter meeting (1973)
A183*	Backward	✓					Full text unavailable	-	Cookson (1962)
A184*	Backward	✓					Full text unavailable	-	Ditmars (1904)
A068*	Initial	✓					Full text unavailable	-	Fink (1943)
A070*	Initial	✓					Full text unavailable	-	Fleming & Skurski (2013)
A224*	Backward	✓					Full text unavailable	-	Font & Gomez-Gomez (1991)
A215*	Backward	✓					Full text unavailable	-	Grisham & Powers (1985)
A222*	Backward	✓					Full text unavailable	-	Naimoli & Powers (2005)
A098*	Initial	✓					Full text unavailable	-	Nil (1981)
A165*	Backward	✓					Full text unavailable	-	Powell (1967)
A216*	Backward	✓					Full text unavailable	-	Powers (1986)
A201*	Backward	✓	✓				Full text unavailable	-	Rensch & Adrian-Hinsberg (1963)
A206*	Backward	✓					Full text unavailable	-	Takemasa & Nakamura (1935)
A144*	Initial	✓	✓				Full text unavailable	-	Williams & Albiniak (1972)
A034	Initial	✓					None reptile	-	Barlow et al (1969)
A156	Backward	✓	✓				None reptile	-	Biederman et al (1964)
A048	Initial	✓					None reptile	-	Cherry et al (1999)
A049	Initial	✓					None reptile	-	Chow et al (2016)
A067	Initial	✓					None reptile	-	Fi (1985)
A246	Forward	✓	✓				None reptile	-	Nomura & Gunji (2000)
A102	Initial	✓					None reptile	-	Ohman et al (1975)
A131	Initial	✓					None reptile	-	Thomas & LaBar (2008)
A135	Initial	✓					None reptile	-	Weir & Marshall (1980)
A136	Initial	✓					None reptile	-	Werness et al (1993)

A008	Initial	✓					Not a learning study	-	Aguilera et al (2014)
A013	Initial	✓					Not a learning study	-	Amiel et al (2011)

Table S2. Summary table containing publications (book section and review papers only) selected based on title to be searched to assure a comprehensive search of the available literature. Given are the label assigned to each publication, during which search it was found (initial search or backward search) and the reference. * next to the label indicated that no full text was available.

Label	Search	Selected by title	Reference
R001*	Initial	✓	Crews & Gans (1992a)
R002*	Initial	✓	Papi (1992)
R003*	Initial	✓	Bauchot (1994)
R004	Initial	✓	Alexander (1985)
R005	Initial	✓	Brown (2013)
R006	Initial	✓	Bulté & Blouin-Demers (2006)
R007	Initial	✓	Burghardt (1978)
R008	Initial	✓	Burghardt (2013)
R009	Initial	✓	Corcoran (1995)
R010	Initial	✓	Crews & Gans (1992b)
R011*	Initial	✓	Crews et al (2009)
R012	Initial	✓	Doody et al (2013)
R013*	Initial	✓	Fleming (2011)
R014	Initial	✓	Hearn & Granger (2008)
R015	Initial	✓	Ickes et al (1997)
R016	Initial	✓	Kroodsma et al 1984)
R017*	Initial	✓	Lea (1984)
R018	Initial	✓	Mrosovsky (1973)
R019	Initial	✓	Northcutt (2013)
R020*	Initial	✓	Roth (2013)
R021	Initial	✓	Roth & Krochmal (2016)
R022	Initial	✓	Samia et al (2015)
R023	Initial	✓	Scapini (1988)
R024	Initial	✓	Thorpe (1956)
R025	Initial	✓	Suboski (1992)
R026	Backward	✓	Bolles (1970)
R027	Backward	✓	Wilkinson & Huber (2012)
R028*	Backward	✓	Brattstrom (1978)
R029*	Backward	✓	Morlock (1989)
R030	Backward	✓	Domjan et al (2004)
R031	Backward	✓	Bitterman (1975)
R032*	Backward	✓	Fink (1954)
R033	Backward	✓	Holtzman (1998)
R034*	Backward	✓	Macphail (1982)
R035	Initial	✓	Matsubara et al (2017)

