JOURNAL OF **Evolutionary Biology** .«eseb

RESEARCH ARTICLE

Multiple paternity is related to adult sex ratio and sex determination system in reptiles

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Abstract

The adult sex ratio (ASR, the proportion of males in the adult population) is an emerging predictor of reproductive behaviour, and recent studies in birds and humans suggest it is a major driver of social mating systems and parental care. ASR may also influence genetic mating systems. For instance male-skewed ASRs are expected to increase the frequency of multiple paternity (defined here as a clutch or litter sired by two or more males) due to higher rates of coercive copulations by males, and/or due to females exploiting the opportunity of copulation with multiple males to increase genetic diversity of their offspring. Here, we evaluate this hypothesis in reptiles that often exhibit high frequency of multiple paternity although its ecological and life-history predictors have remained controversial. Using a comprehensive dataset of 81 species representing all four non-avian reptile orders, we show that increased frequency of multiple paternity is predicted by more male-skewed ASR, and this relationship is robust to simultaneous effects of several life-history predictors. Additionally, we show that the frequency of multiple paternity varies with the sex determination system: species with female heterogamety (ZZ/ZW sex chromosomes) exhibit higher levels of multiple paternity than species with male heterogamety (XY/ XX) or temperature-dependent sex determination. Thus, our across-species comparative study provides the first evidence that genetic mating system depends on ASR in reptiles. We call for further investigations to uncover the complex evolutionary associations between mating systems, sex determination systems and ASR.

KEYWORDS
extra-pair paternity, genetic mating system, multiple mating, phylogenetic comparative analysis, sex chromosome, social behaviour

1 | INTRODUCTION

Social environment is an important determinant of reproductive investment of animals (Clutton-Brock, 2021; Gonzalez-Voyer et al., 2022). Variation in the social environment influences the evolution of several reproductive traits, including the investments into gamete production, mating competition and parental behaviour (Clutton-Brock, 2021; Emlen & Oring, 1977; Fitzpatrick & Lüpold, 2014; Royle et al., 2013). In sexually reproducing organisms, an important aspect of social environment is the adult sex ratio (ASR, the proportion of males in the adult population) because it determines both the number of same-sex competitors for mating and

the availability of mates (Schacht et al., 2017; Székely et al., 2014). Consistently with theoretical expectations, recent studies identified ASR as a major predictor of various reproductive traits, including fertilization success, social mating systems, mate desertion and parental care in a wide range of animals, including humans (Hesketh & Xing, 2006; Liker et al., 2013, 2014; Schacht et al., 2017; Székely et al., 2014; Vahl et al., 2013). In birds, for example, high frequency of social polygyny and predominant (or exclusive) female care typically occur in species that have female-skewed ASRs (Gonzalez-Voyer et al., 2022; Liker et al., 2013, 2014).

Multiple mating by females with different males is a major component of mating system variation, which can result in multiple paternity, when offspring originating from a single reproductive event (i.e., in a clutch or litter) are sired by two or more fathers. Multiple paternity is common in nature as it has been shown in all major animal taxa including insects, molluscs, fishes, amphibians, birds and mammals (Brouwer & Griffith, 2019; Lee et al., 2018; Petrie & Kempenaers, 1998; Simmons, 2002; Taylor et al., 2014; Uller & Olsson, 2008). Mating with multiple males by females and the resulting multiple paternity plays an important role in the evolution of various reproductive and sexually selected traits, because it may affect both male and female fitness (Jennions & Petrie, 2000; Taylor et al., 2014), and the selection for traits used in pre- and post-copulatory mate choice (Kokko & Jennions, 2008) and parental care (Queller, 1997).

Previous studies highlighted that the social environment can be a key driver of the evolution of multiple paternity, although most studies considered only the effects of breeding synchrony and density (reviewed for example by Westneat & Stewart, 2003; Maldonado-Chaparro et al., 2018). Consequently, although ASR is expected to affect multiple paternity, their relationship has remained poorly explored. Two hypotheses have been proposed for why skewed ASRs may influence the frequency of multiple paternity. First, multiple paternity can be a consequence of male harassment and forced copulations (Westneat & Stewart, 2003). Therefore, its frequency may increase when ASR is skewed toward males, because more males can force copulations more often (Johnson et al., 2021; Le Galliard et al., 2005). Second, multiple paternity may emerge via female-initiated copulations and female choice if females can gain fitness benefits by mating with multiple males (Jennions & Petrie, 2000; Maldonado-Chaparro et al., 2018; Westneat & Stewart, 2003). Both theoretical models and experiments show that male-skewed ASRs may facilitate multiple mating by females because (1) females can find mates more easily (due to higher encounter rate) resulting in higher mating rate than in populations with even (or female-skewed) ASRs, and (2) higher variation in male quality may increase the chance that an already mated female finds an optimal/better partner after her first mating (Jirotkul, 1999, Bleu, Bessa-Gomes & Laloi 2012; Vahl et al., 2013).

