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1 **The genetic sex-determination system predicts**

2 **adult sex ratios in tetrapods**

3
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17

18 **Adult sex ratio (ASR) has critical effects on behaviour, ecology and population**
19 **dynamics¹⁻³, but the causes of variation in ASRs are unclear^{4,5}. Here we assess whether**
20 **the type of genetic sex determination influences ASR using data from 344 species in 117**
21 **families of tetrapods. We find that taxa with female heterogamety have a significantly**
22 **more male-biased ASR (mean proportion of males: 0.55 ± 0.01 SE) than taxa with male**
23 **heterogamety (0.43 ± 0.01). The genetic sex-determination system explains 24% of**
24 **interspecific variation in ASR in amphibians and 36% in reptiles. We consider several**
25 **genetic factors that could contribute to this pattern, including meiotic drive and sex-**
26 **linked deleterious mutations, but further work is needed to quantify their effects.**
27 **Regardless of the mechanism, the effects of the genetic sex-determination system on the**
28 **adult sex ratio are likely to have profound impacts on the demography and social**
29 **behaviour of tetrapods.**

30
31 Adult sex ratio (ASR) varies widely in nature, ranging from populations that are heavily
32 male-biased to ones composed only of adult females⁵⁻⁸. Birds and schistosome parasites
33 tend to have male-biased ASR, for example, while mammals and copepods usually exhibit
34 female-biased ASR⁵. Extreme bias occurs among marsupials (Didelphidae and
35 Dasyuridae): males die after the mating season, so there are times when the entire
36 population consists of pregnant females⁹. Understanding the causes and consequences of
37 ASR variation is an important goal in evolutionary biology, population demography and
38 biodiversity conservation because ASR impacts behaviour, breeding systems, and
39 ultimately population fitness^{1,2,10-13}. It is also a significant issue in social sciences, human
40 health and economics, since unbalanced ASRs have been linked to violence, rape, mate
41 choice decisions and spread of diseases like HIV¹⁴⁻¹⁶. The causes of ASR variation in wild
42 populations, however, remain obscure^{5,13,17}.

43

44 One factor that could impact the ASR is the genetic sex-determination system^{7,8,18}. Taxa
45 such as mammals and fruit flies have XY sex determination (males are heterogametic),
46 whereas taxa such as birds and butterflies have ZW sex determination (females are
47 heterogametic). Sex-determination systems could affect the ASR in several ways. A
48 skewed ASR might result from an unbalanced sex ratio at birth caused by sex ratio
49 distorters¹⁹. Alternatively, a biased ASR could develop after birth if sex chromosomes
50 contribute to sex differences in mortality^{8,18,20,21}. Differential postnatal mortality is likely
51 to be the main driver of biased ASR in birds and mammals, since birth sex ratios in these
52 classes tend to be balanced⁷.

53

54 Here we use data from the four major clades of tetrapods (amphibians, reptiles, birds, and
55 mammals) to assess whether adult sex ratios differ between taxa with XY and ZW sex
56 determination (Fig. 1; Supplementary Table 1). While mammals and birds are fixed for
57 XY and ZW sex determination, respectively, reptiles and amphibians provide particularly
58 attractive opportunities for this study since transitions between sex-determination systems
59 have occurred many times within these clades^{22,23}. We compiled published data on adult
60 sex ratios in wild populations and their sex-determination systems (Supplementary Table
61 1). To control for phylogenetic effects, we used phylogenetic generalized least squares
62 (PGLS)²⁴ to test for differences in ASRs between XY and ZW taxa, and Pagel's discrete
63 method (PDM)²⁵ to test whether XY and ZW systems are evolutionarily associated with
64 female-biased and male-biased sex ratios, respectively. Phylogenies were taken from
65 recent molecular studies (see Methods for details).

66

67 Both the ASR and the sex-determination system are highly variable across tetrapods (Fig.
68 1, Supplementary Table 1). We find that ASR and sex determination are correlated.
69 Before controlling for phylogenetic effects, we find that ASRs are significantly more
70 male-biased in species with ZW sex determination than in those with XY sex
71 determination (Fig. 2, Table 1, Extended Data Table 1). Similarly, the proportion of
72 species with male-biased ASRs is greater among ZW than among XY species (Fig. 1,
73 Table 1). These differences are significant within amphibians, within reptiles, and across
74 tetrapods as a whole (Table 1, Extended Data Table 1).

