



Do female amphibians and reptiles have greater reproductive output if they have more mates?

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Abstract

In general, males mate with multiple females to increase individual reproductive success. Whether or not, and under what circumstances, females benefit from multiple mating has been less clear. Our review of 154 studies covering 184 populations of amphibians and reptiles showed that polyandry was widespread and variable among and within taxonomic groups. We investigated whether amphibian and reptile females had greater reproductive output as the number of sires for offspring increased. Meta-analysis revealed significant heterogeneity in the dataset of all taxa. Expected heterozygosity was a significant moderator (covariate) of positive relationships between female reproductive output and the number of sires, but a sensitivity test showed the result was tenuous. Significant heterogeneity remained despite controlling for expected heterozygosity and other variables but was resolved for most taxonomic groups with subgroup meta-analyses. Subgroup meta-analyses showed that only female salamanders (Caudata) had significantly greater reproductive output with an increased number of sires. For many species of Caudata, males cannot coerce females into accepting spermatophores. We therefore suggest that if females control the number of matings, they can use polyandry to increase their fitness. Caudata offers ideal models with which to test this hypothesis and to explore factors enabling and maintaining the evolution of female choice. Outstanding problems may be addressed by expanding taxonomic coverage and data collection and improving data reporting.

Significance Statement

Many factors and combinations of factors drive polyandry. Whether or not females benefit from mating with more than one male remains equivocal. Focusing on amphibians and reptiles, our analyses demonstrate that female salamanders produced more offspring when mated with multiple males, whereas this was not the case for reptiles. Unlike many other species in our dataset, the polyandrous female salamanders fully control sperm intake and have chosen to mate multiple times. We further highlight problems and key directions for future research in the field.

Keywords Female reproductive success · Heterozygosity · Mate choice · Meta-analysis · Multiple paternity · Polyandry

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Introduction

Mating is costly for the participants, so convention is that the more highly invested sex (usually the female) should restrict mating to the minimum required for fertilisation whereas the less constrained sex (usually the male) should benefit from mating with many individuals (Bateman 1948; Trivers 1972). However, the theory that polyandry (females mating with more than one male in the same breeding season; see Table 1) has no fitness benefit for females is questionable because it does not explain why polyandry occurs for so many species (Slatyer et al. 2012; Taylor et al. 2014). Polyandry can be simultaneous, when sperm from different males fertilise the same clutch or litter to result in multiple paternity, or sequential, in which offspring partitioned into separate clutches are fertilised by different males (Table 1). Molecular-based paternity testing within and between the clutches or litters of offspring is a means of detecting multiple sires. Incidence of multiple paternity in clutches or litters is used to indicate incidence of polyandry, but is not accurate if not all mating events resulted in fertilisation (Bretman and Tregenza 2005). Additionally, polyandry resulting in different sires between the clutches or litters of the same female will not be detected by assessing the paternity of only one clutch or litter. However, multiple paternity can only happen if the female had mated with at least two different males at some point in the past. Thus, even if the correspondence may not be one-to-one, in general, the incidence of multiple paternity should scale with the incidence of polyandry—there is, for example, evidence that multiple paternity

increases with mate availability (Jensen et al. 2006; Sandrin et al. 2015). Multiple paternity detected for many species is evidence that polyandry is a common behaviour, even for socially monogamous species (see Supporting Information S11, Table S1).

To explain widespread polyandry, mating with multiple males is suggested to benefit females despite the well-known costs of mating (Table 2 (adaptive explanations), also see Olsson and Madsen 2001; Uller and Olsson 2008; Parker and Birkhead 2013; Forstmeier et al. 2014). Having sperm from multiple males increases the diversity of offspring (Jennions and Petrie 2000) and allows for insurance against male infertility and/or bet-hedging against incompatible matings (Garcia-Gonzalez et al. 2015), sperm competition (Friesen et al. 2020) and post-copulatory mate choice by females (cryptic female choice) (Birkhead 2000; Firman et al. 2017). Genetically acquired benefits may further manifest as increased offspring viability (Olsson and Madsen 2001). Indeed, one view is that multiple mating is nearly always beneficial to females but is logistically constrained by mate acquisition (Avisé and Liu 2011). Notwithstanding these hypotheses, the question of whether or not females benefit from polyandry still stands, because even with the focus in behavioural ecology shifting from the male to the female perspective (e.g. Lyons et al. 2021), there remains no consensus on the matter, with reviews of various taxonomic groups and topics reaching equivocal or different conclusions (S11, Table S1).

Ultimately, to demonstrate that a female benefits from polyandry, we need to show that her fitness increases. *Sensu*

Table 1 Definitions of some of the specialist terms mentioned in the text

Terms	Definition
Amplexus	External fertilisation that occurs when males mount females, and eggs and sperm are released simultaneously
Convenience polyandry	Females mate multiple times to reduce the costs imposed upon them by harassing males, such as injury and energy expenditure
Explosive mating strategy (explosive breeders)	Where mating occurs intensively over a brief period of time (as opposed to the prolonged mating strategy of prolonged breeders)
Multiple amplexus	During external fertilisation, when sperms of other males are released in the vicinity of the amplexant pair (see amplexus) or when males sneak sperm into nests or eggs guarded by other males
Multiple paternity	Where the offspring of the same clutch or litter were sired by more than 1 male
Polyandry	When females mate with multiple different males within the same reproductive period (within 1 breeding season) and her offspring may have more than 1 sire; the term may be used interchangeably with ‘multiple mating by females’
Polygynandry	When both males and females mate multiple times with different individuals during a single reproductive period (within 1 breeding season)
Polygyny	When males mate with multiple different females during a single reproductive period (within 1 breeding season)
Sequential polyandry	When females produce multiple clutches of eggs over the course of 1 reproductive period (within a breeding season), which can be fertilised by different males in separate mating events
Simultaneous polyandry	When the sperm of 2 or more males fertilise the same clutch or litter (see also multiple paternity)
Spermatophore transfer	When a sperm packet (the spermatophore) deposited by the male is taken up by the female in her cloaca; among vertebrates, this fertilisation method is unique to Caudata

stricto, an individual's fitness is defined in terms of all of its descendants, but lifetime reproductive success (all progeny produced in her lifetime) is considered an appropriate, and a more readily quantifiable, proxy (Brommer et al. 2004). Still, collecting data on lifetime productivity is more suited for laboratory settings and difficult to obtain for individuals in wild populations, especially when they may be long lived. A more tractable indicator is the reproductive output of one breeding event, which contributes to individual fitness irrespective of the mechanisms involved in producing that output. A short-term measure of reproductive output may still provide a broad indication of total lifetime reproductive success (Nguyen and Moehring 2015). If polyandry has fitness benefits for females, then, regardless of the drivers, we may expect the number of offspring (reproductive output) of those females to increase with the number of sires.

Nonetheless, a key problem is that empirical evidence of females benefiting from polyandry has been hard to find (e.g. Olsson and Madsen 2001; Noble et al. 2013); therefore, alternative explanations have been proposed (Table 2 (neutral (null) explanations)). One is sexual conflict, whereby males coerce females into extra matings (Boulton et al. 2018). Male–male competition may be particularly influential in driving polyandry when density is high, and sex ratio is male-biased (Lyons et al. 2021). Females may also mate according to the mate encounter rate of the population (e.g. Lee et al. 2018), which may be likely where mates are limited or if females cannot predict whether they are likely to meet further mates (Gowaty 2013; Kokko and Mappes 2013).

