

UC Davis

UC Davis Previously Published Works

Title

Adult sex ratio, sexual dimorphism and sexual selection in a Mesozoic reptile

Permalink

<https://escholarship.org/uc/item/1vg1s6bv>

Journal

Proceedings of the Royal Society B, 282(1815)

ISSN

0962-8452

Authors

Motani, Ryosuke

Jiang, Da-yong

Rieppel, Olivier

et al.

Publication Date

2015-09-22

DOI

10.1098/rspb.2015.1658

Peer reviewed



Research

Cite this article: Motani R, Jiang D, Rieppel O, Xue Y, Tintori A. 2015 Adult sex ratio, sexual dimorphism and sexual selection in a Mesozoic reptile. *Proc. R. Soc. B* **282**: 20151658.
<http://dx.doi.org/10.1098/rspb.2015.1658>

Received: 9 July 2015

Accepted: 24 August 2015

Subject Areas:

palaeontology

Keywords:

adult sex ratio, sexual size dimorphism, sexual selection, gompertz allometry, sauropterygia

Authors for correspondence:

Ryosuke Motani

e-mail: rmotani@ucdavis.edu

Da-yong Jiang

e-mail: djiang@pku.edu.cn

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1658> or via <http://rspb.royalsocietypublishing.org>.

Adult sex ratio, sexual dimorphism and sexual selection in a Mesozoic reptile

Ryosuke Motani¹, Da-yong Jiang², Olivier Rieppel³, Yi-fan Xue² and Andrea Tintori⁴

¹Department of Earth and Planetary Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA

²Laboratory of Orogenic Belt and Crustal Evolution, Ministry of Education; Department of Geology and Geological Museum, Peking University, Yiheyuan Street 5, Beijing 100871, People's Republic of China

³Center of Integrative Research, The Field Museum, Chicago, IL 60605-2496, USA

⁴Dipartimento di Scienze della Terra, Università degli Studi di Milano, Via Mangiagalli, Milan 34-20133, Italy

RM, 0000-0001-5022-1053; DJ, 0000-0002-4668-2081

The evolutionary history of sexual selection in the geologic past is poorly documented based on quantification, largely because of difficulty in sexing fossil specimens. Even such essential ecological parameters as adult sex ratio (ASR) and sexual size dimorphism (SSD) are rarely quantified, despite their implications for sexual selection. To enable their estimation, we propose a method for unbiased sex identification based on sexual shape dimorphism, using size-independent principal components of phenotypic data. We applied the method to test sexual selection in *Keichousaurus hui*, a Middle Triassic (about 237 Ma) sauropterygian with an unusually large sample size for a fossil reptile. *Keichousaurus hui* exhibited SSD biased towards males, as in the majority of extant reptiles, to a minor degree (sexual dimorphism index = 0.087). The ASR is about 60% females, suggesting higher mortality of males over females. Both values support sexual selection of males in this species. The method may be applied to other fossil species. We also used the Gompertz allometric equation to study the sexual shape dimorphism of *K. hui* and found that two sexes had largely homogeneous phenotypes at birth except in the humeral width, contrary to previous suggestions derived from the standard allometric equation.

1. Introduction

There is a substantial gap in our knowledge of the evolutionary history of sexual selection through geologic time because studies of sexual selection and dimorphism in fossil organisms are hampered by many obstacles [1]. The problem is rooted in the limitation of information content of a fossil specimen. Most fossils only preserve morphologies of hard tissues, so even such basic information as the sex of an individual remains unknown except in some rare cases where, for example, a genital bone (e.g. baculum of some mammals) is preserved, or unetched embryos are found in the body cavity to indicate that the individual is a gravid female [2–4]. This restriction led palaeontologists to explore sexual shape dimorphism in an attempt to identify sexes in the absence of direct evidence [1,5,6]. However, methodologies for sex identification based on sexual shape dimorphism suffer from a systematic bias, as discussed below.

Well-corroborated sex identifications would allow estimation of two important ecological metrics in a fossil population, namely adult sex ratio (ASR) and sexual size dimorphism (SSD). Both ASR and SSD are considered important ecological parameters in extant vertebrates, and skewedness of each metric is interpreted as an indication of different selection mechanisms [7,8]. Male-biased SSD, in particular, is considered sexually selected (i.e. larger males have higher success of mating and thus large male size is selected) in most mammals, reptiles and birds [9–11]. Female bias in SSD, in contrast, is often interpreted as fecundity selected, but this is not as well established as the sexual selection of male-biased SSD [12]. ASR and SSD have rarely been quantified in fossil vertebrates using the