75

76 The pattern remains significant after controlling for phylogenetic effects. Both the mean of
77 ASR across species (analyzed using PGLS) and the proportion of species with male-
78 biased sex ratios (analyzed using PDM) are significantly different between XY and ZW
79 systems within amphibians, within reptiles, and across tetrapods as a whole (Table 1,
80 Extended Data Table 1). The effect is strong in clades with variation in sex determination:
81 the type of genetic sex determination explains up to 24% of the interspecific variance in
82 ASR among amphibians and 36% in reptiles (estimated using PGLS, Extended Data Table
83 2). The results remain significant when we treat three large clades with invariant sex-
84 determination systems as a single datum each (snakes, ZW; birds, ZW; mammals, XY;
85 Extended Data Table 1), when we make different assumptions about branch lengths in the
86 phylogeny (Extended Data Table 2), and when we use arc-sine transformed ASR values
87 and control for variance in sample size (see Methods).

88

89 Body size and breeding latitude correlate with life-history traits in many organisms and
90 these traits could affect ASR^{26–28}. Sexual size dimorphism is linked to differential sexual
91 selection acting on males and females and thus influences sex-specific mortality, and has

92 been suggested to drive the evolution of genetic sex-determination systems²⁹.
93 Nevertheless, we find that neither body size nor breeding latitude explains the ASR in
94 phylogenetically controlled multi-predictor analyses (Table 2). Sexual size dimorphism is
95 significantly associated with ASR in reptiles and across tetrapods as a whole, but the
96 effect of the genetic sex-determination system remains significant when size dimorphism
97 is included in the analysis (Table 2).

98

99 Sex differences in dispersal may also result in biased ASRs. However, dispersal is
100 unlikely to explain the relationship between ASR and sex-determination systems. First,
101 male-biased dispersal is typical in reptiles regardless of sex-determination system
102 (Supplementary Material 1)^{30,31}. Second, there is no relationship between ASR and sex
103 bias in dispersal distance in birds (Supplementary Material 1). Finally, the relationship
104 between sex determination and ASR remain significant when the influence of sex-biased
105 dispersal is controlled for in multi-predictor models in tetrapods (Supplementary Material
106 1).

107

108 The sex-determination system may affect the ASR in the directions seen in the data in a
109 number of ways. First, sexual selection can fix mutations that increase male mating
110 success and decrease male survival. They will accumulate on Y but not W chromosomes,
111 and will accumulate more readily on X than Z chromosomes if they tend to be recessive.
112 Second, biased ASRs could result from recessive mutations at loci carried on the X (or Z)
113 but absent from the Y (or W) chromosome since they are not masked in the heterogametic
114 sex (the “unguarded sex chromosome” hypothesis)^{7,8,18}, and from deleterious mutations
115 carried on the Y (or W) but not on the X (or Z). At loci carried on both sex chromosomes,
116 alleles on the Y (or W) can show partial degeneration³². Population genetic models

117 suggest deleterious mutation pressure alone may not be adequate to explain ASR biases as
118 large as those observed (Supplementary Material 2), but the models do not include factors
119 that could be important, notably degeneration of Y and W chromosomes by genetic drift³².
120 A third hypothesis is imperfect dosage compensation, which may be deleterious to the
121 heterogametic sex³³. Fourth, distorted sex ratios can result from meiotic drive acting on
122 sex chromosomes^{34,35}. Drive more often produces female-biased sex ratios in XY systems
123 at birth³⁶. There is little data on drive in ZW systems, but if it operates in a symmetric
124 fashion then we expect it to cause male-biased sex ratios. Fifth, Y and W chromosomes
125 might degenerate during the lifespan, for example by telomere shortening or loss of
126 epigenetic marks, more rapidly than X and Z chromosomes. A final possibility is that sex-
127 antagonistic selection acting on sex-linked loci could lead to biased sex ratios, but unlike
128 the preceding hypotheses there does not seem to be a robust prediction about the direction
129 of the ASR bias it will produce (see Supplementary Material 2).