Various factors may affect the incidence of polyandry. For example, with regard to female fecundity, species with larger brood sizes have greater numerical opportunity for multiple paternity compared with those with smaller brood sizes (Avisé and Liu 2011; Correia et al. 2021; Lyons et al. 2021). Other factors may be environmental: mating incidence may vary with latitude because temperature influences longevity, breeding seasonality and mate encounter rates (Olsson et al. 2011; Taylor et al. 2014). Some studies have tested offspring and maternal phenotypic characteristics, offspring heterozygosity, rates of offspring survival or viability and population factors (e.g. density) as possible covariates (Table 2). However, given the variability of behavioural characteristics across species and how the optimum mating strategy at any given time is conditional on population and environmental and individual circumstances (Gowaty 2013; Lyons et al. 2021), it is unlikely for there to be only a single driving factor, even for the same species (Lyons et al. 2021). Variables potentially affecting polyandry become increasingly difficult to resolve as species have more complicated mating behaviours and ecologies.

Focusing on amphibians and reptiles, our aim was to address the question of whether or not females have greater

reproductive output if they have more mates. The causes of polyandry may potentially be more easily teased apart for these taxa compared with vertebrates that have more complex and obligate social and mating behaviours (e.g. mammals and birds) (Uller and Olsson 2008). However, two reviews of anuran amphibians and reptiles published over a decade ago used descriptive approaches to conclude that there was little evidence that females of these species benefited from polyandry (Uller and Olsson 2008; Roberts and Byrne 2011). Here, we extended previous reviews with updated literature. Further, we extended previous approaches by taking an empirical approach in examining whether or not female reproductive output increased with polyandry. We used meta-analytical methods to summarise and organise information and to test the relationship between the number of offspring and the number of sires. To compare results from different studies, we used a standardised effect size (a statistic reflecting the strength of the relationship between the variables; Borenstein et al. 2009). We also tested a number of methodological, environmental and biological variables as possible moderators (covariates) of the effect sizes.

Methods

Assembling the global dataset and extraction of data

We searched Web of Science and Scopus through to August 2019 (S11, Fig. S1). We limited searches to peer-reviewed journals and to studies that used molecular data for paternity analyses. We considered only studies based on amphibians or reptiles that could express natural mating behaviour. Experimental studies were excluded as they may not reflect natural patterns of polyandry and constitute a different body of literature (examples in S11, Table S1, and see Hettyey et al. 2010). We accepted studies of reintroduced/translocated populations and of wild-caught individuals temporarily held in captivity, where individuals had mated naturally (details in S11).

We extracted data on multiple paternity and on numbers of sires and offspring in clutches or litters from the text or tables of studies. If presented in graphs, values were extracted using *DataThief* (Tummers 2006) or the *R* package *metaDigitise* (Pick et al. 2019). As often as possible, two people independently extracted data. Otherwise, the same person re-extracted data at least one other time, but on a different occasion (i.e. not immediately after the first extraction).

We used the multiple paternity data to estimate the percentage of females in the population with evidence of polyandry. A sample for the prevalence of polyandry (hereafter 'PA') was one group of offspring produced in the same

reproductive season by a female. We pooled multiple paternity data for cases where multiple clutches or litters in the same breeding season were sampled for the same female (see SI1 for worked examples). However, offspring produced in different breeding seasons were considered independent samples, because many factors such as maternal body condition, environmental conditions and mate or resource availability could have changed between seasons, with the differences likely more pronounced between rather than within the same season.

To avoid over-representation of well-studied populations, we only had a single PA estimate for any one population (called a ‘case’, K). Data across consecutive breeding seasons were combined. For example, if polyandry was found for 2 of 10 samples in one season and 4 of 14 samples in another season, PA would be estimated as 25% (6 out of 24 samples with evidence of polyandry). However, if different data were collected with an interval of several years, if the studies used different methods or if some of the same data was used in different studies, we chose the data from the study that was more recent, reported more samples and/or used more advanced methods (see Supplementary Data, SI2).

Preliminary analyses led to exclusion of cases with fewer than five samples for analyses involving the PA variable. Cases with small sample sizes inflated the frequency of either 0% or 100% values for PA in the dataset (see SI1, Fig. S2; note that SI2 lists all cases, including those with fewer than five samples).

We also extracted data on a number of variables previously suggested to affect polyandry: latitude, average heterozygosity (observed and expected), average clutch or litter sizes and indicators of the sampling effort (e.g. number of loci, average number and average percentage of offspring genotyped). Data on average heterozygosity (observed and expected) were those estimated for the adult population and limited to cases using microsatellite loci for parentage and/or population genetic analysis. We tested sampling effort because methodological differences between studies may introduce error (Borenstein et al. 2009). For example, evidence of polyandry may become easier to detect as sampling effort increases (Griffith et al. 2002). In some cases, the data for variables were from associated literature (see SI1 for details) or missing. Cases with a missing variable were excluded from analyses involving the missing variable.

Datasets

Summary statistics were estimated for all data and for data in major taxonomic groups: Anura (frogs and toads), Caudata (newts and salamanders), Crocodylia

(crocodiles and alligators), Lacertilia (lizards, skinks, geckos, iguanas and dragons), Serpentes (snakes) and Testudines (tortoises and turtles). We also obtained summary statistics for Cheloniidae (marine turtles, a family of Testudines) because this was the only family with sufficient cases to summarise the data for genera. Lacertilia and Serpentes are squamates, but we treated them separately as they are groups with distinct biological differences and large membership. Included in the summary statistics of the full dataset were data for single representatives of their respective taxonomic groups: the caecilian *Boulengerula taitanus* (Gymnophiona, Herpelidae) and the tuatara *Sphenodon punctatus* (Rhynchocephalia, Sphenodontidae).

Effect size data

We estimated the standardised effect size, Fisher’s z -transformation of the correlation coefficient (Z_r). We calculated the correlation coefficient r (Pearson’s r) between the number of offspring and the number of sires. If there was only summary information (means, variances and sample sizes), we used the *escalc()* function of the R package *metafor* (Viechtbauer 2010) to calculate the bias-corrected standardised mean difference (Hedges’ g) between singly sired and multiply sired groups of offspring, which was then converted to correlation coefficient (r). We used reported r values if raw or summary data were not available. We then converted r values and their sample sizes to Z_r and its variance (Var_{Z_r}) (Borenstein et al. 2009) (see SI1 for formulae).

Some studies tested for relationships between the number of offspring and the number of sires but did not include the information required for effect size calculation (SI1, Table S2). These studies used a variety of tests: t tests, ANOVA, ANCOVA, GLM, GLMM and logistic regression. While it may be possible to convert between some types of effect sizes (Rosenberg et al. 2000), converting the results of statistical models that include multiple variables or tests that control for covarying factors may not be appropriate. Conversions make assumptions about the underlying data, and if these assumptions were violated or if there were substantive differences between the studies, then the validity of the meta-analysis will be impacted (Borenstein et al. 2009). We preferred to take a conservative approach by excluding these studies.

Statistical analyses

We performed statistical analyses in R v. 3.6.1 (R Core Team 2019) using R Studio v. 1.1.453 (RStudio Team 2015) and used the R package *metafor* (Viechtbauer 2010) for meta-analyses. The multilevel meta-analytical framework in

metafor fits random-effects models weighted by the inverse of the marginal variance–covariance matrix estimated for the effect sizes (Viechtbauer 2010). We used the *rma.mv()* function to build random-effects meta-models with the default restricted maximum likelihood estimation (REML) method and the option ‘test’ set to ‘t’ (see S11 for R scripts). Random effects were the statistic used for effect size calculation (correlation r or Hedges’ g), common ancestry (phylogeny) and estimates from the same study or from the same species. Funnel plots (the *funnel()* function), Egger’s tests (the *regtest()* function) and estimation of ‘fail-safe’ numbers (the *fsn()* function) enabled the examination of the model results for the presence of heterogeneity and publication bias (Rothstein et al. 2005). We used the *influence()* function for diagnostic tests of influential outliers. We used the *cumul()* function to observe how summary effect sizes accumulated with a specific variable (e.g. the year of publication).