While theoretical arguments posit ASR for a key role in driving multiple paternity, evidence from empirical studies is mixed. Females were found to be more frequently polyandrous in male-skewed populations in two species of Darwin's finches (Grant & Grant, 2019).

However, studies of the viviparous lizard (*Zootoca vivipara*) yielded inconsistent results, as multiple paternity was either unrelated to sex ratio or the relationship varied with the age of females (Dreiss et al., 2010; Fitze et al., 2005). The only across-species comparative study we are aware of found that the frequency of multiple paternity was higher in species with male-skewed ASR across bird species (Liker et al., 2014).

Motivated by both the theoretical expectations and the paucity of studies and the inconsistencies between their results, we investigated the relationship between multiple paternity and ASR in a phylogenetic comparative study across reptiles. Reptiles are well-suited for this work because they exhibit large variation across species in both ASR (Bókony et al., 2019) and the frequency of multiple paternity, including species with up to 100% multiple paternity (Uller & Olsson, 2008). Most reptiles do not have social pair bonds between males and females, and multiple paternity can arise when females mate with more than one male before producing a clutch or litter. This is facilitated by sperm storage, which is widespread and can last for long periods, even spanning multiple reproductive cycles (Uller & Olsson, 2008). Furthermore, male harassment, which is common in some reptile taxa, may also result in multiple paternity (Fitze et al., 2005; Le Galliard et al., 2005).

In this study, we tested whether the frequency of multiple paternity is related to ASR. Based on the above considerations, we expected higher frequency of multiple paternity with more male-skewed ASR. Furthermore, we tested the robustness of this relationship by taking into account the potential effects of the following life-history and ecological predictors of multiple paternity. (1) Clutch size varies widely in reptiles and previous studies reported more frequent multiple paternity in species with large clutches both at the intra- and interspecific levels. This may be because larger number of eggs can be fertilized more easily with sperm from more males (Uller & Olsson, 2008). (2) Body size is often tied to life-history traits such as longevity and age at maturation (Angilletta et al., 2004; Lislevand et al., 2007), some of which can influence multiple mating. For example, longer-living species may store sperm from more males or for longer period, which may increase the frequency of multiple paternity in their clutches (Uller & Olsson, 2008). (3) Sexual size dimorphism is often related to reproductive traits like fecundity and mating competition (Shine, 1994), and thus may be an important factor in both forced copulations and female choice. (4) Reproductive mode of reptiles can be oviparity where eggs are laid, viviparity when the embryos develop in their mother's body and get born as juveniles, and ovoviviparity when eggs form inside females but hatch before birth and juveniles are born. These reproductive modes can be associated with social structures like grouping or solitary living, which may affect the frequency of multiple paternity (Halliwell et al., 2017; While et al., 2009). (5) Geographic latitude influences environmental characteristics which then shape relevant aspects of the social environment like population density (Kiester, 1991; Uller & Olsson, 2008). Accordingly, some studies demonstrated that the frequency of multiple paternity varies between geographic regions (Taylor et al., 2014; Valcu et al., 2021). (6) The type of sex

determination system (i.e., temperature-dependent, or genetic with XX/XY or ZZ/ZW sex chromosome systems) has been linked to ASR (Pipoly et al., 2015) as well as to other major life-history traits such as longevity (Sabath et al., 2016), age of maturation (Bókony et al., 2019), and sexual size dimorphism (Katona et al., 2021). (7) Finally, major taxa of reptiles differ strongly in ecology and reproductive biology which may influence the frequency of multiple paternity and its relationship with ASR (Uller & Olsson, 2008). In the present study, first we tested the relationships of multiple paternity with ASR and with each of the above species-characteristics in bivariate analyses to maximize sample size and thus statistical power. Then, we used a multi-predictor approach to test whether the frequency of multiple paternity is predicted by ASR when the effects of other, potentially confounding predictors are statistically controlled for.

2 | MATERIALS AND METHODS

2.1 | Frequency of multiple paternity

We used published data to conduct across-species comparative analyses. We searched the literature published until 2019 for paternity studies in reptiles using Web of Science and Google Scholar, with the combination of keywords 'multiple paternity' AND 'reptile' or, alternatively, 'multiple paternity' and the scientific name of species for which we already had ASR data. We included data from studies which investigated multiple paternity in wild populations using molecular genetic techniques (i.e., DNA fingerprinting, microsatellite analysis). In these studies, samples for genetic analyses were collected from newly hatched or newly born offspring either in the field ($N=18$ species including 3 viviparous ones) or in laboratory ($N=63$ species including 22 viviparous ones; henceforth we refer to both hatchlings and newborns as "hatchlings"). In the case of laboratory studies, field-collected gravid females or eggs were kept in captivity and incubated in terraria until egg laying, birthing or hatching (Jones & Ardren, 2003; Zajdel et al., 2019).