130

131 The limited data that are available do not provide clear support for any of these
132 hypotheses, although critical tests are lacking. For instance, the meiotic drive process
133 predicts biased sex ratios at birth. Although a recent comparative analysis in birds
134 suggests that sex ratios at birth are unrelated to biased ASRs¹⁰, offspring sex ratios have
135 not been compared between different sex-determination systems. Additional insight might
136 come from study of dioecious plants with biased sex ratios³⁷, but their skewed ASR could
137 result from selection on the gametophytic stage that is absent from animals³⁸.

138 Evolutionary feedbacks from the ASR to the sex-determination system are also possible:
139 for example, the ASR could influence sexual size dimorphism and sexual conflict, which
140 in turn could trigger transitions in sex determination^{29,39,40}.

141

142 In conclusion, we demonstrate strong and phylogenetically robust associations between
143 genetic sex-determination systems and a demographic property of populations, ASR.
144 Although the mechanisms that drive this association need further theoretical and empirical
145 analyses, the observed pattern is biologically important for two reasons. First, changes in
146 sex-determination systems are expected to have knock-on effects on social behaviour.
147 Theory suggests that ASR affects violence, pair bonds, infidelity and parental care^{1,41}, and
148 field-based studies support these predictions^{4,13,15,16}. For instance, female-biased ASRs co-
149 occur with polygyny and female care, whereas male-biased ASRs tend to co-occur with
150 polyandry and male care in birds⁴. Second, sex-determination systems may have important
151 demographic consequences through skewed birth sex ratios and sex-biased survival. Such
152 biases may not only impact upon the productivity and growth of populations, but also their
153 genetic composition and viability. Further theoretical, experimental, and comparative
154 studies are clearly needed to understand the linkages between sex determination,
155 demography, and social behaviour.

156

157 **Methods Summary**

158 We collected ASR data for 39 amphibian, 67 reptile, 187 bird and 51 mammal species
159 from the literature. When more than one estimate was available for a species we used their
160 mean. Because genetic sex-determination systems of amphibians vary between closely
161 related species⁴², we used only those species in which sex determination was characterized
162 at the species level^{22,43}. Sex determination is evolutionarily less labile in reptiles, thus we
163 included all species for which sex determination was known either at the family level or,
164 in variable families, at the species level^{22,44,45}. Breeding latitude was calculated as the
165 distance from the Equator in latitudinal degrees (averaged if multiple records were

166 available for a species). Sexual dimorphism in body size was calculated as $\log_{10}(\text{male}$
167 $\text{size}) - \log_{10}(\text{female size})$. All data and their sources are given in Supplementary Table 1.

168

169 We controlled for phylogenetic effects in two ways. First, we tested whether ASR bias
170 (female- or male-biased) is evolutionary associated with the type of sex determination
171 using Pagel's discrete method (PDM)²⁵ as implemented in *BayesTrait*. Second, we tested
172 for differences in ASR with phylogenetic generalized least squares (PGLS)²⁴ using the R
173 package *caper*⁴⁶. We used recently published phylogenies for amphibians⁴⁷, reptiles⁴⁸⁻⁵⁰,
174 birds⁵¹, and mammals^{52,53}. The branching topology between these four major clades was
175 based on recent tetrapod phylogenies^{54,55} (Fig. 1).

176

177 We developed simple population genetic models of the effects that deleterious mutation
178 and sex-antagonistic selection can have on the ASR (Supplementary Material 2). The
179 results regarding deleterious mutations reported in the text assume the mutations are
180 largely or entirely recessive and have multiplicative fitness effects across loci, that the loci
181 are in linkage equilibrium, and that selection is strong relative to mutation and drift. The
182 loci are assumed to be fully sex-linked, and those carried on the one type of sex
183 chromosome (e.g. the X) are assumed to have no homologue on the other type (e.g. the Y)
184 that could otherwise mask a deleterious mutation. Fitness effects of mutations in
185 hemizygotes and homozygotes are assumed equal. In our models of sex-antagonistic
186 selection the loci are fully sex-linked and carried on an X or Z chromosome. The models
187 for both deleterious mutation and sex-antagonistic selection are deterministic. They
188 therefore do not account for stochastic processes (such as “Muller’s ratchet”) that are
189 thought important to sex chromosome evolution³². It is possible that the conclusions
190 would change qualitatively if the models were extended to include those additional effects.