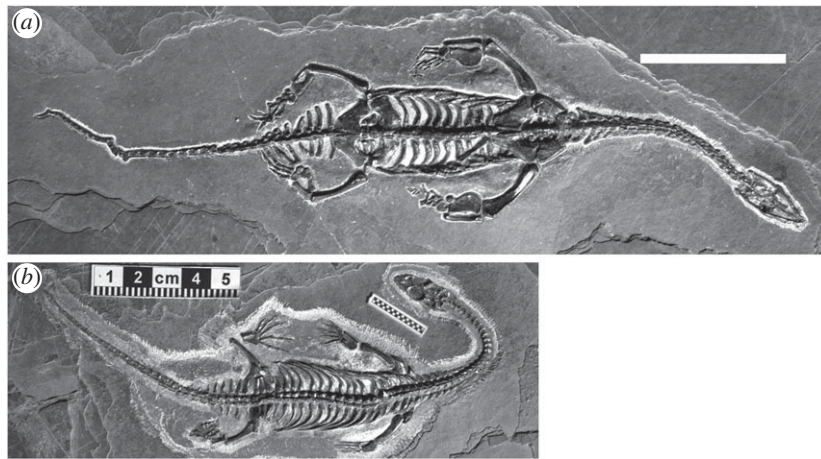


Figure 1. Sexual dimorphism of *K. hui*. (a) Male; (b) young female. Forelimbs of males tend to be more enlarged and robust relative to the body compared with female forelimbs. Scale bar, 5 cm.

formulae for extant vertebrates, with one notable exception [5]. The main reason for this scarcity is the aforementioned difficulty of sex identification in fossils, coupled with the generally small sample sizes.

The sample size problem may be reconciled in selected fossil species, such as *Keichousaurus hui*, a sauropterygian reptile from the Ladinian (Middle Triassic) of Guizhou Province, China [13]. It is considered a pachypleurosaur, although there is uncertainty in the monophyly of Pachypleurosauria [14,15]. The species is known from hundreds of specimens commonly seen in museum displays across China. Many of them are not well prepared but the rest still provide a sufficiently large sample size that enables statistical analyses of morphology that are often not feasible in fossil reptiles, such as quantification of sexual shape dimorphism [6,16]. Two morphotypes have been recognized, where one has enlarged and more robust forelimbs for a given body size than the other (figure 1) [6]. The morphotype with smaller and slenderer limbs has unambiguously been identified as female based on the find of two well-preserved gravid specimens [2]. This led previous workers to interpret the enlargement of the limbs as a secondary sexual character of males [6]. Enlarged limbs in males probably led to improved reproductive success, as seen in salamanders with analogous dimorphism where males use their enlarged limbs during amplexus in water [17,18]. Also, enlarged limbs may have stabilized the body during courtship display in water, as in marbled newt (*Triturus marmoratus*) [19].

Studies of sexual shape dimorphism in *K. hui* have encountered two major obstacles, which are relevant to other fossil species in general [6,16]. First is a systematic bias inherent to the traditional method of sex identification based on sexual shape dimorphism, where specimens are sexed based on a combination of skeletal ratios [5,6]. During ratio-based sex identification, a threshold ratio is set for each pair of skeletal measurements related to pronounced sexual shape dimorphism in adults to delineate between two sexes. However, secondary sexual characters are only evident in adult males in *K. hui*, while juvenile specimens do not exhibit many characters to allow sex identification. Thus, small males, with skeletal ratios similar to those of females, may be identified as females based on these ratios. Also, given that secondary sexual characters usually exhibit positive allometry, the line representing the threshold ratio, which inherently has a slope of 1 in log–log space, intersects with the distribution of the data, dividing it

into two size-dependent groups (figure 2a). Thus, the use of a ratio systematically causes exaggeration of SSD in the resulting series of sex identification. There is a need for a method to account for this systematic bias.

The second obstacle is the use of the standard allometric equation to interpret the relative growth of secondary sexual characters. Although the equation is known to effectively illuminate scaling effects in morphological data, its logical foundation cannot be fully reconciled with the growth of sexually dimorphic features. Many secondary sexual characters grow fast during adolescent years, after which growth decelerates, whereas the standard allometric equation assumes exponential growth of relevant characters throughout life, without acceleration or deceleration [20]. Graphically speaking, in a double-logarithmic space of features x versus y , the standard allometric equation represents a line, when secondary sexual characters often form curves. Then, it is useful to apply an allometric equation that appears curved on the same plot by accounting for growth acceleration and deceleration.

In the present contribution, we try to address those two problems in a study of sexual selection and dimorphism in *K. hui*. We first devised a method to enable sex identification across all body sizes while removing a systematic bias inherent to the traditional method. The new method permits statistically sound quantification of SSD and ASR for the first time in fossil vertebrates, which in turn will allow a test of sexual selection. We will then apply the Gompertz allometric equation [20], which accounts for acceleration and deceleration of growth rates, to the resulting sex sets in order to investigate the effects of growth acceleration and deceleration on our interpretation of secondary sexual characters (see Material and methods for an explanation of the Gompertz allometric equation). The combined results will allow us to discuss the possibility of sexual selection and dimorphism in this fossil reptile, from a perspective that has been lacking in other studies.