We calculated the frequency of multiple paternity as the proportion of clutches or litters with more than one sire, that is, number of clutches/litters having two or more genetic fathers divided by total number of clutches/litters examined in the population (henceforth we refer to both clutches of oviparous species and litters of viviparous species as "clutches"). We only included studies where paternity was tested in at least 5 clutches per population. We found paternity data for 81 species, representing all four reptile orders (*Squamata*: 46 species; *Testudines*: 24 species; *Crocodylia*: 10 species; *Rhynchocephalia*: 1 species). The proportion of clutches that had multiple paternity varied widely between species, ranging from 0 to 1 (Figure S1A). Whenever we found paternity data for more than one population of the same species we used the unweighted average value in the analyses. To verify this approach, we checked the within-species (among-population) repeatability of the multiple paternity estimates using a mixed-effect model (as implemented in

the *rptR* R package; Nakagawa & Holger, 2020), in which multiple paternity for each population was the response, and species were the random effect.

2.2 | Adult sex ratio

The majority of ASR data were taken from two earlier comparative studies (Bókony et al., 2019; Pipoly et al., 2015). We also searched the published literature for additional ASR data for those species for which we had information on multiple paternity. We collected ASR estimates that were representative for the population composition and thus provided reliable sex ratio data, similarly to other studies (Ancona et al., 2017; Bókony et al., 2019; Pipoly et al., 2015). Thus, we used ASR information from studies that investigated population demography by either mark-recapture methods or total population counts to determine the number of males and females. We accepted only those studies which (1) used sexually mature individuals to calculate sex ratio, (2) used a reliable sex identification method, (3) sampling was not sex-selective and (4) individuals were uniquely identified to ensure every individual was counted only once. If the authors indicated possible bias in the methods or results, we rejected the study. We were able to find ASR estimates for 60 species for which we also have paternity information (Figure S1B). Data for ASR often were not available from the populations used in the paternity studies, so we used ASR estimates from other populations of the same species. Whenever we found ASR estimates from more than one population of the same species, we averaged these for each species and used the unweighted average ASR in the analyses. According to Bókony et al. (2019), ASR estimates of reptiles has a moderately high repeatability for species with genetic sex determination (intraclass correlation coefficient $\pm$ SE $= 0.55 \pm 0.10$, $p < 0.001$, $N=146$ populations of 93 species), and lower but significant repeatability for species with temperature-dependent sex determination (0.14 ± 0.06, $p = 0.002$, $N=334$ populations of 72 species). The latter reflects the high within-species variances of sex ratios in reptiles with temperature-dependent sex determination (Bókony et al., 2019), which is likely a biological phenomenon rather than a sign of reduced data quality.

2.3 | Other predictor variables

To represent body size, we collected data on snout-vent length (distance from tip of snout to cloaca, in meters) for *Squamata*, *Crocodylia* and *Rhynchocephalia* ($N=57$ species), and carapace length (measured between nuchal notch and posterior marginal tip, in meters) for Testudines ($N=24$ species) from primary sources and compilations (e.g., Regis & Meik, 2017; Shine, 1994). We preferred to collect sex-specific body size estimates separately for males and females, and used average size values of unsexed individuals only when sex-specific data were not available. Where we had the sex-specific information, we averaged the male and female data to calculate mean

body size for each species. Thus, we had mean body size data for all 81 species. Using the sex-specific length data, we also calculated sexual size dimorphism (SSD) using the formula log_{10}(male length/female length), which is an appropriate proxy for measuring SSD (Liker et al., 2021; Smith, 1999). The positive values of this SSD index mean that males are larger than females, whereas the negative values indicate that females are larger than males. We found sex-specific body size and thus SSD data for 74 species. Our earlier study using a partially overlapping set of reptile species showed that SSD has a high repeatability between populations (Katona et al., 2021).

We collected information on mean clutch size of wild populations for all 81 species from review papers and published databases (Iverson et al., 1993; Scharf et al., 2015; Thorbjarnarson, 1996). Since most information for clutch size were obtained from species-level databases, we could not test its between-population repeatability. However, the variation of clutch size among species in our data set is much higher (range: 2–123 eggs) than the typical variation within species (e.g., 4.3–9.8 in the most widely-ranging terrestrial reptile included in this study, the viviparous lizard; Roitberg et al., 2013). Thus it is unlikely that any imprecisions in our estimate of mean clutch size would mask existing relationships.