To control for phylogenetic relatedness (Lajeunesse 2009), we acquired the correlation matrix of phylogenetic relationships. We used the R package *rotl* (Michonneau et al. 2016) to interface with the ‘Open Tree of Life’ (opentreeof-life.org) database (Redelings and Holder 2017) and retrieve phylogenetic trees (S11, Fig. S3). With the R package *ape* (Paradis and Schliep 2018), we used the *compute.brlen()* function to estimate branch lengths, and the *vcv()* function to construct the correlation matrix.

We ran a random-effects model using the *rma.mv()* function to estimate a pooled (summary) effect size. The random-effects model allows the true effect size to vary from case to case, so we estimated heterogeneity (variation in true effect sizes) from observed effects as the statistic T^2 , which includes both true heterogeneity and random error (Borenstein et al. 2009). We calculated Cochran’s Q to test for heterogeneity (this tests for differences between the effect sizes of cases and the meta-analytical mean effect size) and the I^2 statistic to show the proportion of heterogeneity that is due to a variation among studies (Borenstein et al. 2009).

We addressed significant heterogeneity in two ways. First, we evaluated separate meta-analytic models for taxonomic subsets of the data (subgroup meta-analyses) to identify where significant heterogeneities were occurring (Borenstein et al. 2009). Second, we carried out meta-analyses that tested for ‘moderators’, which are variables that are case-level covariates of effect sizes (Viechtbauer 2010). We used the *pairs.panels()* function of the R package *psych* (Revelle 2018) to estimate correlations between variables that were potential moderators and effect sizes (Zr) and to estimate pairwise correlations among these variables. We then conducted meta-analyses incorporating and testing for moderators. These models included random factors (see previous text for details of random effects) and controlled for time-lag bias (mean-centred publication year, which is the year of publication minus the mean of all years of publications)

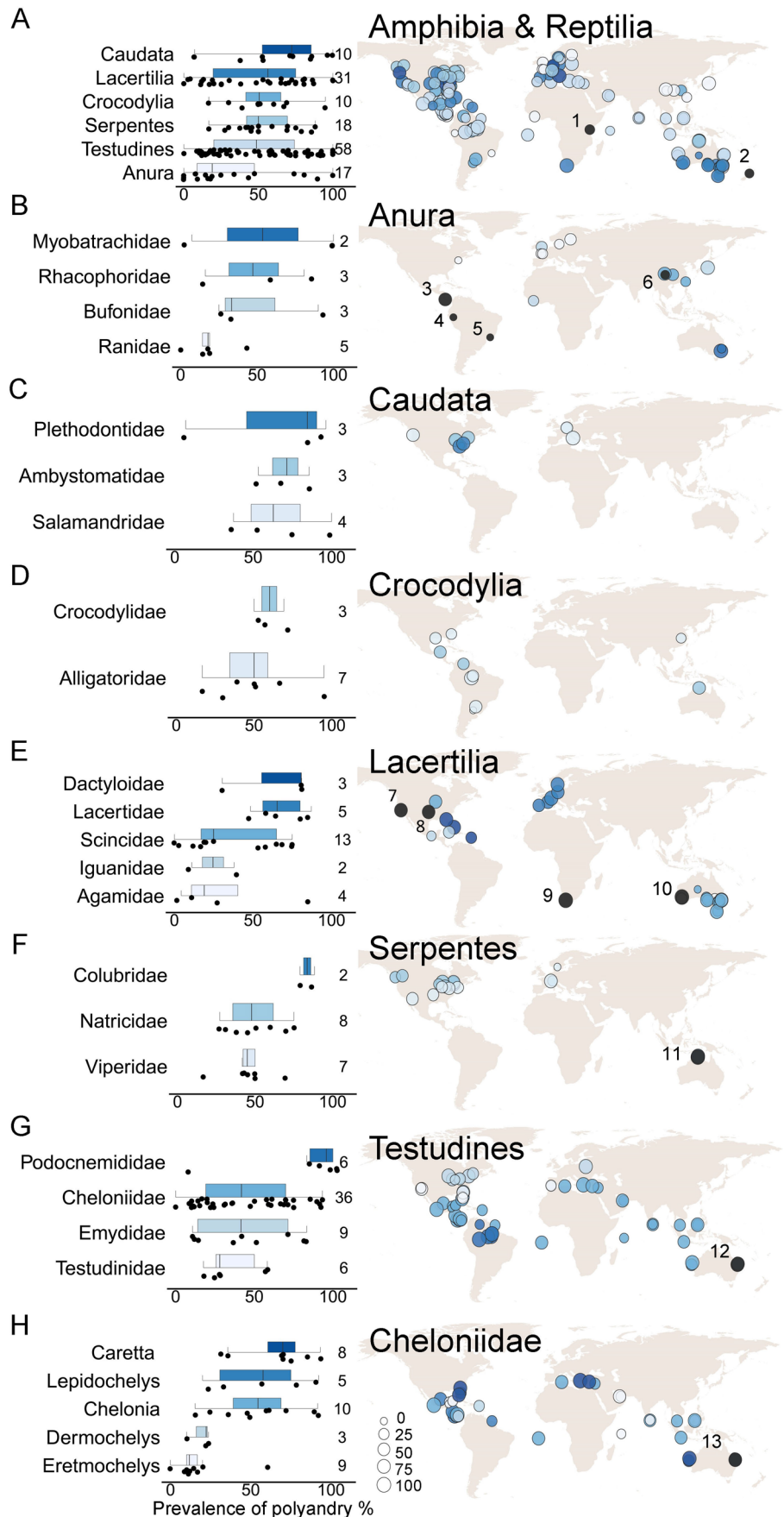
and small study effect (inverse of Zr standard error, which is $(1/\sqrt{N-3})$) (see S11 for R scripts). The program *metafor* tested whether variables were significant moderators and tested for remaining residual heterogeneity. We initially fitted a model including all candidate moderators. Next, we fitted models with single candidates to work out the best (according to the test of the moderator) to include in models with two moderators. We further considered whether the test for residual heterogeneity remained significant and used corrected Akaike information criterion values (AIC_C) to confirm the model best fitting the data. We then tested combinations of two candidates for variables that were not significantly correlated with each other. Finally, we tested between models with different numbers of moderators and ran a sensitivity test (see S11 for details).

Results

In assessing the full-text articles of 370 studies, we found 154 reporting on the occurrence of multiple paternity among clutches or litters from 184 different amphibian and reptile populations (see also S11 Fig. S1; S12 lists all studies and references). The majority, 172 of 184 cases, used microsatellite loci. Of the others, one used single nucleotide polymorphisms (SNPs), two used amplified fragment length polymorphism (AFLP), six used allozymes, two used multilocus DNA fingerprinting (minisatellites or variable number of tandem repeats (VNTRs)) and one used both multilocus DNA fingerprinting and a single-locus DNA probe (see S12 for all references). We estimated PA at 48% after excluding 36 cases with fewer than five samples and two with unknown sample sizes ($SD = 30\%$, $K = 146$ cases; *N.B.*, for all 184 cases, $PA = 49\%$, $SD = 34\%$). There were more cases reported for the northern hemisphere than for the southern hemisphere (100 versus 46 for cases with $N \geq 5$) (Fig. 1A; see also S11, Fig. S4).