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311

312 **Supplementary Information** is linked to the online version of the paper at

313 www.nature.com/nature.

314

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325 T.S., A.L. and V.B. designed the study. I.P., V.B., P.F.D. and A.L. collected the reptile,
326 amphibian, mammal and bird data, respectively. I.P., V.B. and A.L. conducted the analyses.
327 M.K. developed the population genetic models. All authors wrote the paper.

328

329 **Author Information**

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333 be addressed to A.L. (aliker@almos.uni-pannon.hu).

334

335 **Table 1. The effect of the sex-determination system on the adult sex ratio.**

Taxon	Number of species	Mean ASR				% species with male-biased ASR		
		XY	ZW	<i>t</i> -test [†]	PGLS [†]	XY	ZW	PDM [†]
Amphibians	39	0.51	0.61	**	**	42.9	90.9	*
Reptiles	67	0.45	0.57	***	***	24.2	76.5	*
Birds	187	--	0.55	--	--	--	76.5	--
Mammals	51	0.37	--	--	--	9.8	--	--
Tetrapods	344	0.43	0.55	***	***	22.3	77.2	***

336

337 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, -- no data or not tested

338 [†]Detailed results of the statistical analyses are presented in Extended Data Table 1.

339 Mean adult sex ratios (ASR, proportion of males in the population), *t*-tests and percentage of

340 species with male-biased ASRs represent species-level statistics and analyses, while

341 phylogenetic generalized least squares (PGLS)²⁴ and Pagel's discrete method (PDM)²⁵ were

342 used for phylogenetically corrected analyses of the difference in ASR between XY and ZW

343 species.

344 **Table 2. The relationships between adult sex ratio, sex-determination system and other**
 345 **factors in phylogenetically corrected multi-predictor analyses.**

346

	Amphibians (<i>n</i> = 39)			Reptiles (<i>n</i> = 67)			Tetrapods (<i>n</i> = 259)		
	<i>b</i> (± SE)	<i>t</i>	<i>P</i>	<i>b</i> (± SE)	<i>t</i>	<i>P</i>	<i>b</i> (± SE)	<i>t</i>	<i>P</i>
Sex-determination system	0.10 (± 0.03)	3.38	0.002	0.10 (± 0.02)	4.56	<0.001	0.10 (± 0.02)	5.23	<0.001
Body size	0. (± 0)	1.41	0.166	0 (± 0)	0.78	0.440	0 (± 0)	0.05	0.962
Breeding latitude	0 (± 0)	0.13	0.898	0 (± 0)	0.04	0.966	0 (± 0)	0.24	0.811
Sexual size dimorphism	-0.32 (± 0.34)	0.92	0.363	-0.31 (± 0.15)	2.17	0.034	-0.38 (± 0.07)	5.57	<0.001

347

348 Results of phylogenetic generalized least squares (PGLS)²⁴. Separate models were
 349 constructed for amphibians, reptiles and tetrapods, that included ASR as response variable.
 350 For sex determination, *b* is the estimated difference in ASR between ZW and XY species.

351

352 **Figure 1. Phylogenetic distribution of adult sex ratio (ASR) and genetic sex-**
353 **determination systems across tetrapods.** Inner band shows the type of sex determination
354 (red: XY, blue: ZW) and the outer band shows the ASR bias for each species included in the
355 study (red: ≤ 0.5 , blue: > 0.5). Sample sizes: 39 species for amphibians, 67 species for
356 reptiles, 187 species for birds and 51 species for mammals (see Supplementary Table 1).