We recorded the latitudinal coordinates of the study populations where the paternity studies were conducted as absolute distance from the Equator in degrees. For populations where the authors did not report the coordinates, we estimated the latitude using Google Earth by searching for the name of the reported study sites. We averaged the latitude values where we had paternity information from more than one population. We had information on absolute latitude from all 81 species. Our dataset contained 19 species from tropical region and 62 species from temperate climate region.

To categorize the sex determination system of the species we used the Tree of Sex database (Ashman et al., 2014), and we updated that information with more recently published data where it was available. We separated the species into three categories: genetic sex determination with XY/XX male-heterogametic sex chromosome system (XY species henceforward, $N=12$), or with ZZ/ZW female-heterogametic sex chromosome system (ZW species henceforward, $N=19$ species), or temperature-dependent sex determination, where offspring sex is determined by the incubation temperature of eggs ($N=39$ species). For species where the sex determination system is unknown but all studied species in their taxonomic genus or family have the same sex determination system, we categorized the species based on the sex determination system of their genus or family ($N=11$ species). We only used genus/family level information when we had information on sex determination system for at least two species in the taxon. We did not categorize the snow skink (*Carinascincus ocellatus*) and the water skink (*Eulamprus heatwolei*) into any sex determination groups because those species have a mixed system with sex chromosomes as well as temperature-dependent sex reversal (Cornejo-Páramo et al., 2020; Hill et al., 2021). No other species with known mixed sex determination system was included in our dataset. We divided species into two groups according to their mode of reproduction: oviparous

($N=56$ species) or viviparous ($N=25$ species, including 3 ovoviviparous species), based on the information available from the Reptile Database (Uetz et al., 2020). To compare multiple paternity between major clades of reptiles, we categorized all species into 4 taxonomic groups according to the four reptile orders following the Reptile Database (*Crocodylia*, *Testudines*, *Squamata* and *Rhynchocephalia*; Uetz et al., 2020).

2.4 | Statistical analyses

We tested the relationships between the proportion of multiple paternity and the predictor variables using Phylogenetic Generalized Least Squares (PGLS; Pagel, 1998). We built the PGLS models using the *gls* function of the *nlme* package (Pinheiro et al., 2021) of the R 4.1.1 statistical software (R Core Team, 2020). To control for phylogenetic relatedness among the species in the analyses, a composite phylogenetic tree (Figure S2) was created based on current phylogenetic information (Guillon et al., 2012; Oaks, 2011; Pyron et al., 2013; Sarre et al., 2011; Thorn et al., 2019). Since composite phylogenies do not have true branch lengths, we used Nee's method to generate branch lengths using the Mesquite software (Maddison & Maddison, 2019). Freckleton et al. (2002) showed that PGLS is relatively insensitive to branch length assumptions, and we got qualitatively the same results using other branch length assumptions (i.e., Pagel's or unit branch length methods; unpublished results). We used the *corPagel* function of the *ape* package to estimate the phylogenetic signal as Pagel's lambda (λ) for each model by the maximum-likelihood method (Freckleton et al., 2002; Pagel, 1999; Paradis & Schliep, 2019). We included sample size (i.e., total number of clutches tested for paternity of a species, combining all populations in the dataset) as a weight variable by setting estimation variance to the inverse of sample size (using the *weights* argument of the *gls* function), to control for the large variability in the estimation uncertainty of multiple paternity due to differences in sample size (Garamszegi, 2014).

First, we tested the relationships of the frequency of multiple paternity (response variable) with ASR and each of the seven other predictors in bivariate models (i.e., each model had a single predictor). We applied arcsine square-root transformation to the proportion of multiple paternity before the analyses to ensure the fit of model residuals to statistical requirements of the models. For categorical predictors with three or more levels (i.e., sex determination system and taxonomic group) we evaluated their overall effects in the models using type 2 analysis-of-deviance tables with *Anova* function of the *car* package (Fox & Weisberg, 2019). Then, we calculated pairwise post-hoc comparisons between either the three sex determination types (TSD, XY or ZW) or three taxonomic groups (*Crocodylia*, *Squamata*, *Testudines*) using the *emmeans* function of package *emmeans* (Lenth, 2018), adjusting p-values with the false discovery rate (FDR) method. Both of these latter functions (*Anova*, *emmeans*) use the PGLS models fitted to the data, and we applied them only to obtain estimates not provided in the summary output of PGLS. For the

model that included taxonomic group as a predictor, we excluded the order *Rhynchocephalia* which has a single species (*Sphenodon punctatus*). The conclusion of this latter analysis was not changed when we re-ran the model by including *S. punctatus* in *Squamata* (the sister group to *Rhynchocephalia*; result not shown). Sample sizes varied between 60 and 81 species in the bivariate analyses, depending on data availability for the predictor variables (Table 1).