PA varied randomly with respect to absolute latitude (Kendall’s rank correlation tau test: $z = 0.84$, $p = 0.402$) and sample size ($z = -1.61$, $p = 0.107$). There were also no significant relationships between PA and the number genotyped per clutch/litter or the proportion genotyped (Kendall’s rank correlation tau tests: $z = 1.53$, $p = 0.126$, for the former after excluding two cases with clutch sizes of over a thousand, and $z = 0.05$, $p = 0.959$, for the latter). For cases based on microsatellite markers, there were no significant relationships between PA and the number of loci nor the average number of alleles (Kendall’s rank correlation tau tests; $z = -1.65$ and 0.45 , $p = 0.100$ and 0.652 , respectively). There were no significant relationships with the average observed or expected heterozygosities (Kendall’s rank correlation tau tests: $z = 1.58$ and 1.88 ,

Fig. 1 A–H The prevalence of polyandry (PA) in amphibian and reptile breeding populations across taxonomic groups and maps of sampling locations (excludes cases with fewer samples than five). Jittered points in graphs are the PA for individual cases within each taxonomic group, with values summarised above as a box plot (central lines in boxes are median values, numbers are the number of cases, boxes correspond to the first and third quartiles and whiskers extend to 1.5 times of the inter-quartile range). Sampling locations are plotted in maps, with the bubble size reflecting the degree of PA and colour corresponding to the colour used in the associated graph. Single-case taxonomic groups (excluded from summary graphs) are plotted on the map with a black bubble and numbered: (1) *Gymnophiona (Boulengerula taitanus)*, (2) *Rhynchocephalia (Sphenodon punctatus)*, (3) *Centrolenidae (Hyalinobatrachium valeriol)*, (4) *Dendrobatidae (Ranitomeya imitator)*, (5) *Leptodactylidae (Thoropa taophora)*, (6) *Megophryidae (Leptobrachium boringii)*, (7) *Phrynosomatidae (Uta stansburiana)*, (8) *Crotaphytidae (Crotaphytus collaris)*, (9) *Chamaeleonidae (Bradypodion pumilum)*, (10) *Diplodactylidae (Oedura reticulata)*, (11) *Pythonidae (Liasis fuscus)*, (12) *Chelidae (Elseya albagula)* and (13) *Cheloniidae (Natator depressus)*



$p = 0.115$ and 0.060 , respectively) or the year of publication ($z = 1.09$, $p = 0.277$).

Patterns across taxonomic groups

PA was widespread and variable across major taxonomic groups (Fig. 1A). There was a large range of PA values within groups, without significant differences among groups (Kruskal–Wallis rank sum test = 8.27 , $df = 5$, $p = 0.142$). One notable pattern was that Anura had the smallest median PA (18.9%; Fig. 1A) with many cases of relatively low values being of Ranidae (the largest value was no more than 44%). The PA data for Anura were significantly lower than those for Caudata (Wilcoxon rank sum test: $W = 41.5$, $p = 0.031$). In contrast, Caudata had the highest median PA (72.4%; Fig. 1A). Thus, cases for Caudata and Anura tended towards opposite ends of the range of values for PA, even though both groups were amphibians. For reptile groups, median PA values were 48.7–56.3% (Fig. 1A).

Within most taxonomic families, PA values ranged widely (Fig. 1B–G), but with some exceptions. Ranidae and Iguanidae were the only families with relatively low PA for all cases ($K = 5$ cases, range: 0–44%, and $K = 2$ cases, range: 11–38%, respectively). While values for the five cases of Ranidae only averaged 19%, these were not significantly different from the PA values of the other genera in Anura (Kruskal–Wallis $\chi^2 = 11.44$, $df = 10$, $p = 0.324$). Iguanidae only had two cases, so it remains to be seen if a greater range of PA values will be reported in future studies. Many taxonomic families were represented by few cases (< 5), so general conclusions would be tentative.

Among the taxonomic groups, Testudines was the most studied ($K = 58$ cases), with PA values spanning the entire range (0–100%; Fig. 1G). PA for Podocnemididae tended towards high values (median = 95.8%), whereas those of Testudinidae were lower (median = 28.1%), but overall, there were no significant differences among families (Kruskal–Wallis $\chi^2 = 8.22$, $df = 4$, $p = 0.084$). Among Testudines, Cheloniidae, the taxonomic family with the greatest number of cases ($K = 36$; 62% of all cases), provided the only opportunity to observe patterns of PA among genera within the family (Fig. 1H). In Cheloniidae, we found a wide range of PA values (0–93%), with one noteworthy pattern. There were significantly lower PA values for *Dermochelys* ($K = 3$, range: 10–24%) and *Eretmochelys* ($K = 8$ with a range of 0–17%, and one case of 61%) compared to PA values of the other genera (Kruskal–Wallis $\chi^2 = 19.03$, $df = 5$, $p = 0.002$; with *Dermochelys* and *Eretmochelys* excluded: $\chi^2 = 1.35$, $df = 3$, $p = 0.716$).

Testing the relationship between the number of offspring and the number of sires

Effect size data (36 cases from 35 studies) obtained from all taxonomic groups, except Anura, were checked for influential cases, outliers and publication bias. Egger's test did not find significant asymmetry in funnel plots (S11, Fig. S6), so publication bias was not an extensive problem. A forest plot of cumulative meta-analysis conducted according to the year of publication showed initial cumulative effect sizes had high values influenced by a few early cases, but as more were added, the cumulative effect sizes settled close to zero (S11, Fig. S7). Influential case diagnostics discovered one case for a population of *Zootoca vivipara* (Eizaguirre et al. 2007), exerting substantial changes in fitted models (see S11 for Fig. S5 and further details). Funnel plots confirmed this case as an outlier (S11, Fig. S6). We therefore fitted meta-analysis models with and without this case (Fig. 2). Summary effect sizes estimated by phylogenetically controlled meta-analyses were not significant (Fig. 2), but significant heterogeneity in the data remained even after the influential outlier was excluded (Table 2), and even though the meta-analysis controlled for phylogenetic non-independence and a number of other random factors (see methods and R script in S11). While heterogeneity may be caused by random error, some may be due to real differences between cases (Borenstein et al. 2009). To clarify the heterogeneity, we used subgroup meta-analyses and tested for moderators.

Subgroup meta-analyses

Subgroup meta-analyses revealed significant heterogeneity in just one taxon, Lacertilia (Table 3). Indeed, values of Z_r for Lacertilia ranged from -0.30 to as high as 1.58 , the latter being the largest effect size in the dataset (Fig. 2). The meta-analysis included species from diverse families: Scincidae (*Tiliqua rugosa* and *Egernia whitii*) (Bull et al. 1998; Chapple and Keogh 2005), Agamidae (*Intelligama lesueurii*) (Frere et al. 2015), Iguanidae (*Cyclura nubila caymanensis*) (Moss et al. 2019) and Lacertidae (*Z. vivipara*) (Eizaguirre et al. 2007). Only two cases had significantly positive effect sizes (Fig. 2): *T. rugosa* (Bull et al. 1998) and *Z. vivipara* (Eizaguirre et al. 2007). However, *T. rugosa* have few offspring (average of two in this case), so the result could be an artefact of multiple paternity being difficult to detect when few offspring are tested. The other case, however, was the outlier identified in influential diagnostics and in funnel plots and likely contributed heterogeneity to the data. The funnel plot for Lacertilia revealed a further case as a possible source of heterogeneity (S11, Fig. S6): a population of *E. whitii* studied by Chapple and Keogh (2005). The two outliers had the largest effect sizes in Lacertilia, but in