357

358 **Figure 2. Variation in adult sex ratio as a function of the sex-determination system in**
359 **amphibians, reptiles, mammals and birds, and tetrapods (all four clades combined).**

360 Central dots and solid whiskers are means ± 1 SE, horizontal bars are medians, and boxes and
361 dashed whiskers show the interquartile ranges and data ranges, respectively, based on species
362 values. Numbers of species are at the bottom of each panel. See Table 1 and Extended Data
363 Table 1 for statistical results and Extended Data Figure 1 for phylogenetically corrected
364 graphs.

365

366 **Methods**

367 **Data collection**

368 We collected data on ASR (proportion of males in the adult population) in amphibians and
369 reptiles from literature published by December 2013, by searching in Google Scholar and
370 Web of Science with the key words "sex ratio" and "reptile" or "amphibian" or the scientific
371 names of species. We also used reviews to identify additional data sources^{43,56}. ASR data for
372 mammals⁷ were obtained from a similar search finished in 2007; and we used avian ASR
373 estimates from our existing data set (Supplementary Information of Liker et al.¹³).

374

375 We specifically collected ASR data for amphibians and reptiles from studies that aimed to
376 obtain representative estimates for the population composition and thus provide reliable sex
377 ratio data⁵⁷. These include either long-term demographic studies applying mark-recapture or
378 sacrificing methods (i.e. each individual was counted only once) with similar capture
379 probabilities for the sexes, or total population counts. When more than one measure was
380 available, we used the total counts of individually marked animals over the study period
381 because this may best approximate the overall ASR. We excluded studies in which the
382 authors explicitly stated or speculated that their data may not represent the population-level
383 ASR, or when the methods were not described in enough detail to assess the reliability of the
384 ASR estimate. Moreover, we tested whether ASR estimates differ between sampling (hand-
385 capture, trap, other) and marking (mark-recapture, sacrifice) methods, and we found no such
386 differences (linear mixed-effects model with species as random factor, sampling: $F_{(3, 105)} =$
387 $0.50, P = 0.683$; marking: $F_{(2, 105)} = 2.18, P = 0.118$; $n = 234$ records). When more than one
388 estimate of ASR was available for the same population (e.g. from several yearly counts at the
389 same location) we took their mean weighted by sample size. When more than one
390 independent record was available for a species from different populations or studies, we used

391 their simple mean. Weighted and non-weighted mean ASRs were highly correlated
392 (amphibians: Pearson's $r = 0.973$, $P < 0.001$, $n = 35$ species; reptiles: $r = 0.995$, $P < 0.001$, $n =$
393 60 species); we used non-weighted averages because not all studies reported sample size.

394

395 We categorized the genetic sex-determination (GSD) systems of the species from published
396 sources either as male-heterogametic (XY) or female-heterogametic (ZW). For amphibians,
397 only species with known GSD system were included^{22,43}, because GSD is an evolutionarily
398 labile trait in amphibians; species within a genus or even populations within a species can
399 differ in GSD⁴². For reptiles, we included all species for which GSD was known either at the
400 family level, or at the species level if both XY and ZW systems were reported in the
401 family^{22,44,45}. Our result for reptiles is not changed qualitatively by restricting our analyses to
402 those species for which GSD is known at species level²², i.e. when species for which we
403 assumed GSD based on other species in the family were excluded (difference between XY
404 and ZW reptile species, phylogenetic generalized least squares model (PGLS)^{24,58}: $b \pm SE =$
405 0.11 ± 0.02 ; $t = 4.70$, $P < 0.001$, $n = 26$; $R^2 = 0.479$). All birds were assigned to ZW, and all
406 mammals to XY sex-determination systems²².

407

408 We also collected data on three additional ecological and behavioural variables to control for
409 their known correlation with ASR and so reduce potential confounding effects in multi-
410 predictor analyses. First, we used body size (in mm) which was measured as snout to vent
411 length for amphibians and squamates, and carapace length for the two turtle species, where
412 possible from the same population for which ASR was reported. Head-body length was used
413 for mammals ($n = 36$)⁵⁹. Since head-body length is not available for the vast majority of birds,
414 we calculated this from the total body length by extracting bill and tail length ($n = 133$;

415 Supplementary Table 1). Where we had sex-specific data, the mean of male and female head-
416 body length was used as body size variable in the analyses.