R036*	Backward	✓	Peterson (1980)
R037	Initial	✓	Swimming Ability of Reptiles (1961)
R038*	Initial	✓	Storm (1967)
R039*	Initial	✓	The sea turtle's tale (1990)
R040*	Initial	✓	Snakes in the grass (1990)
R041*	Initial	✓	Managing reptile behaviour (2004)
R042	Initial	✓	Growing interest in reptile behaviour (2004)
R043*	Initial	✓	Broussard (2014)
R044*	Backward	✓	Powers (1990)
R045*	Backward	✓	Bruce (2007)
R046	Initial	✓	Booth (2018)
R047	Initial	✓	Bull et al (2017)

Table S3. Raw data for the analysis of sex differences based on trials to criterion. The study code and citation (source) are given from which data were extracted. Learning task includes discrimination and reversal learning and stimuli used are either spatial (position, e.g. left/ right), colour, or a compound stimulus of colour and shape or position. The learning criterion used in each study is also included as well as scientific species name, family and the age (A – adult, J- juvenile) of subjects. $\bar{x}_{female}$ – mean trials to criterion for females, s_{female} – standard deviation of trials to criterion for females, $\bar{x}_{male}$ – mean trials to criterion for males, s_{male} – standard deviation of trials to criterion for males, lnRR* – effect size (unbiased log response ratio), and $\sigma^2_{lnRR^*}$ – variance of lnRR*, U1-4 – unpublished studies. U3** was recently published (Szabo, Noble, & Whiting, 2019).

Study	Age	Family	Species	Criterion	Stimulus	Learning task	$\bar{x}_{female}$	s_{female}	$\bar{x}_{male}$	s_{male}	lnRR*	$\sigma^2_{lnRR^*}$	Source
A047	A	Scincidae	*Eulamprus quoyii*	7/8 or 8/8	Position	Discrimination	10.2	3.0	13.1	3.8	-0.25	0.0142	Carazo et al (2014)
A089	A	Dactyloidae	*Anolis evermanni*	6/6	Colour	Discrimination	6.0	0.0	6.5	0.7	-0.08	0.0059	Leal & Powell (2012)
A225	J	Scincidae	*Egernia striolata*	5/6	Position	Discrimination	12.3	5.6	4.3	6.3	0.89	0.3271	Riley et al (2016)
							7.7	9.3	2.4	3.5	0.89	0.6275	
A270	A	Scincidae	*Egernia striolata*	6/6 or 7/8	Shape/ Colour	Discrimination	54.4	20.6	50.6	24.3	0.07	0.0485	Szabo et al (2018)
						Reversal	31.1	24.9	9.6	4.1	1.20	0.1316	
						Discrimination	39.7	29.6	24.2	10.1	0.52	0.1168	
						Reversal	45.6	35.8	28.6	16.0	0.48	0.1529	
						Discrimination	45.1	25.8	39.4	36.4	0.07	0.2037	
						Reversal	30.2	20.5	37.6	33.9	-0.25	0.2457	
						Discrimination	34.3	25.8	37.0	33.4	-0.09	0.3021	
						Reversal	40.0	31.9	39.4	35.7	0.01	0.3225	
U1	A	Lacertidae	*Podarcis bocagei*	7/7 or 7/8	Colour	Discrimination	10.9	4.0	12.6	7.8	-0.04	0.0646	Damas, Unpublished raw data 1
						Reversal	21.7	5.5	27.3	8.1	0.24	0.0548	
					Colour	Discrimination	11.3	6.5	11.8	6.6	-0.16	0.0511	