Model fit was checked by inspection of diagnostic residual plots for all models. We also checked the sensitivity of PGLS models to the influence of outlier data points, which were identified visually from the plots. Whenever potentially influencing points were apparent, we repeated the models without these data points. Only models containing mean body size (two outliers) and clutch size (one outlier) were concerned in this sensitivity analysis, and the results of both models remained qualitatively unchanged after we excluded outliers from the analyses (Table S1). Therefore, in the main text, we only present the results from the models using all available data, including the outliers.

To infer the robustness of the relationship between multiple paternity and ASR to the potentially confounding effects of other predictors, we first tested whether the relationship between multiple paternity and ASR is different in species with different sex determination systems. For this purpose, we created a model which contained the ASR×sex determination system interaction term. We evaluated the interaction effect using a type 3 analysis-of-deviance table with *Anova* function of the *car* package. Second, we built a multi-predictor model which included only those predictor variables that were significant in the bivariate models. Sample size for this model was 51 species due to missing data for some variables. Variance inflation factor (VIF), a measure of multi-collinearity, was low in this multi-predictor model (between 1.01 and 1.89 for each predictor). We did not include all the predictors that we tested in the bivariate analyses into a single model, because in that case multi-collinearity would be unacceptably high (VIF up to 5.63), leading to inflated standard errors and unreliable p-values (Graham, 2003).

To further investigate the relative importance of ASR among the predictors of multiple paternity, we performed multi-model inference based on Akaike's information criterion (AIC) as the measure of model fit. In this analysis, we included all predictors, because the set of predictors that yields the best explanatory power can be correctly identified by model selection based on model fit statistics even when multi-collinearity is present (Burnham & Anderson, 2002). Therefore, we created a candidate model set using all possible combinations of all 8 predictors, resulting in 256 models (Table S2), and we compared the models based on their AICc values (AIC corrected for sample size) to identify the most supported models (Burnham & Anderson, 2002) using the *aictab* function of the *AICcmodavg* R package (Mazerolle, 2012). Because of missing data in some

TABLE 1 Multiple paternity (response variable, arcsine square-root transformed) in relation to adult sex ratio (expressed as proportion of males in the adult population) and other predictors in reptiles. The table shows the results of bivariate phylogenetic generalized least-squares (PGLS) models each containing a single predictor (eight separate models). Statistically significant *p*-values (*p* < 0.05) are highlighted in bold (see also Figures 1 and 2). Parameter estimates (*ß*) express the slope of the relationship for continuous predictors (i.e., adult sex ratio, clutch size, body size, sexual size dimorphism, latitude) and the difference between groups for categorical predictors (i.e., reproductive mode, sex determination system, taxonomic group). Pagel's *λ* indicates the strength of the phylogenetic signal, and *N* is the number of species.

Predictor variables	$ß \pm SE$	t	p	$λ$	N
Adult sex ratio	0.937 ± 0.279	3.354	**0.001**	0.528	60
Clutch size	-0.0002 ± 0.001	−0.254	0.801	0.337	81
Body size	0.016 ± 0.067	0.245	0.801	0.329	81
Sexual size dimorphism	0.072 ± 0.501	0.144	0.886	0.192	74
Reproductive mode (Oviparity—viviparity)	0.119 ± 0.073	1.625	0.108	0.321	81
Latitude	0.002 ± 0.002	0.794	0.429	0.292	81
Sex determination system[a]		18.288[A]	**<0.001**[B]	0.191	70
TSD—XY	0.045 ± 0.093	0.485	0.630		
TSD—ZW	-0.323 ± 0.081	−3.973	**0.001**		
XY—ZW	-0.368 ± 0.107	−3.453	**0.002**		
Taxonomic group[a]		6.450[A]	**0.040**[B]	0.323	80
Crocodylia—Squamata	-0.070 ± 0.172	−0.407	0.688		
Crocodylia—Testudines	0.142 ± 0.161	0.600	0.582		
Squamata—Testudines	0.212 ± 0.085	1.844	0.054		

Note: Asts between marginal means, with FDR-corrected

Abbreviations: TSD, temperature-dependent sex determination; XY and ZW, genetic sex determination with XY/XX or ZZ/ZW sex chromosome systems, respectively.