417

418 Second, we estimated sexual size dimorphism (SSD) as $\log_{10}(\text{male body size}) - \log_{10}(\text{female}$
419 $\text{body size})$. For birds, we used body mass dimorphism (data available for $n = 181$ species)⁶⁰
420 due to the lack of sex-specific body length data. The results of the multivariate PGLS model
421 of tetrapods presented in Table 2 remain qualitatively the same when wing length dimorphism
422 (data available for $n = 153$ species) is used for birds instead of body mass dimorphism (effect
423 of sex determination: $b \pm SE = -0.10 \pm 0.02$, $t = 4.97$, $P < 0.001$; body size: $b \pm SE = 0 \pm 0$, $t =$
424 0.06 , $P = 0.949$; latitude: $b \pm SE = 0 \pm 0$, $t = 0.223$, $P = 0.823$; size dimorphism: $b \pm SE = -$
425 0.52 ± 0.12 , $t = 4.33$, $P < 0.001$; $n = 248$ species).

426

427 Third, we included breeding latitude as the geographic coordinates of the ASR studies for
428 amphibians and reptiles, taking absolute values to represent distance from the Equator in
429 latitudinal degree. When the authors did not report latitude, we used Google Earth to estimate
430 it on the basis of the description of the study site. For birds and mammals, we used the
431 latitudinal midpoint of the breeding range of the species ($n = 182$ and 44 species, for birds and
432 mammals, respectively; sources: V. Remes, A. Liker, R. Freckleton and T. Székely
433 unpublished data for birds, and the PanTHERIA database for mammals⁶¹, respectively). Mean
434 values of these variables were used if multiple data of body size, latitude or size dimorphism
435 per species were available.

436

437 Other possible confounding factors include the lifespan of individuals and sex-specific
438 dispersal distances. First, longer average lifespan may lead to exaggeration of ASR bias.

439 However, in species with available data⁶², lifespan is unrelated to ASR (PGLS, birds: $b \pm SE$

440 = 0 ± 0 , $t = 0.196$, $P = 0.845$, $n = 71$ species; mammals: $b \pm SE = 0 \pm 0$, $t = 0.751$, $P = 0.457$,
441 $n = 35$ species) and also to the absolute deviation of ASR from 0.5 (i.e. when assuming that
442 longer lifespan can exaggerate ASR bias in either direction; birds: $b \pm SE = 0 \pm 0$, $t = 1.543$, P
443 = 0.127 , $n = 71$ species; mammals: $b \pm SE = 0 \pm 0$, $t = 0.180$, $P = 0.858$, $n = 35$ species).
444 Second, sex-specific dispersal can bias ASR due to the higher mortality in the sex with longer
445 dispersal distances. However, we found no evidence of a relationship of sex bias in dispersal
446 either with GSD in reptiles, or with ASR in birds (Supplementary Material 1). For these
447 reasons, as well as because data on lifespan and/or sex-specific dispersal are not available for
448 most species in our ASR data set, we did not include these variables in the main multi-
449 predictor models (see Supplementary Material 1 for additional models including dispersal).

450

451 Our final dataset comprises data on 39 amphibian species and 67 reptile species (in total $n =$
452 229 ASR records from different populations), 187 bird species and 51 mammalian species (a
453 total of 344 species). We could not find body size and latitude data for some species, thus
454 sample sizes were reduced in multi-predictor models. All species-level data and their sources
455 are given in Supplementary Table 1.