			Podarcis carbonelli			Reversal	26.5	6.0	22.8	3.5	0.15	0.0177	
			Podarcis sicula		Colour	Discrimination	20.7	9.9	16.2	9.2	-0.10	0.0374	
						Reversal	20.2	6.0	22.1	9.8	-0.23	0.0219	
U2	Both	Scincidae	*Tiliqua scincoides*	6/6 or 7/8	Shape/ Colour	Discrimination	35.8	13.1	34.0	18.1	0.04	0.0459	Szabo, Unpublished raw data 2
						Reversal	42.0	6.2	24.0	16.4	0.53	0.0673	
						Discrimination	32.3	16.6	26.3	17.0	0.19	0.1053	
						Reversal	28.6	20.5	15.0	7.1	0.67	0.1619	
						Discrimination	22.0	13.8	38.3	21.7	-0.55	0.1592	
						Reversal	24.0	7.3	16.8	10.3	0.32	0.1133	
						Discrimination	16.3	1.5	33.3	18.1	-0.75	0.0741	
U3**	A	Scincidae	*Eulamprus quoyii*	6/6 or 7/8	Shape/ Colour	Discrimination	27.6	17.7	25.5	0.7	0.11	0.0529	Szabo, Unpublished raw data 3
A050	J	Scincidae	*Bassiana duperreyi*	5/6	Colour/ Position	Discrimination	10.5	4.8	19.5	4.9	-0.63	0.0512	Clark et al (2014)
					Colour	Discrimination	6.0	1.4	5.5	0.7	0.09	0.0133	
						Reversal	17.0	3.8	14.0	0.0	0.20	0.0071	
A266	J	Scincidae	*Egernia striolata*	7/8	Colour/ Position	Discrimination	11.3	5.0	8.8	1.8	0.26	0.0279	Riley et al (2018)
U4	A	Scincidae	*Tiliqua rugosa*	7/8 or 8/9	Shape/ Colour	Discrimination	44.5	22.5	21.3	6.7	0.75	0.0982	Szabo, Unpublished raw data 4
						Reversal	28.7	26.7	44.0	24.0	-0.36	0.4678	
						Discrimination	32.3	9.5	39.5	17.7	-0.24	0.1240	

Table S4. Raw data for the analysis of sex differences based on errors to criterion. The study code and citation (source) are given from which data were extracted. Learning task includes discrimination and reversal learning and stimuli used are either spatial (position, e.g. left/ right), colour, or a compound stimulus of colour and shape or position. The learning criterion used in each study is also included as well as scientific species name, family and the age (A – adult, J- juvenile) of subjects. $\bar{x}_{female}$ – mean errors to criterion for females, s_{female} – standard deviation of errors to criterion for females, $\bar{x}_{male}$ – mean errors to criterion for males, s_{male} – standard deviation of errors to criterion for males, lnRR* – effect size (unbiased log response ratio), and $\sigma^2_{lnRR^*}$ – variance of lnRR*, U1-4 – unpublished studies. U3** was recently published (Szabo, Noble, & Whiting, 2019).

Study	**Age**	**Family**	**Species**	**Criterion**	**Stimulus**	**Learning task**	$\bar{x}_{female}$	s_{female}	$\bar{x}_{male}$	s_{male}	**lnRR***	$\sigma^2_{lnRR^*}$	**Source**
A047	A	Scincidae	*Eulamprus quoyii*	7/8 or 8/8	Position	Discrimination	1.8	1.7	3.6	2.3	-0.65	0.132	Carazo et al (2014)
A226	A	Scincidae	*Scincella lateralis*	5/5	Pattern	Discrimination	0.3	0.1	0.3	0.1	0.30	0.055	Paulissen (2014)
A225	J	Scincidae	*Egernia striolata*	5/6	Position	Discrimination	5.0	3.5	3.0	3.7	0.42	0.310	Riley et al (2016)
							4.7	5.7	2.0	2.6	0.64	0.591	
A270	A	Scincidae	*Egernia striolata*	6/6 or 7/8	Shape/ Colour	Discrimination	23.7	9.9	22.6	12.3	0.04	0.061	Szabo et al (2018)
						Reversal	13.4	11.4	1.8	2.0	1.93	0.335	
						Discrimination	18.1	14.3	9.4	3.2	0.69	0.116	
						Reversal	20.7	18.3	11.6	8.4	0.58	0.217	
						Discrimination	18.0	12.4	15.8	16.5	0.05	0.266	
						Reversal	12.4	9.4	16.0	17.5	-0.32	0.334	
						Discrimination	14.3	14.9	13.8	13.9	0.07	0.491	
						Reversal	15.0	13.3	16.2	19.0	-0.12	0.454	
U1	A	Lacertidae		7/7 or 7/8	Colour	Discrimination	1.9	1.8	3.1	3.4	-0.21	0.329	Damas, Unpublished

