

## 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 1<sup>st</sup> 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 20<sup>th</sup> 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 doctoral 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 ( $s_{\lnRR}^2$ ) for bias due to small study sample size (Lajeunesse, 2015) as follows:

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

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

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

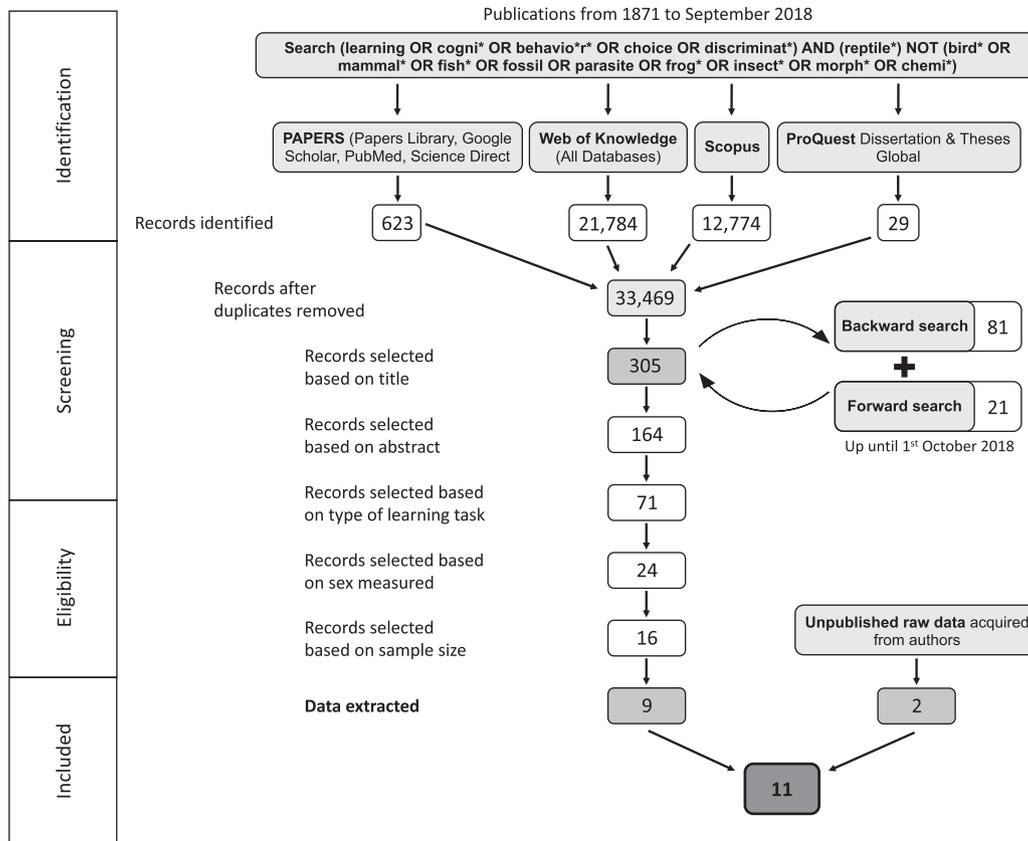


Fig. 1. PRISMA diagram showing the systematic search for literature on learning in non-avian reptiles. Included are the search terms, which datasets were searched and when, how many entries were identified and a step-by-step description of the selection of data for the meta-analysis.

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

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

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

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

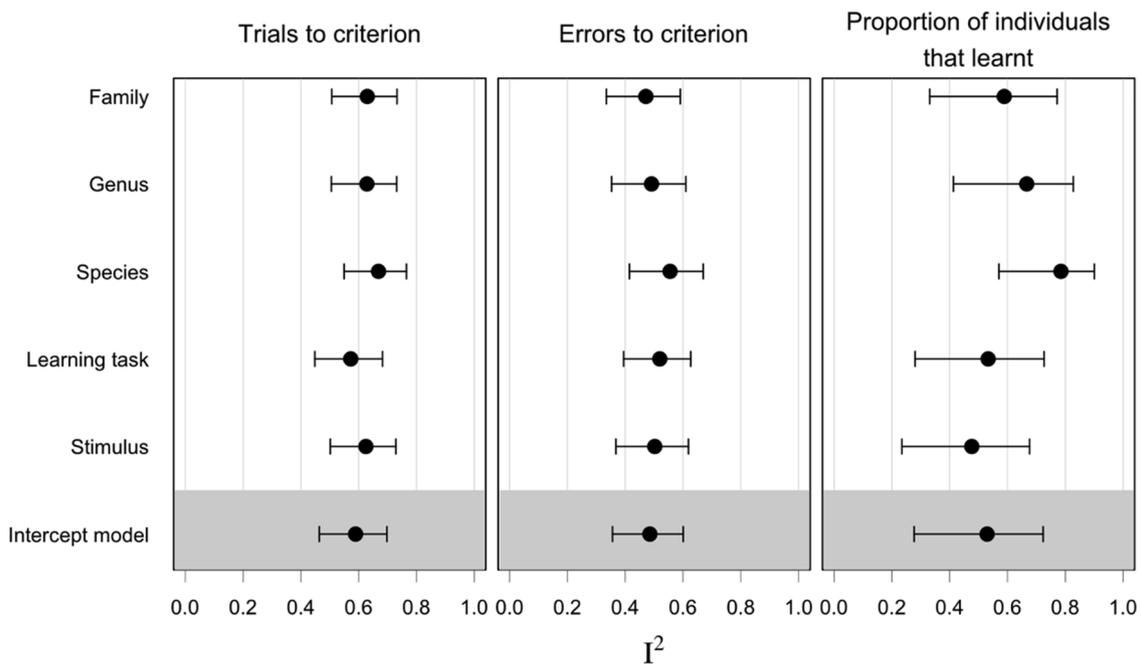


Fig. 2. Total heterogeneity ( $I^2$ ) with 95% confidence interval for trials to criterion, errors to criterion and the proportion of individuals that learnt. Rows indicate the different models (MLMR) run for each of the five moderators. The MLM model is highlighted in grey. For raw values see electronic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