456

457 **Data analysis**

458 To assess the reliability of the amphibian and reptile ASR estimates, we calculated the
459 repeatability of ASR as the intraclass correlation coefficient (ICC) following Lessells &
460 Boag⁶³, using only those species for which we had at least two ASR estimates from different
461 populations. These analyses show a moderate repeatability of ASR, and that a significant part
462 of ASR variation is interspecific (amphibians: $ICC = 0.559$, $F_{(22,96)} = 7.27$, $P < 0.001$, $n = 23$
463 species, $n = 120$ records; reptiles: $ICC = 0.524$, $F_{(13,26)} = 4.11$, $P = 0.001$, $n = 14$ species, $n =$
464 40 records). For birds, our earlier analyses showed that nearly half (44%) of the ASR

465 variation was interspecific, and that the direction of ASR (i.e. male- or female-biased) was
466 highly conserved: in 44 species out 55 (80%), the direction of ASR bias was the same for all
467 repeated estimates⁵. For mammals, we did not find enough multiple ASR data within species
468 to estimate repeatability.

469

470 In the comparative analyses we used the topology of Pyron & Wiens⁴⁷ for amphibians, a
471 composite phylogeny for reptiles⁴⁸⁻⁵⁰, Jetz et al.⁵¹ for birds¹³, the family-level relationships
472 of Meredith et al.⁵² and the genus/species level relationships of Fritz et al.⁵³ for mammals.
473 For analyses across tetrapods, the branching topology between these four major clades
474 was based on recent tetrapod phylogenies^{54,55} (Fig. 1). Since we did not have branch
475 length information for these composite phylogenies, we ran the analyses using arbitrary
476 gradual branch lengths according to Nee's method⁶⁴. However, our results remained
477 consistent when we repeated the analyses with other branch length assumptions (Pagel's
478 method and unit branch lengths⁶⁴; Extended Data Table 2).

479

480 To test the association between ASR bias (male- versus female-biased) and GSD (XY versus
481 ZW) in phylogenetically corrected analyses, we used Pagel's discrete method²⁵ as
482 implemented in *BayesTrait*⁶⁵. We used maximum likelihood methods to fit independent and
483 dependent models for transitions in ASR bias and GSD states, and compared the fit of these
484 two models by a likelihood ratio test²⁵. To test the ASR difference between XY and ZW
485 species, we used PGLS models with maximum likelihood estimates of Pagel's lambda
486 values²⁴ using the R⁶⁶ package *caper*^{46, 58}. ASR was the response variable in all models, and
487 genetic sex-determination system was fitted as the predictor (Table 1, Extended Data Table
488 1). The parameter estimate b shows the difference in ASR (proportion of males in the
489 population) between ZW and XY species. To test the robustness of the bivariate results, we

490 added body size, breeding latitude and SSD as predictors in multi-predictor models to control
491 for their potential confounding effects (Table 2). As in earlier ASR studies^{5,7}, the distribution
492 of ASR values did not deviate significantly from normal in the four clades separately as well
493 as in tetrapods as a whole; our results remain qualitatively identical when ASR is arc-sine
494 transformed before PGLS analyses (amphibians: $b \pm SE = 0.10 \pm 0.03$, $t_{37} = 3.44$, $P = 0.001$, n
495 $= 39$; reptiles: $b \pm SE = 0.12 \pm 0.02$, $t_{65} = 5.95$, $P < 0.001$, $n = 67$; tetrapods: $b \pm SE = 0.11 \pm$
496 0.02 , $t_{342} = 5.24$, $P < 0.001$, $n = 344$).

497

498 The difference between XY and ZW systems for tetrapods is not sensitive to the inclusion of
499 large clades with uniform sex-determination systems (snakes and birds are all ZW, mammals
500 are all XY) since it remains unchanged when each of these clades is reduced to a single datum
501 of its mean ASR (PGLS: $b \pm SE = 0.10 \pm 0.02$, $t = 5.07$, $P < 0.001$, $R^2 = 0.232$, $n = 87$).