			Podarcis bocagei			Reversal	9.2	2.6	12.6	5.4	0.35	0.126	raw data 1
			Podarcis carbonelli	7/7 or 7/8	Colour	Discrimination	2.4	3.2	3.0	3.6	-0.51	0.207	
						Reversal	12.3	3.2	11.0	2.5	0.11	0.028	
			Podarcis sicula	7/7 or 7/8	Colour	Discrimination	6.8	5.3	4.8	3.9	-0.13	0.067	
						Reversal	8.2	3.6	9.3	5.3	-0.33	0.036	
U2	Both	Scincidae	*Tiliqua scincoides*	6/6 or 7/8	Shape/ Colour	Discrimination	15.4	6.6	14.3	9.3	0.06	0.066	Szabo, Unpublished raw data 2
						Reversal	18.4	4.0	8.7	7.5	0.70	0.106	
						Discrimination	12.6	7.1	10.4	9.5	0.14	0.176	
						Reversal	11.4	10.9	4.0	3.2	1.06	0.345	
						Discrimination	7.4	6.2	18.3	11.5	-0.88	0.244	
						Reversal	8.8	6.3	7.5	9.0	0.04	0.435	
						Discrimination	5.3	0.6	13.3	10.7	-0.99	0.154	
U3**	A	Scincidae	*Eulamprus quoyii*	6/6 or 7/8	Shape/ Colour	Discrimination	12.3	9.8	8.5	0.7	0.40	0.087	Szabo, Unpublished raw data 3
A266	J	Scincidae	*Egernia striolata*	7/8	Colour/ Position	Discrimination	2.3	2.2	1.2	0.4	0.68	0.124	Riley et al (2018b)
U4	A	Scincidae	*Tiliqua rugosa*	7/8 or 8/9	Shape/ Colour	Discrimination	16.8	9.6	8.7	4.7	0.65	0.180	Szabo, Unpublished raw data 4
						Reversal	8.3	9.5	13.5	7.8	-0.35	0.673	
						Discrimination	9.7	3.8	13.5	3.5	-0.33	0.086	

Table S5. Raw data for the analysis of sex differences based on the number of males and females that successfully learnt a task. The study code and citation (source) are given from which data were extracted. Learning task includes discrimination and reversal learning and stimuli used are either spatial (position, e.g. left/ right), colour, patter (stripes) or a compound stimulus of colour and shape or position. The learning criterion used in each study is also included as well as scientific species name, family and the age (A – adult, J- juvenile) of subjects. N_F – number of females total, S_F – number of successful females, F_F – number of unsuccessful females, N_M– number of males total, S_M – number of successful males, F_M – number of unsuccessful males, lnOR – effect size (log odds ratio), and σ^2_{lnOR} – variance of lnOR, U1-4 – unpublished studies. U3** was recently published (Szabo, Noble, & Whiting, 2019).

Study	**Age**	**Family**	**Species**	**Criterion**	**Stimulus**	**Learning task**	**N_F**	**S_F**	**F_F**	**N_M**	**S_F**	**F_M**	**lnOR**	**σ^2_{lnOR}**	**Source**
A047	A	Scincidae	*Eulamprus quoyii*	7/8 or 8/8	Position	Discrimination	31	9	22	31	18	13	1.219	0.289	Carazo et al (2014)
A089	A	Dactyloidae	*Anolis evermanni*	6/6	Colour	Discrimination	3	2	1	3	2	1	0.000	3.000	Leal & Powell (2012)
A226	A	Scincidae	*Scincella lateralis*	5/5	Pattern	Discrimination	14	3	11	18	8	10	-1.076	0.649	Paulissen (2014)
A225	J	Scincidae	*Egernia striolata*	5/6	Position	Discrimination	10	9	1	4	3	1	1.099	2.444	Riley et al (2016)
A270	A	Scincidae	*Egernia striolata*	6/6 or 7/8	Shape/ Colour	Discrimination	12	9	3	12	7	5	0.762	0.787	Szabo et al (2018)
						Reversal	12	7	5	12	5	7	0.673	0.686	
						Discrimination	12	7	5	12	5	7	0.673	0.686	
						Reversal	12	7	5	12	5	7	0.673	0.686	
						Discrimination	12	7	5	12	5	7	0.673	0.686	
						Reversal	12	5	7	12	5	7	0.000	0.686	
						Discrimination	12	4	8	12	5	7	-0.357	0.718	
						Reversal	12	4	8	12	5	7	-0.357	0.718	