[a]For the overall effect of sex determination system and taxonomic group, A is the χ2 value and B is the p-value from a type 2 analysis of deviance. Pairwise comparisons between groups are shown as linear contrasts between marginal means, with FDR-corrected p-values.

predictors, sample size in this latter analysis was $N=47$ species for all candidate models.

3 | RESULTS

The repeatability analysis showed a moderate within-species repeatability of multiple paternity and suggested that a significant part of multiple paternity variation is interspecific (c$\pm$SE$=0.420\pm0.104$, $p<0.001$, $N=161$ populations of 81 species). The frequency of multiple paternity was associated with the adult sex ratio (Tables 1 and 2): the proportion of clutches with multiple paternity increased with male-skewed ASR (Figure 1). This relationship remained significant in a multi-predictor model that included potential confounds (Table 2) which were significant in the bivariate associations, i.e., sex determination system and taxonomic group. Moreover, AICc-based model selection that included all putative predictor variables supported two models with ΔAICc <2, both of which contained ASR as a predictor. The most supported model included ASR and sex determination system as predictors, whereas the second supported model included only ASR (Table S2).

Our analyses also revealed that the frequency of multiple paternity significantly differed between the three major types of sex determination systems (Table 1). Specifically, we found that reptiles with ZW sex determination had the highest frequency of multiple paternity, XY species had the lowest, whereas TSD species exhibited an intermediate level of multiple paternity (Figure 2). In bivariate analyses, ZW species differed significantly from both XY and TSD species, whereas TSD and XY species did not differ significantly from each other (Table 1, Figure 2). Sex determination and multiple paternity remained significantly associated in the multi-predictor model (Table 2), with the same direction of differences between species of different sex determination systems as in the
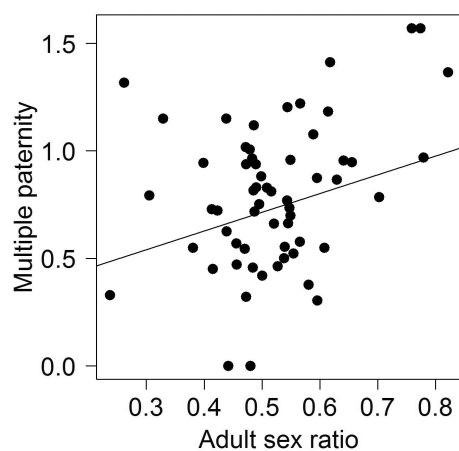
TABLE 2 Multiple paternity (response variable, arcsine square-root transformed) in relation to adult sex ratio (expressed as proportion of males in the adult population), sex determination system and taxonomic group in a multi-predictor phylogenetic generalized least-squares (PGLS) model. Results of type 2 analysis of deviance, and pairwise comparisons among groups of the categorical predictors are shown (the full model's Pagel's $\lambda=0.418$; $N=51$ species). Statistically significant ($p<0.05$) p-values are highlighted in bold.

Predictor variables	df	χ^2	p
Adult sex ratio	1	12.751	**<0.001**
Sex determination system	2	7.420	**0.024**
	$\beta\pm$SE	t	p
TSD−XY[1]	0.055 ± 0.144	0.385	0.702
TSD−ZW[1]	-0.241 ± 0.152	−1.588	0.183
XY−ZW[1]	-0.296 ± 0.110	−2.684	**0.032**
Taxonomic group	2	0.672	0.714
	$\beta\pm$SE	t	p
Crocodylia−Squamata[2]	0.071 ± 0.223	0.316	0.756
Crocodylia−Testudines[2]	0.128 ± 0.170	0.753	0.756
Squamata−Testudines[2]	0.057 ± 0.155	0.368	0.756

Note: Pairwise comparisons between groups are shown as linear contrasts between marginal means, with FDR-corrected p-values from this multi-predictor model where [1] ASR and sex determination system or [2] ASR and taxonomic group are controlled for.

Abbreviations: TSD, temperature-dependent sex determination; XY and ZW, genetic sex determination with XY/XX or ZZ/ZW sex chromosome systems, respectively.
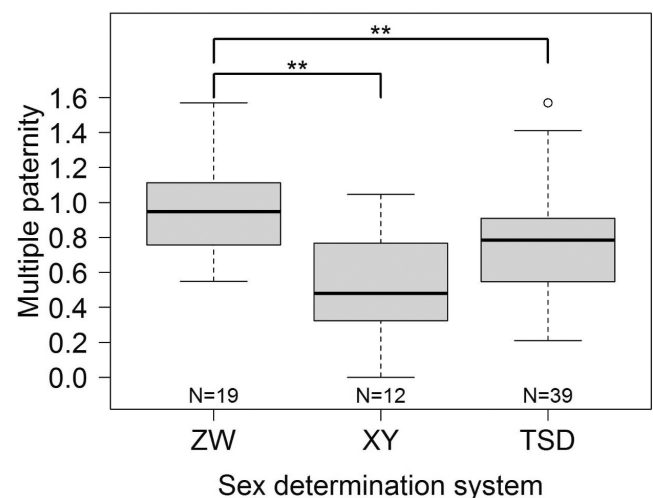