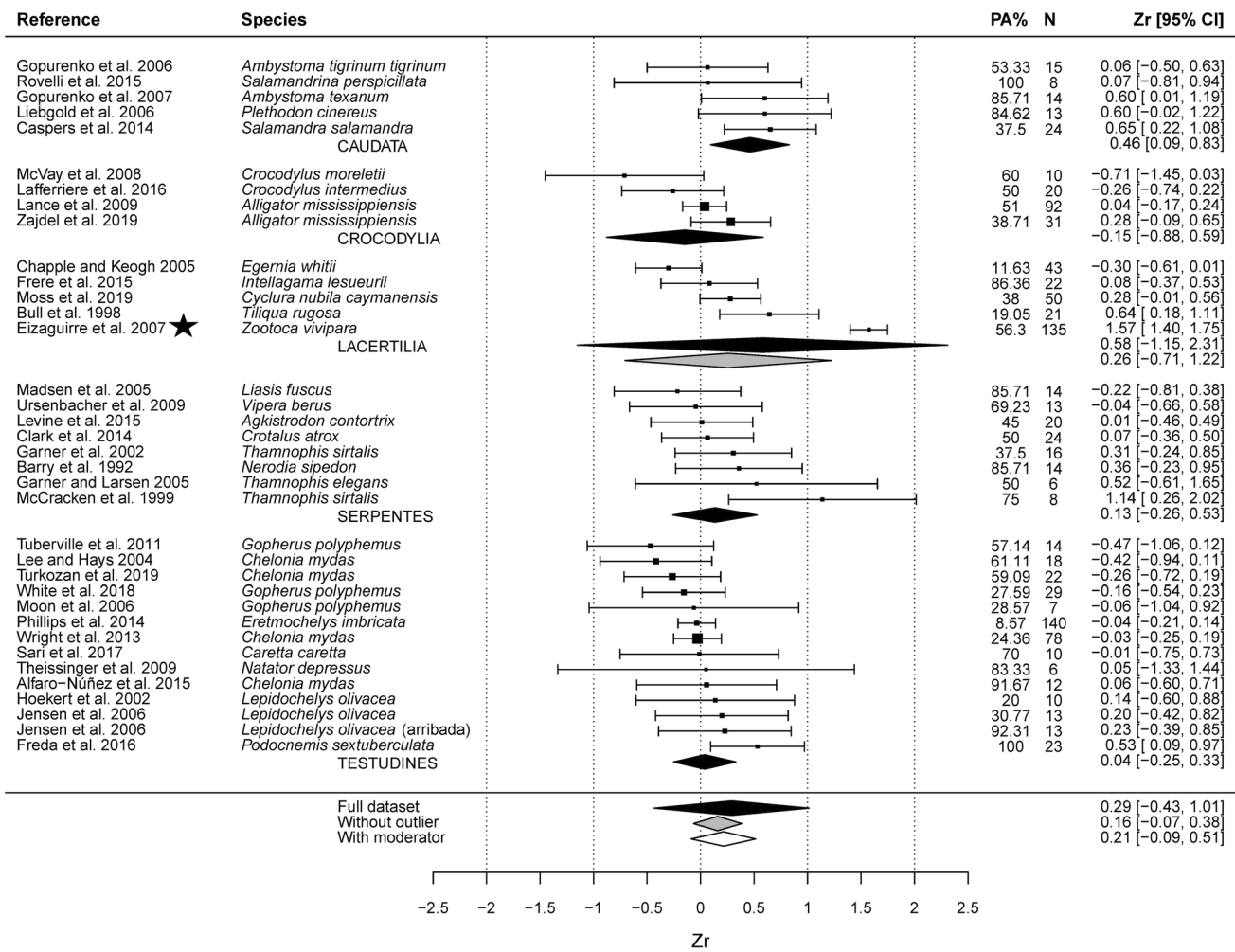


Fig.2 Forest plot of effect sizes, and summary effect sizes estimated by phylogenetically controlled meta-analysis (random-effects maximum likelihood method) of the relationship between the number of offspring and the number of sires. The star indicates the outlying influential case (see text). Within taxonomic subgroups, cases are organised by the effect size (Z_r) and labelled with the reference of the study. Point sizes are proportional to the precision of the estimates, and whiskers, 95% confidence intervals (CI). An effect size is considered significantly different from zero if its 95% confidence interval is either larger than or smaller than zero. Positive values indicate that there are larger numbers of offspring in groups of siblings and half-siblings with more sires, whereas negative values indicate the opposite. ‘PA %’ is the estimated prevalence of polyandry in the population with sample size ‘N’. The black diamond polygon below each

subgroup is the estimated summary effect size including the 95% confidence interval, labelled by the taxonomic name of the subgroup. The grey diamond polygon is the summary effect size excluding the outlying influential case. Summary effect sizes for the whole dataset are represented by diamond polygons at the bottom of the graph. The black polygon represents the estimate for all cases (36 cases, labelled ‘Full dataset’), the grey polygon represents the estimate for cases without the outlier (35 cases, labelled ‘Without outlier’) and the white polygon represents the estimate based on a mixed-effects model that included average expected heterozygosity as a moderator (27 cases, labelled ‘With moderator’). The latter excluded the outlying influential case, and cases that were missing data for average expected heterozygosity (see also Fig. 3)

opposite directions (Fig. 2). Maternal size was reported as significantly correlated with the number of mates and the number of offspring in the study on *Z. vivipara* (Eizaguirre et al. 2007). However, we could not control for maternal size in our meta-analysis because the information was lacking for other cases. Significant heterogeneity remained after leaving out the influential outlier (Table 3). Excluding both outliers reduced heterogeneity to non-significance ($I^2 = 35.5%$, $Q = 3.37$, $p = 0.185$), but left only three cases for Lacertilia.

Subgroup meta-analysis showed Caudata as the only group with a significant summary effect size (Fig. 2). Total heterogeneity for Caudata was low ($I^2 = 2.5%$, $Q = 3.82$, $p = 0.431$; Table 3), suggesting that the effect sizes were consistent in supporting the summary effect size for the group. All species were salamanders, and of the five, effect sizes for *Ambystoma texanum* (Gopurenko et al. 2007) and *Salamandra salamandra* (Caspers et al. 2014) were significant. Individual effect sizes for *Ambystoma tigrinum*

Table 2 Hypotheses proposed to explain the occurrence of polyandry, with some examples from studies of amphibians and reptiles

	Indicator	Examples
Adaptive explanations		
Increases fertilisation success	Increase in offspring number	CAU (Caspers et al. 2014), LIZ (Noble et al. 2013)
Increases likelihood of male–female genetic compatibility (allows for sperm competition)	Increase in offspring viability ¹	SER (Blouin-Demers et al. 2005; Madsen et al. 2005)
Insures against nest failure	Increase in offspring survivorship	ANU (Byrne and Keogh 2009)
Inbreeding avoidance	Increase in offspring heterozygosity ¹	LIZ (Moss et al. 2019)
Genetic bet-hedging: genetic contributions spread among multiple sires to minimize variance in male quality	Increase in offspring heterozygosity or genetic diversity among offspring ¹	LIZ (Moss et al. 2019), TUR (Bouchard et al. 2018)
Enables female cryptic choice based on males' genetic dissimilarity	Increase in offspring heterozygosity ¹	CAU (Rovelli et al. 2015)
Enables female choice of best sire genes for their progeny to alleviate the costs of sexual conflict	Increase in genetic diversity among offspring ¹	LIZ (Calsbeek et al. 2007)
Increases likelihood that some offspring will survive unpredictable/novel environments	Increase in genetic diversity among offspring	LIZ (Calsbeek et al. 2007; Eales et al. 2010), TUR (Bouchard et al. 2018)
Neutral (null) explanations		
Larger litters provide greater opportunity for multiple paternity to occur	Increase in offspring number	SER (Prosser et al. 2002)
More fecund (e.g. larger/older or more mobile/experienced) females attract/encounter more mates	Increase in offspring number or size; increase in maternal size or age	CRO (Lance et al. 2009), SER (Garner et al. 2002; Prosser et al. 2002; Garner and Larsen 2005), LIZ (Eizaguirre et al. 2007), TUR (Pearse et al. 2002; Zbinden et al. 2007; McGuire et al. 2013)
Multiply mated females are stimulated to oviposit more eggs	Increase in offspring number	TUR (Pearse et al. 2002)
Smaller (younger, less experienced) females less able to reject males, or not as well guarded	Decrease in maternal size/age or experience	TUR (Moon et al. 2006)
Females accept unwanted mates to avoid costs of rejecting mates ('convenience polyandry' ²)	Increase in breeding density	TUR (Lee and Hays 2004)
Increased mating opportunities (mate encounter rate) lead to females mating more often	Increase in breeding density	LIZ (Garner et al. 2002), TUR (Lee and Hays 2004)
Male-skewed sex ratios lead to increased mate encounter rate and females mating more often	Male-skewed operational sex ratios	TUR (McGuire et al. 2013, 2014)
Stored sperm from a current or a previous breeding season mixing with sperm from the current mating	Offspring of different clutches of the same female sharing the same sire within or between breeding seasons	TUR (Fitzsimmons 1998; Pearse et al. 2002; Roques et al. 2004, 2006; McGuire et al. 2014; Phillips et al. 2017)