U1	A	Lacertidae	*Podarcis bocagei*	7/7 or 7/8	Colour	Reversal	10	6	4	10	8	2	-0.981	1.042	Damas, Unpublished raw data 1
			Podarcis carbonelli				10	4	6	10	5	5	-0.405	0.817	
			Podarcis sicula				10	9	1	10	7	3	1.350	1.587	
U2	Both	Scincidae	*Tiliqua scincoides*	6/6 or 7/8	Shape/ Colour	Discrimination	11	9	2	11	9	2	0.000	1.222	Szabo, Unpublished raw data 2
						Reversal	11	7	4	11	7	4	0.000	0.786	
						Discrimination	11	7	4	11	6	5	0.377	0.760	
						Reversal	11	5	6	11	4	7	0.377	0.760	
						Discrimination	11	5	6	11	4	7	0.377	0.760	
						Reversal	11	4	7	11	4	7	0.000	0.786	
						Discrimination	11	3	8	11	4	7	-0.421	0.851	
U3**	A	Scincidae	*Eulamprus quoyii*	6/6 or 7/8	Shape/ Colour	Discrimination	10	8	2	10	2	8	2.773	1.250	Szabo, Unpublished raw data 3
A050	J	Scincidae	*Bassiana duperreyi*	5/6	Colour/ Position	Discrimination	29	11	18	31	2	29	2.18	0.681	Clark et al (2014)
					Colour	Discrimination	29	11	18	31	2	29	2.18	0.681	
						Reversal	29	7	22	31	1	30	2.26	1.222	
U4	A	Scincidae	*Tiliqua rugosa*	7/8 or 8/9	Shape/ Colour	Discrimination	8	4	4	6	3	3	0.00	1.167	Szabo, Unpublished raw data 4
						Reversal	8	3	5	6	2	4	0.18	1.283	
						Discrimination	8	3	5	6	2	4	0.18	1.283	

Table S6. Summary table of calculated total study heterogeneity (I^2) of six models including no moderator (MLM) or one of five moderators (stimulus and learning task, as well as species, genus and family; MLMR) for trials to criterion, errors to criterion and the proportion of individuals that learnt the task. Also shown are the within study and between study variance (sigma). CI_{lower} – lower 95% confidence interval of I^2, CI_{upper} – upper 95% confidence interval of I^2. Grey highlighted is the intercept only model.

Measurement	Model	I^2	CI_{lower}	CI_{upper}	τ^2_{within}	$\tau^2_{between}$
Trials to criterion	Intercept	0.5893	0.4638	0.6976	0.5893	0.4638
	Stimulus	0.6250	0.5017	0.7287	0.6250	0.5017
	Learning task	0.5726	0.4484	0.6825	0.5726	0.4484
	Species	0.6686	0.5500	0.7652	0.6686	0.5500
	Genus	0.6286	0.5056	0.7317	0.6286	0.5056
	Family	0.6298	0.5069	0.7328	0.6298	0.5069
Errors to criterion	Intercept	0.4851	0.3560	0.6006	0.4851	0.3560
	Stimulus	0.5020	0.3676	0.6185	0.5020	0.3676
	Learning task	0.5194	0.3944	0.6270	0.5194	0.3944
	Species	0.5549	0.4144	0.6699	0.5549	0.4144
	Genus	0.4908	0.3526	0.6096	0.4908	0.3526
	Family	0.4713	0.3346	0.5905	0.4713	0.3346
Proportion of individuals that learnt	Intercept	0.5296	0.2771	0.7235	0.0000	1.0261
	Stimulus	0.4766	0.2345	0.6764	0.0000	0.8198
	Learning task	0.5332	0.2802	0.7266	0.0000	1.0422
	Species	0.7849	0.5702	0.9005	0.0000	3.5515
	Genus	0.6667	0.4133	0.8278	0.0000	1.8859
	Family	0.5890	0.3311	0.7716	0.0000	1.3251

Table S7. Percent total heterogeneity (I^2_{total}), heterogeneity based on the error (I^2_{error}) and between study heterogeneity (I^2_{study}) of the MLM for each measurement of learning. 95% confidence intervals are given within brackets.