FIGURE 1 Multiple paternity (proportion of clutches having multiple paternity, arcsine-square root transformed) in relation to adult sex ratio (proportion of males in the adult population) in reptiles. Each dot represents one species, and the slope of the regression line was estimated by phylogenetic generalized least-squares model (see Table 1 for statistics, $N=60$ species).

FIGURE 2 Multiple paternity (proportion of clutches having multiple paternity, arcsine-square root transformed) of reptiles with different sex determination systems (TSD: temperature-dependent sex determination, XY and ZW: genetic sex determination with XY/XX or ZZ/ZW sex chromosome systems, respectively). The thick horizontal lines in the boxes are the medians, boxes show the interquartile ranges, and whiskers correspond to 1.5 times the interquartile range, based on species values. Number of species is given below the boxplot of each group. Asterisks indicate significant differences (**$0.001<p<0.01$). See Table 1 for details of statistics.

bivariate models. Note that sex determination system was also included in the model best supported by AICc-based model selection (Table S2). The relationship between multiple paternity and ASR did not differ across species with different sex determination systems, because the interaction between ASR and sex determination was not significant (type 3 ANOVA: $\chi^2 = 2.868$, $p = 0.238$, $N = 52$ species).

Although the major reptilian taxa exhibited different levels of multiple paternities (Table 1), this relationship was no longer significant in the multi-predictor model (Table 2), nor supported by the AICc-based model selection (Table S2). Body size, sexual size dimorphism, clutch size, latitude, and reproductive mode were not significantly associated with the frequency of multiple paternity in bivariate models (Table 1) and were not supported by AICc-based model selection (Table S2).

4 | DISCUSSION

Our study shows to our knowledge for the first time that multiple paternity increases with ASR across reptile species, consistent with studies on birds (Grant & Grant, 2019; Liker et al., 2014). We propose two mutually non-exclusive explanations for this association. First, females may find multiple mating partners more easily when males are in excess, and by doing so, they may increase the viability of their young (Jennions & Petrie, 2000). This proposition has been supported by within-species studies of reptiles showing that clutches fertilized by multiple males had higher genetic diversity and offspring viability than single-sired clutches (Fitze et al., 2005; Noble et al., 2013; Olsson & Madsen, 2001). However, a recent meta-analysis investigating female benefits from multiple mating in reptiles showed that female reproductive output did not increase consistently with increasing number of sires (Lee et al., 2022). Alternatively, according to the second explanation, multiple paternity in reptiles may be driven more by males than by females: males may force copulations more frequently when females are scarce, as their chances of finding a receptive female is low. For example, studies on the viviparous lizard showed that male aggression toward females increased when ASR was male-skewed (Le Galliard et al., 2005), so that multiple paternity increased with ASR (Dreiss et al., 2010). In a population of Hermann's tortoise (*Testudo hermanni*) where ASR is heavily male-skewed, males harass females to such extent that they injure females, causing significant increase in female mortality (Bonnet et al., 2016; Golubovic et al., 2018). These within-species results suggest that male harassment emerging from male-skewed ASR likely increases the frequency of multiple paternity in reptiles. Further studies are needed to assess whether female choice or forced copulations by males contribute more to the across-species association between ASR and multiple paternity we found in this study. It would be also interesting to investigate whether males or females, or both sexes, have specific adaptations to exploit the potential benefits (or to avoid the costs) of multiple mating in species that have male-skewed ASRs.

Importantly, we also found that the frequency of multiple paternity differed among sex determination systems, being highest in ZW species and lowest in XY species, and species with temperature-dependent sex determination falling between the two genetic sex determination systems. As far as we are aware, our study is the first that found significant differences in multiple paternity between different sex determination systems in any taxon. We propose four potential explanations for this pattern. First, the intensity of male–male competition may differ between XY, ZW and TSD reptiles. A theoretical model, supported by empirical evidence, proposes that selection for male-biased sexual size dimorphism (a trait that is often interpreted as indicating the strength of male–male competition) favours the evolution of XY sex determination (Adkins-Regan & Reeve, 2014; Katona et al., 2021). This would predict higher frequency of multiple paternity in XY species because larger males may force copulations with fertile females more effectively. However, this explanation is inconsistent with our present results because reptiles with XY systems had the lowest proportion of multiple paternity out of the three sex determination groups, and also because SSD was not associated with multiple paternity frequency in our analyses. Alternatively, if males in XY species are larger than females (which seems to be the case in some, but not all reptile lineages: Adkins-Regan & Reeve, 2014; Katona et al., 2021), then males may monopolize females or territories more successfully, thus females may have less opportunities to copulate with multiple partners, which would be consistent with the pattern we found.