Hypotheses can be grouped as either (A) adaptive (fitness benefit for the female) or (B) neutral or null (no benefit for the female) explanations. Non-adaptive hypotheses (explanations for maintenance of a character despite reducing fitness; see Forstmeier et al. 2014) are not listed as these have not been considered for reptiles and amphibians. 'Indicators' are variables within a clutch or litter of offspring predicted to covary with polyandry. Examples are from reptile or amphibian studies used in this review, with three letter codes indicating taxonomic groups (ANU Anura (frogs and toads), CAU Caudata (newts and salamanders), CRO Crocodylia (crocodiles and alligators), LIZ Lacertilia (lizards, skinks, geckos, iguanas and dragons), SER Serpentes (snakes), TUR Testudines (turtles and tortoises))

¹ Ultimately, these genetic or indirect benefits should result in an increase in the number of offspring produced by the female

² Usually considered a null hypothesis, but sometimes argued as a benefit to females because it mitigates the costs of resistance (e.g. Boulton et al. 2018)

Table 3 Estimates of heterogeneity for the full dataset, datasets excluding the influential outlier and taxonomic subsets of the data

Dataset	Number of cases <i>K</i>	Estimated heterogeneity		Proportion of heterogeneity due to a variation among cases <i>I</i> ² (%)	Test for heterogeneity		
		<i>T</i> ²	<i>SE</i>		<i>Q</i>	<i>df</i>	<i>P</i>
Full	36	0.158	0.055	78.7	304.56	35	<0.001*
Full excluding the outlying influential case	35	0.043	0.024	46.9	59.65	34	0.004*
Caudata	5	0.002	0.061	2.5	3.82	4	0.431
Crocodylia	4	0.063	0.089	61.8	7.01	3	0.072
Lacertilia	5	0.504	0.379	95.5	145.56	4	<0.001*
Lacertilia excluding the outlying influential case	4	0.115	0.124	77.1	13.09	3	0.005*
Serpentes	8	0.000	0.044	0	8.42	7	0.297
Testudines	14	0.000	0.012	0	13.46	13	0.413

* $p < 0.05$, a significant result of the test for heterogeneity

tigrinum (Gopurenko et al. 2006), *Salamandrina perspicillata* (Rovelli et al. 2015) and *Plethodon cinereus* (Liebgold et al. 2006) were also positive in value, though not significant (Fig. 2).

For *Serpentes*, the effect size for one population of *Thamnophis sirtalis* was significant (McCracken et al. 1999), but those of the other population (Garner et al. 2002) and for other species (Barry et al. 1992; Garner and Larsen 2005; Madsen et al. 2005; Ursenbacher et al. 2009; Clark et al. 2014; Levine et al. 2015) were not (Fig. 2). However, two singly sired litters in the *T. sirtalis* case only had four offspring each (McCracken et al. 1999), so this may be an artefact of having few offspring to test in paternity analysis.

The summary effect size for three species of *Crocodylia* (McVay et al. 2008; Lance et al. 2009; Lafferriere et al. 2016; Zajdel et al. 2019) was non-significant, lacked heterogeneity and showed a negative trend (Fig. 2; Table 3).

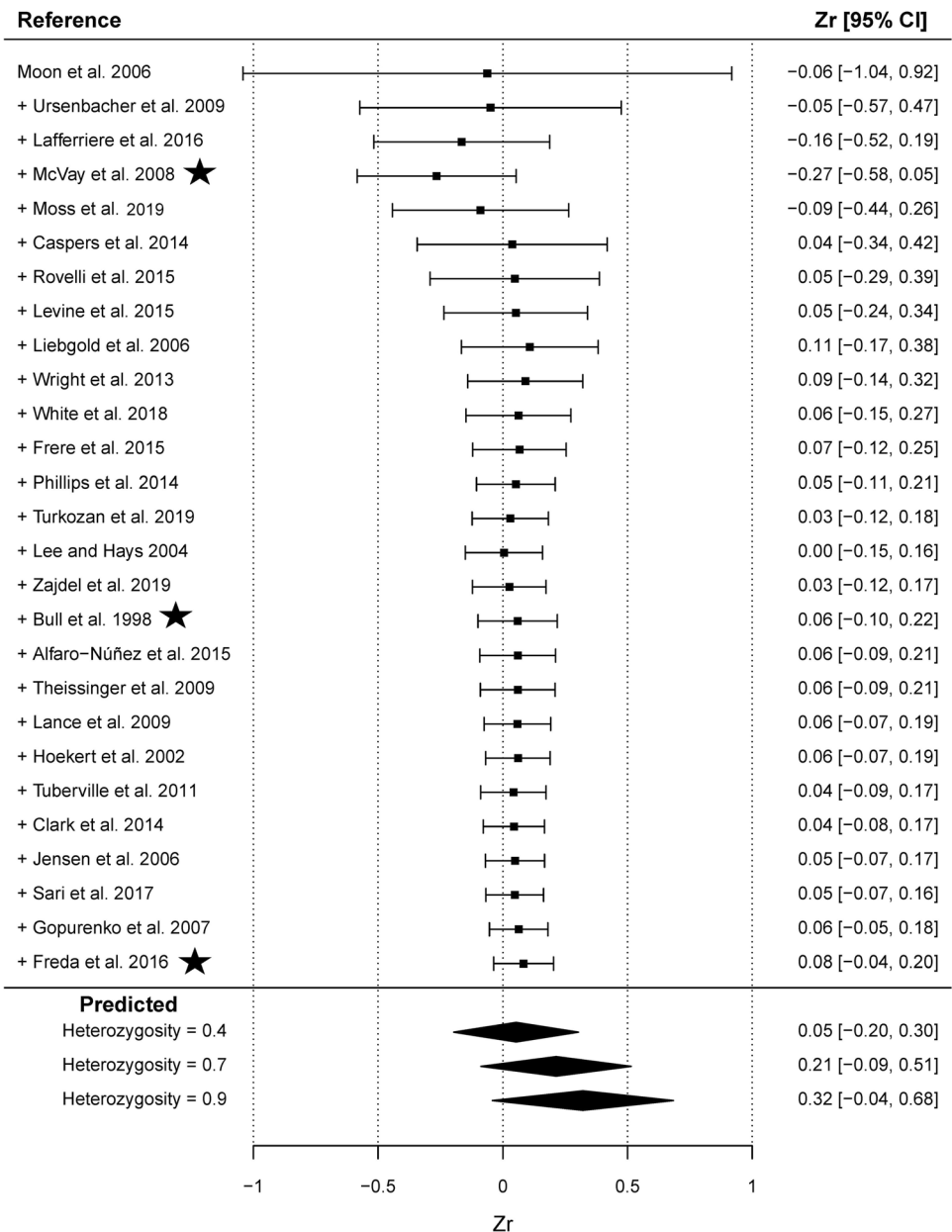
Subgroup meta-analysis of *Testudines* included *Gopherus polyphemus* (Testudinidae) (Moon et al. 2006; Tuberville et al. 2011; White et al. 2018), *Podocnemis sextuberculata* (Podocnemididae) (Freda et al. 2016) and species of Cheloniidae: *Chelonia mydas* (Lee and Hays 2004; Wright et al. 2013; Alfaro-Núñez et al. 2015; Turkozan et al. 2019), *Eretmochelys imbricata* (Phillips et al. 2014), *Caretta caretta* (Sari et al. 2017), *Natator depressus* (Theissinger et al. 2009) and *Lepidochelys olivacea* (Hoekert et al. 2002; Jensen et al. 2006). This resulted in a non-significant summary effect size (Fig. 2) with individual effect sizes not significant except for *P. sextuberculata* (Fig. 2). Given the lack of significant heterogeneity (Table 3), we did not partition *Testudines* any further for meta-analysis.