MLM	**I^2_{total} [CI_{low} to CI_{up}]**	**I^2_{error} [CI_{low} to CI_{up}]**	**I^2_{study} [CI_{low} to CI_{up}]**
Trials to criterion	59 [46 - 70]	41 [30 – 54]	10^{-10} [29^{-11} – 22^{-10}]
Errors to criterion	49 [36 – 60]	52 [40 – 64]	2 [0.5 – 5]

Proportion that learnt	53 [28 – 72]	47 [28 – 72]	53 [28 – 72]

Table S8. Summary table of estimates generated for MLM (no moderators) and MLMR including one of five predictors (stimulus, learning task, species, genus and family) based on trials to criterion, errors to criterion and the proportion of males and females that learnt a task. Given are estimates for each level as well as confidence intervals. Significant levels are indicated in bold. – no data available.

Model	Levels	Trials to criterion			Errors to criterion			Proportion of individuals that learnt		
		Estimate	95% $\mathrm{CI}_{\mathrm{low}}$	95% $\mathrm{CI}_{\mathrm{up}}$	Estimate	95% $\mathrm{CI}_{\mathrm{low}}$	95% $\mathrm{CI}_{\mathrm{up}}$	Estimate	95% $\mathrm{CI}_{\mathrm{low}}$	95% $\mathrm{CI}_{\mathrm{up}}$
MLM	none	0.07	-0.06	0.19	0.12	-0.08	0.31	-0.32	-1.10	0.46
Stimulus	Colour	0.01	-0.19	0.21	-0.95	-0.48	0.29	-0.83	-2.25	0.59
	Colour & Position	-0.14	-0.59	0.32	0.68	-0.30	1.67	-1.28	-3.42	0.86
	Position	0.03	-0.46	0.53	-0.09	-0.80	0.63	0.63	-1.15	2.41
	Shape & Colour	0.17	-0.03	0.36	0.18	-0.08	0.44	-0.56	-1.61	0.49
	Pattern	-	-	-	0.30	-0.54	1.14	1.08	-1.30	3.45
Learning task	Discrimination	-0.01	-0.16	0.14	0.06	-0.19	0.32	-0.35	-1.17	0.48
	Reversal	0.20	-0.09	0.41	0.26	-0.10	0.61	-0.26	-1.20	0.68
Species	*A. evermanni*	-0.08	-0.67	0.51	-	-	-	0.00	-5.02	5.02
	B. duperreyi	-0.06	-0.42	0.31	-	-	-	-2.20	-6.03	1.63
	E. striolata	**0.34**	**0.05**	**0.63**	**0.43**	**0.05**	**0.80**	-0.63	-3.58	2.32
	E. quoyii	-0.10	-0.57	0.37	-0.08	-0.79	0.63	-0.55	-3.42	2.31
	P. bocagei	-0.20	-0.68	0.28	-0.39	-1.08	0.31	0.98	-3.22	5.18
	P. carbonelli	0.07	-0.41	0.56	0.02	-0.70	0.74	0.41	-3.69	4.50
	P. sicula	0.06	-0.33	0.56	0.08	-0.62	0.77	-1.35	-5.79	3.09
	S. lateralis	-	-	-	0.30	-0.60	1.21	1.08	-2.94	5.09
	T rugosa	0.19	-0.37	0.76	0.02	-0.66	0.70	-0.12	-4.02	3.79
	T. s. scincoides	0.06	-0.26	0.37	0.01	-0.42	0.44	0.12	-3.87	3.64
Genus	*Anolis*	-0.08	-0.62	0.46	-	-	-	0.00	-4.33	4.32
	Bassiana	-0.05	-0.39	0.29	-	-	-	-2.20	-5.07	0.68
	Egernia	**0.34**	**0.06**	**0.62**	**0.42**	**0.07**	**0.78**	-0.58	-2.86	1.70
	Eulamprus	-0.10	-0.54	0.34	-0.07	-0.74	0.59	-0.42	-2.64	1.80
	Podarcis	-0.02	-0.29	0.24	-0.10	-0.47	0.28	0.21	-2.73	3.14

	Scincella	-	-	-	0.30	-0.52	1.12	1.08	-2.04	4.20
	Tiliqua	0.09	-0.17	0.35	0.01	-0.33	0.35	-0.12	-2.15	1.91
Family	Dactyloidae	-0.08	-0.63	0.46	-	-	-	0.00	-4.08	4.08
	Lacertidae	-0.02	-0.29	0.24	-0.09	-0.46	0.27	0.21	-2.33	2.75
	Scincidae	0.11	-0.04	0.27	0.19	-0.03	0.40	-4.20	-1.36	0.52

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