Second, female preferences for showy male traits (and also the preferred male traits themselves) may evolve more easily in ZW than in XY systems (Reeve & Pfennig, 2003), and thus female choice may be more important in ZW than in XY species. This might explain the high level of multiple paternity in ZW species if high selectivity by females is accompanied by high frequency of multiple paternity. For example, the females' ability to discriminate among males of different quality may increase the benefit of mating with multiple males, because females can more effectively select the most appropriate males (e.g., those that provide the highest genetic diversity of offspring in the clutch). According to this idea, female choice between males of different qualities is documented in reptiles (Laloi et al., 2011; Olsson et al., 1996), although it is rather rare (Olsson & Madsen, 1995) and we do not know whether this is more frequent and/or more discriminative in ZW species than in other reptiles.

Third, reptiles with different sex determination systems have different ASR, which may generate differences in multiple paternity. As Pipoly et al. (2015) showed, reptiles with ZW sex determination exhibit more male-skewed ASRs than reptiles with XY systems. This may lead to higher multiple paternity rates in ZW species if there is a general positive relationship between ASR and multiple paternity as we have found here. However, this explanation is not likely, because our results from the multi-predictor model showed that both ASR and sex determination had significant effects on multiple paternity, suggesting that the effect of sex determination may be at least partially independent of the effect of ASR (and vice versa).

Fourth, the potential confounding effect of taxonomy on the relationship between multiple paternity and sex determination cannot be fully excluded because most ZW species are snakes (14 snakes out of 19 species with ZW system in our dataset) and most TSD species are turtles (21 turtles out of 39 species with TSD in our dataset), and snakes have a high frequency of multiple paternity (Rivas & Burghardt, 2005). However, the sex determination effect cannot be attributed solely to a taxon effect because sex determination was associated with multiple paternity even when the taxon effect was controlled for in the multi-predictor model. Clearly, more research including other taxa with variable sex determination would be required to explore the generality of the association between multiple paternity and the type of sex determination, and to uncover the underlying evolutionary causes of the relationship.

Finally, our analyses did not support the effects of body size, sexual size dimorphism, clutch size, latitude and reproductive mode on multiple paternity frequency, despite the fact that some of these predictors were associated with multiple paternity in other comparative studies of reptiles (Kiester, 1991; Taylor et al., 2014; Uller & Olsson, 2008). One limitation of our study, shared with many other comparative analyses, is that different kinds of data are rarely available from the same population of each species; that is, our data for various predictors represented populations different from those that provided the ASR and/or paternity data. Thus, variation among populations in life-history traits like body size and clutch size may lead to noise in the analyses, making it more difficult to detect relationships. However, within-species variation is often trumped by among-species variation, yielding fair repeatability for several life-history traits (Bókony et al., 2019; Katona et al., 2021), which facilitates the reliability of comparative analyses like the present study. In addition to the above limitation, our results may also be affected by a geographic bias in the data because we found information for a relatively small number of tropical species.

In conclusion, we found a positive relationship between ASR, a fundamental element of individuals' social environment, and multiple paternity, an aspect of the mating system in reptiles, demonstrating that the frequency of multiple paternity increases with increasing preponderance of males in the adult population. We also found differences in the frequency of multiple paternity between reptiles with different sex determination systems, and the latter finding raises interesting hypotheses for future studies. Our result contributes to recent studies (Liker et al., 2021; Schacht et al., 2017; Schacht & Mulder, 2015; Székely et al., 2014) suggesting that variation in ASR, which can promote frequency-dependent selection, may play a major role in the evolution of reproductive behaviour across a broader range of taxa than currently acknowledged.

AUTHOR CONTRIBUTIONS

TS and AL conceived the study. IP, MG, AL and TS designed data collection and analyses. IP, RD, MG, VB and BV collected the data. IP and AL conducted the analyses with inputs from VB and TS. IP, MG and AL wrote the first draft of the paper. All authors contributed to the writing of the paper.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jeb.14185.

DATA AVAILABILITY STATEMENT

The data analysed in this study will be publicly available upon acceptance, and are reposited here: https://datadryad.org/stash/share/lHocVE1lVgy7KuK1PALoAQbFcFEHQ-kqJcNSKSO2lXY.

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SUPPORTING INFORMATION

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