Testing for moderators of the effect size data

In fitting a model with all candidate moderators, we obtained a non-significant result for the omnibus test of moderators and significant residual heterogeneity (see SI1, Table S3). Some candidate moderators were significantly correlated (SI1, Fig. S8). In testing candidate moderators individually (SI1, Table S3B), we found that the model including latitude had the best fit to the data for models based on 35 cases (SI1, white box in Table S3B), but latitude proved not to be a significant moderator of effect size data. Among models with fewer cases (fewer because of missing data), only average expected heterozygosity was found to be a significant moderator ($t = 2.213$, $p = 0.037$, $K = 27$; see SI1, Table S3B). The model with average expected heterozygosity also had the best fit to the data for models that could be compared (see SI1: comparison of AIC_C values in a light grey box in Table S3B). A cumulative meta-analysis show how predicted summary effect sizes increases with increasing average expected heterozygosity (Fig. 3).

We next fitted models including average expected heterozygosity and other candidate moderators (SI1, Table S3C), excluding those that were significantly correlated with average expected heterozygosity (i.e. observed heterozygosity, the number of loci sampled and the average number of alleles per locus; see SI1, Fig. S8). However, fitting models with two candidate moderators did not result in discernibly better models: omnibus results were non-significant, and residual heterogeneity remained significant (SI1, Table S3C). Differences between models with one, two or three moderators were non-significant (SI1, Table S4). We ceased further model fitting.

Fig.3 Forest plot of a cumulative meta-analysis for relationships between the number of offspring and the number of sires, cumulated according to the average expected heterozygosity estimated for the population. Points are cumulative effect sizes (Zr) with 95% confidence intervals (CI) and labelled with the reference of the study (see Fig. 2 for species names). The data for each study is cumulated progressing from top to bottom (each addition symbolized with ‘+’). The plot excludes cases that lack data for average expected heterozygosity. Diamond polygons at the bottom show summary effect sizes including the 95% confidence interval that are predicted for various values of average expected heterozygosity (minimum, mean and maximum of the dataset), for a mixed-effects model fitted with average expected heterozygosity specified as the moderator. This model also controlled for time-lag bias and small study effect and included random factors. The predicted effect size based on the mean value of average expected heterozygosity is also displayed as a white polygon in Fig. 2. Stars mark cases that, when left out of the dataset, result in non-significant results in tests of average expected heterozygosity as a moderator



Curiously, the average expected heterozygosity was not a significant moderator for the reduced dataset of 26 cases (S11, Table S3B). A sensitivity test (models were fitted repeatedly, leaving out a different case each time) revealed three cases that, when each was excluded, resulted in non-significant tests (the cases are marked by stars in Fig. 3). Furthermore, differences between models with or without average expected heterozygosity as a moderator were not significant (S11, Table S4). These tests highlighted the tenuous nature of average expected heterozygosity as moderating the effect size data.

Discussion

Our tests showed that Caudata females had significantly more offspring with increasing numbers of sires (Fig. 2), whereas there was no evidence for this relationship among reptiles. Summary effect sizes for Testudines and Serpentes were non-significant (Fig. 2), with little heterogeneity among cases (Table 3). This was also true for a smaller number of Crocodylia cases, but effect sizes tended towards negative values (Fig. 2), which implied that multiple paternity may incur costs for Crocodylia (e.g. Zajdel et al. 2019). Results

for Lacertilia were less clear because significant heterogeneity could not be resolved, but individual effect sizes for species and populations were mostly non-significant (Fig. 2). Lacertilia is the largest group of living reptiles, and families are diverse with different morphologies, habitats, reproductive modes (e.g. egg-laying or live bearing), mating systems (monogamy, polygyny, polyandry and polygynandry; see Table 1) and behaviours (e.g. social bonds, community living, territoriality, male dominance hierarchies and male combat). Many are capable of sperm storage, and male competition for females can be intense (Wapstra and Olsson 2014). There are over twenty-five families of Lacertilia, yet studies of polyandry have only been reported for nine (Fig. 1E). Taxonomically limited and biased studies meant patchy coverage of Lacertilia in our meta-analysis, which probably exacerbated the problem with heterogeneity. Overall, we concluded that most female reptiles that produced offspring with different sires did not have more offspring than monogamous females. For cases where polyandrous females did have significantly more offspring, authors offered alternative explanations, proposed other benefits to females or discovered confounding factors such as maternal condition, age or attractiveness (e.g. Table 2).

Among amphibians, Anura are mostly external fertilisers, which allows simultaneous polyandry to result from multiple amplexus (Table 1) (e.g. Sztatecsny et al. 2006) or from the presence of free swimming sperm from multiple males (e.g. Hase and Shimada 2014). However, we found relatively low PA, with some populations exhibiting little or no evidence of polyandry (Fig. 1A). There was a lack of data on whether or not female Anura produced more offspring from polyandrous matings. Counting the number of offspring to estimate female reproductive output for some species is not straightforward since females may produce hundreds to thousands of eggs in a single deposition. Anura capable of sequential polyandry may insure against nest failure by partitioning eggs among multiple males (Byrne and Keogh 2009), but aside from this, there has been little other evidence that female Anura could benefit from polyandry (Roberts and Byrne 2011; Table 2).

Thus, among amphibians, we only have evidence of female salamanders having increased reproductive success with polyandry (Fig. 2). Many Caudata use spermatophore transfer (Table 1) to internally fertilise eggs, which accords females greater control over sperm acquisition than other amphibians and reptiles, since they can choose to reject or pick up spermatophores. Polyandry for some species is further facilitated by sperm storage (e.g. Adams et al. 2005) or explosive breeding (Table 1) (e.g. Myers and Zamudio 2004). Interestingly, female Caudata also had relatively high levels of polyandry (highest median PA among amphibians and reptiles; Fig. 1). Even socially monogamous species of Caudata were found to be predominantly genetically

polyandrous (Liebgold et al. 2006). Female Caudata having virtually complete pre-copulatory choice have little need for post-copulatory choice (Jones et al. 2002; Rafinski and Osikowski 2002; Gopurenko et al. 2006). There is evidence that female choice may be contingent on relatedness—with preferred mates being genetically similar (Caspers et al. 2014) or dissimilar from themselves (Rovelli et al. 2015). For some species, females may require multiple insemination events because eggs are produced over extended periods (Osikowski and Rafiński 2001). Thus, having the pre-copulatory choice to be polyandrous seems a key to enhancing female reproductive success for Caudata. Experimental studies suggest the females of some species ensured fertilisation by mating with the first encountered male, but thereafter choose higher-quality (Gabor and Halliday 1997) or more genetically compatible mates (Garner and Schmidt 2003). Furthermore, mate choice may be condition- (Bos et al. 2009) or context-dependent (Chandler and Zamudio 2008), which may explain contrasting patterns found for some populations (e.g. Caspers et al. 2014 versus Rovelli et al. 2015).