502 Furthermore, our result is also robust to between-species differences in sample size: when we
503 added $\log(\text{no. individuals})$ to the previous model, the effect of sex determination remained
504 significant ($b \pm SE = 0.15 \pm 0.07$, $t = 2.08$, $P = 0.041$) while sample size had no significant
505 effect on ASR ($b \pm SE = 0 \pm 0.01$, $t = 0.35$, $P = 0.72$, $n = 78$). Furthermore, sample size was
506 not a significant predictor of ASR when we added it as a fourth confounding variable in the
507 full PGLS model ($b \pm SE = 0 \pm 0.01$, $t = 1.16$, $P = 0.250$, $n = 78$), and the effect of other
508 predictors remained qualitatively the same as in Table 2. Finally, the results do not change
509 when we only used the most reliable ASR data (based on mark-recapture or sacrifice
510 methods): sex-determination system is significantly related to ASR in amphibians, reptiles
511 and tetrapods (PGLS results, amphibians: $b \pm SE = 0.09 \pm 0.03$, $t = 3.07$, $P = 0.004$, $n = 35$
512 species; reptiles: $b \pm SE = 0.11 \pm 0.03$, $t = 3.974$, $P < 0.001$, $n = 22$; tetrapods with snakes,
513 birds and mammals included as single data points: $b \pm SE = 0.10 \pm 0.02$, $t = 4.23$, $P < 0.001$, n
514 $= 55$).

515

516 **Population genetic models**

517 We developed population genetic models of the effects that deleterious mutation and sex-
518 antagonistic selection might have on the ASR (Supplementary Material 2). The models
519 assume that deleterious mutations are largely or entirely recessive, that they have
520 multiplicative fitness effects across loci, that the loci are fully sex-linked and in linkage
521 equilibrium, that mutation is not sex-biased, and that selection is strong relative to
522 mutation and drift. Fitness effects of mutations in hemizygotes and homozygotes are
523 assumed equal. Full details of the models are given in Supplementary Material 2. Here we
524 summarize key results.

525 When deleterious alleles reach a mutation-selection balance, with X-Y sex
526 determination the mean viability of males relative to females is

527

$$528 \quad \bar{W}_m \approx \exp\{-3U_X - U_Y\},$$

529

530 where U_X and U_Y are the total rates of mutation to deleterious alleles across all loci on the
531 X and Y chromosomes. With Z-W sex determination, the mean viability of females to
532 males is

533

$$534 \quad \bar{W}_f \approx \exp\{-3U_Z - U_W\},$$

535

536 where U_Z and U_W are the total rates of mutation to deleterious alleles across all loci on the
537 Z and W chromosomes. Using very rough estimates for rates of deleterious mutations
538 appropriate for human sex chromosomes, we estimate that mutation-selection balance
539 might bias the ASR by a few percent. This degree of bias is substantially less than what is

540 seen in our data. We emphasize that the conclusion could be quite different using other
541 parameter values, or if the model was extended to include stochastic effects.

542 The second hypothesis to explain biased ASRs that we explored with models is sex-
543 antagonistic selection, the situation in which alleles are selected differently in females and
544 males⁶⁷. In Supplementary Material 2, we use numerical examples to show that under both
545 XY and ZW sex determination, either a female-biased or male-biased ASR can result.
546 Thus there does not seem to be a robust generalization about how sex-antagonistic
547 selection will bias the ASR.

548

549 **Methods References**

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576 **Extended Data titles and legends**

577

578 **Extended Data Table 1. Detailed analyses of the effect of sex-determination system**
579 **on the adult sex ratio.**

580 These are extensions of Table 1 in the text showing details of the phylogenetically
581 uncorrected (t-tests) and phylogenetically corrected analyses (PGLS²⁴ and PDM²⁵). Birds and
582 mammals were not tested with phylogenetic control because there is no variation in the type
583 of sex-determination system within birds and mammals.

584

585 **Extended Data Table2. Phylogenetically controlled analyses of the relationship**
586 **between adult sex ratio and genetic sex-determination system using different branch**
587 **length assumptions.**

588 These are results of phylogenetic generalized least squares models (PGLS)²⁴ as implemented
589 in the R package ‘caper’⁴⁶. The models assume gradual branch lengths calculated either by
590 Nee’s or by Pagel’s method, or unit branch lengths⁶¹.

591

592 **Extended Data Figure 1. Phylogenetically corrected mean and standard error of adult**
593 **sex ratio in clades with different sex-determination systems.**

594 Parameter estimates for means and the associated standard errors were calculated by
595 phylogenetic generalized least squares models (PGLS)²⁴ presented in Extended Data Table 2
596 (with branch lengths estimated by Nee's method).