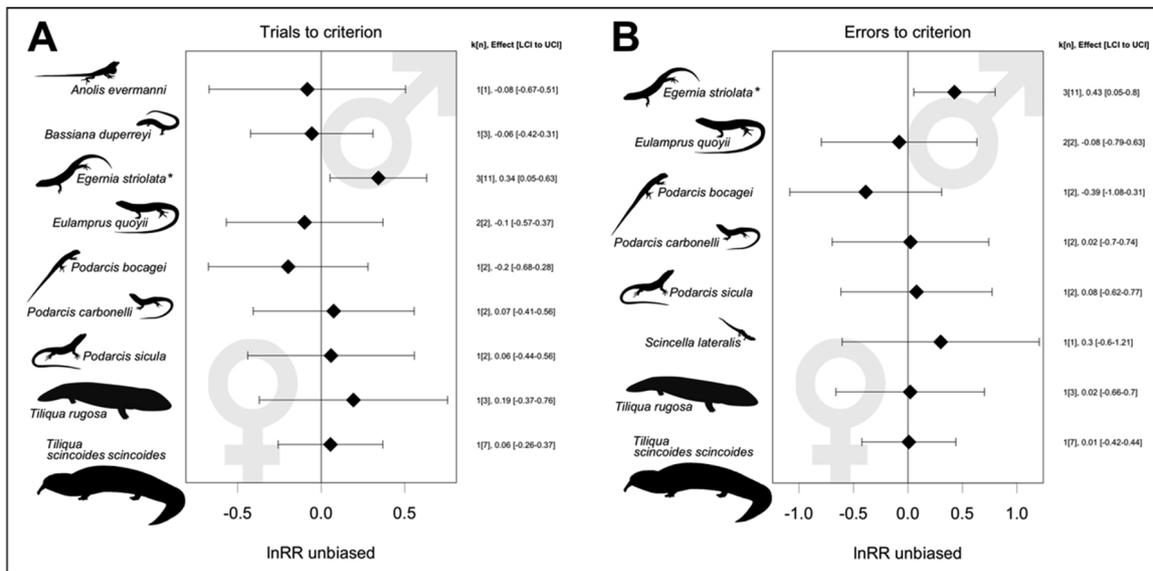
## 3. Results

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 predetermined 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 ( $\pm$  standard deviation) sample size for males was 12.4 ( $\pm$  7.5 standard deviation) and for females 12.6 ( $\pm$  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

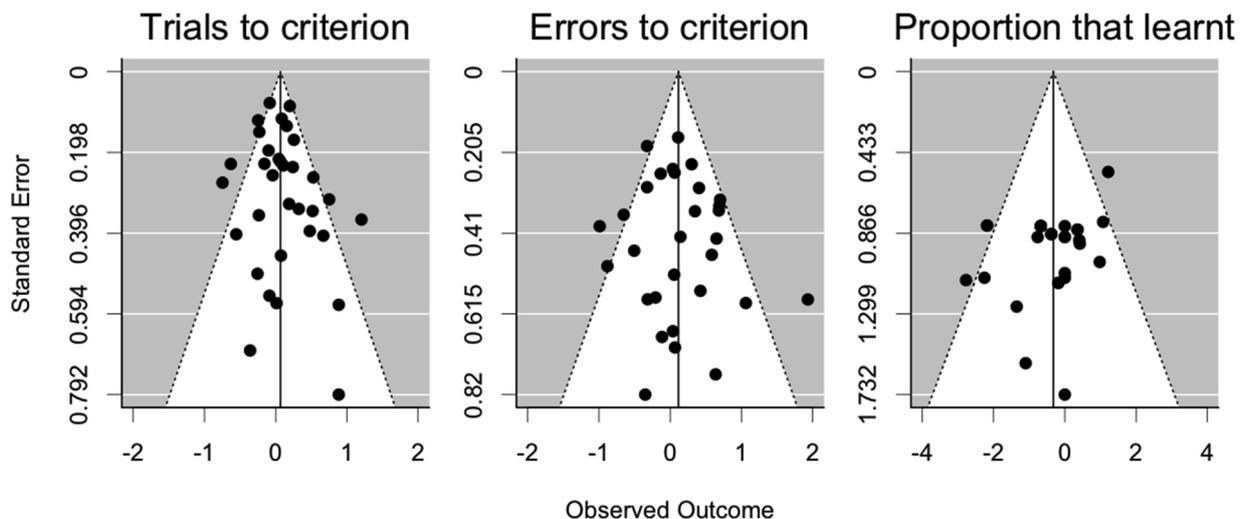
Visual inspection of the funnel plots indicated some asymmetry and suggests the possibility of missing studies (Fig. 4). However, Egger's tests revealed no significant asymmetry (Trials to criterion: estimate = 0.054, t-value = 0.69,  $CI_{low} = -0.105$ ,  $CI_{up} = 0.212$ ,  $P = 0.495$ ; Errors to 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 (*Eulamprus 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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