Our study tested one indicator of a benefit for females (reproductive output), but there may be other benefits for female reptiles and amphibians (Table 2). Polyandry facilitated by sperm storage extends the potential for female choice when mating opportunities or choice of mates is limited or unpredictable. Stored sperm can be used in the same season (e.g. Fitzsimmons 1998; Roques et al. 2004, 2006), between years (e.g. Pearse et al. 2002; Roques et al. 2006; Anthonysamy et al. 2014; McGuire et al. 2014; Phillips et al. 2014; Riley et al. 2021) or over decades in some species (Whitaker 2006; Murphy et al. 2007). Female Caudata may have little need for post-copulatory choice, but for other species of amphibians and reptiles, cryptic choice enables the female to diversify offspring characteristics and/or to select optimal genotypes/phenotypes for offspring (e.g. Calsbeek and Bonneaud 2008). For social reptiles, inbreeding avoidance could be achieved through polyandry (While et al. 2014), which may be important for socially monogamous species with limited choice of mates beyond close kin.

One certain outcome of polyandry is that the diversity of paternal alleles will be greater for groups of offspring with multiple sires compared with groups of offspring with only one sire (e.g. Calsbeek et al. 2007; Bouchard et al. 2018; Moss et al. 2019): some argue that the augmented genetic diversity of offspring per se benefits females. For example, greater diversity could boost the chances of offspring surviving variable or unpredictable environments and reduce sibling competition (Calsbeek et al. 2007; Eales et al. 2010; Bouchard et al. 2018). Offspring viability may be improved with increased offspring heterozygosity or genetic diversity (examples in Table 2), potentially because of better male–female

genetic compatibility (Madsen et al. 2005). These are intriguing examples, but definitive genetic benefits have been difficult to detect (e.g. Noble et al. 2013; also see reviews listed in SI1, Table S1). Perhaps a more general route for genetic benefits is through “heterozygosity-fitness-correlations” (HFCs), in which genome-wide multilocus heterozygosity is interpreted as a proxy for the degree of inbreeding and, thereby, the potential for inbreeding depression (Chapman et al. 2009). From a female’s perspective under an HFC scenario, multiple sires for her offspring increase mean heterozygosity and reduce risks of loss of viability, survival or fecundity to inbreeding depression. We did detect average expected heterozygosity of the population as a moderator of the effect size data (Fig. 3). The calculation of expected heterozygosity is based on the relative frequencies of alleles at loci surveyed for unrelated adults in a population. Therefore, an increase in expected heterozygosity may simply be a by-product of relatively more individuals (males) mating in the system (Rafajlović et al. 2013), even though the HFC model would argue that this would have fitness benefits. However, because our evidence proved tenuous (leaving out one of three cases led to non-significant results), it remains for future work to re-examine links between heterozygosity, polyandry and reproductive success when more cases become available.

Problems, solutions and future research directions

Paternity analysis will continue to be an invaluable tool underpinning studies on the behaviour, ecology, evolution and conservation of amphibians and reptiles (Lee 2008; Flanagan and Jones 2019). For example, paternity data helps identify the genetic mating system (Gardner et al. 2002; Chapple and Keogh 2005; Clark et al. 2014), and comparisons between different seasons or populations reveal variation in mate encounter rate and mating opportunity for the different sexes (Lodé et al. 2005; Olsson et al. 2011; Lasala et al. 2013, 2018; Lee et al. 2018), while temporal changes potentially track population decline or recovery (Figgenger et al. 2016). Paternal alleles determined from offspring provide genetic data about breeding males, which, for some species, cannot be easily obtained in any other way (Madsen et al. 2005; Lee et al. 2007). The current study has additionally demonstrated the value of obtaining data on polyandry across a broad diversity of populations and species. However, in terms of understanding global and trans-taxa patterns of polyandry, there remains outstanding problems with current methods of study and particularly, with sampling.

Sampling across all levels, from within-study, to across geographical locations and within and among taxa, was a critical issue. Sampling was extremely limited in some studies: 18% of cases in our dataset had sample sizes fewer

than five. Furthermore, estimates of polyandry for many species were based on a single case. There are still gaps in our knowledge of female reproductive strategies for many amphibian and reptile species, and limited data for many taxonomic groups. For example, Caudata could offer original, powerful, under-tested models for advancing understanding of polyandry, and some species are already used in experiments on sexual selection, sperm competition and mate choice (e.g. Jones et al. 2004; Chandler and Zamudio 2008; Bos et al. 2009). However, we had few cases for Caudata (ten in Fig. 1 and five in Fig. 2). Some of the other taxonomic groups were even more poorly represented—only by a single case (numbered black points in Fig. 1). The geographical distribution of cases was biased towards temperate and the northern hemisphere, and studies of species from larger groups, such as Lacertilia, Serpentes and Anura, concentrated on certain families (Scincidae, Natricidae and Ranidae, respectively), perhaps reflecting interests of researchers rather than species distribution. Improved coverage within and among species will lead to estimates that are more accurate, and accumulation of data for many more populations and species will facilitate hypothesis testing (e.g. Zbinden et al. 2007; Lee et al. 2018).

Heterogeneity in the effect size data across studies was a significant problem. We attempted to include available data from any species of amphibian or reptile in one meta-analysis, but could not resolve the heterogeneity, even by controlling for random factors and candidate moderators. However, most subgroup meta-analyses did not suffer from significant heterogeneity. We recommend that future meta-analyses may be more appropriately conducted at lower taxonomic levels, such as at the family or subfamily level.

Another problem was the lack of information in some studies. For example, out of 154 studies, we only had 36 cases suitable for meta-analysis. Clearly, future meta-analyses would be facilitated if studies reported further data. Aside from measures of reproductive output, we suggest reporting on maternal and offspring characteristics. Most studies reporting the number of offspring provided no further information (e.g. viability, fledging/survival success, sizes, development, relative performance, fecundity). A few reported maternal condition, but we could not test this variable because we lacked the data for most cases. Limited data restricts the scope for meta-analyses and constrains the opportunities for comparing species with contrasting life histories.

We examined the link between polyandry and female reproductive success, but questions that were beyond this study were whether polyandry or female benefits varied according to the method of reproduction (i.e. egg-laying versus live-birth), sexual dimorphism, lifetime reproductive potential or environmental conditions. How these factors may affect polyandry for amphibians and reptiles remains

avenues for future research. To progress our understanding of polyandry, other reviews of mating systems have advocated integration of observational and experimental approaches, and a more holistic view of the entire reproductive process to include consideration of multiple drivers, both male- and female-based, that may vary within and between species (Uller and Olsson 2008; Wapstra and Olsson 2014; Lyons et al. 2021). We would extend on these suggestions to propose meta-analysis as a powerful tool in consolidating information on polyandry across studies, populations and species. We further urge researchers to take a broader taxonomic view and to continue studying polyandry within and among taxa. Recording and reporting more widely to expand the baseline data will undoubtedly improve future attempts at meta-analysis and support experimental and comparative studies. Establishing a taxonomically well-sampled framework will enhance the utility of amphibians and reptiles as model systems and stimulate growth in the evolutionary and ecological study of male and female reproductive strategies.

Supplementary information

SI1 Additional detail further to those presented in the main text and R scripts.

SI2 Data and data references. Includes: all cases of multiple paternity and associated references; references for excluded studies, and reasons for exclusion; data used in meta-analyses.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03194-6>.

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Data availability Data and R scripts used in analyses are available as Supplementary Information.

Declarations

Competing interests The authors declare no competing interests.

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