2. Material and methods

(a) Specimens and measurements

The data for *K. hui* were derived from a table in our previous study [16]. Of the three body size variables in the original data,

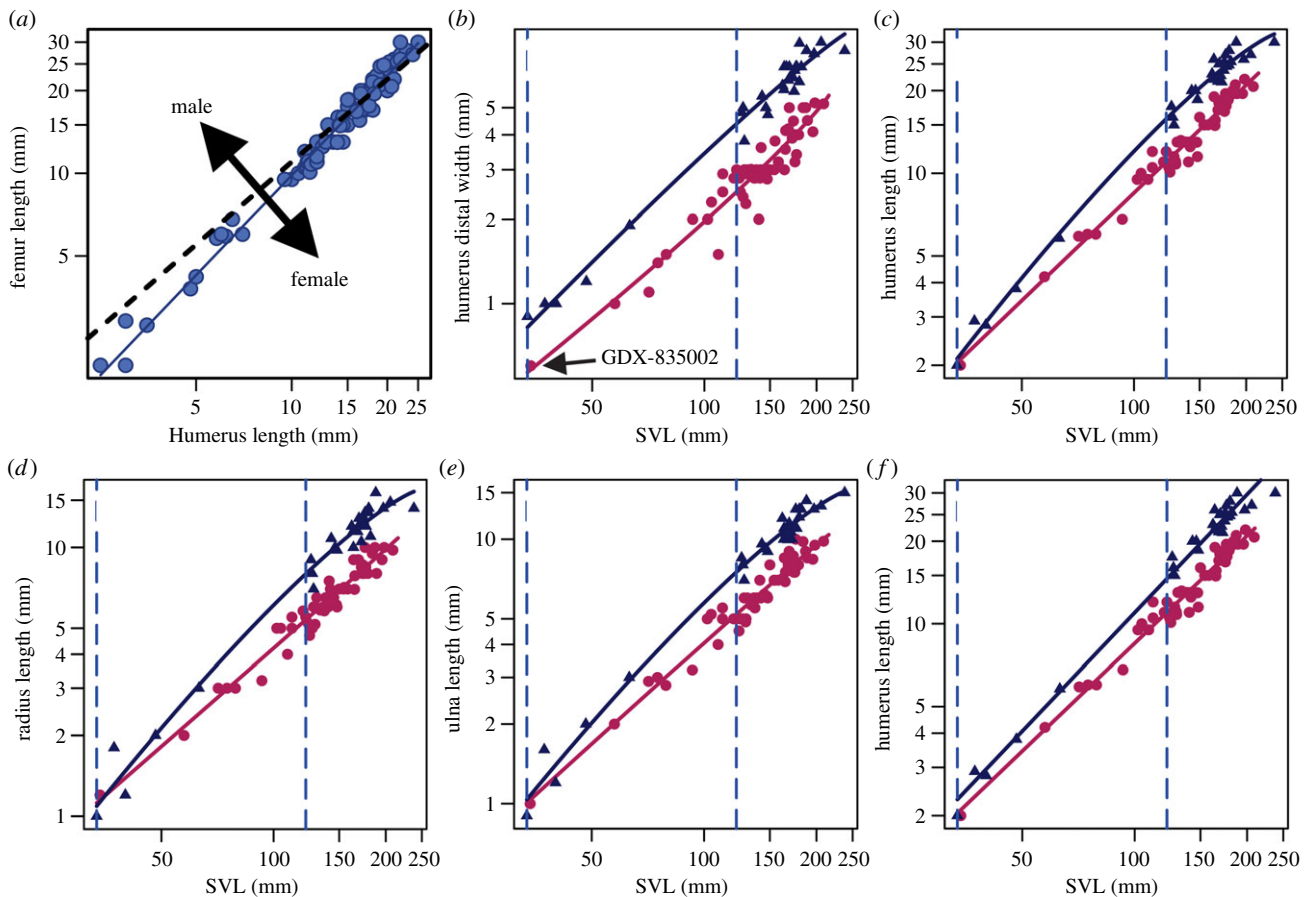


Figure 2. Allometric relationships of limb and body dimensions. (a) Femoral length relative to humeral length in *K. hui*. Broken line represents the ratio that was traditionally used for sex segregation. Ratios inherently have a slope of 1 in log–log space, dividing the sample into two size-based groups, exaggerating SSD and biasing ASR. (b) Distal humeral width versus SVL in *K. hui*, with Gompertz allometric curves. (c) Same as (b) but with humeral length. (d) Same as (b) but with radial length. (e) Same as (b) but with ulnar length. (f) Same as (c) but with standard allometric lines for comparison. In (b–d), vertical broken lines indicate approximate SVL at birth and sexual maturity, while blue and red colours represent males and females, respectively.

we only retained SVL. For sex identification, we only used a subset of limb characters that showed sexual differences when plotted against SVL, namely the distal width of humerus and the lengths of the following elements: humerus, radius, ulna, femur, tibia and fibula. Other characters were removed to reduce noises. Obvious outliers and specimens lacking any of the measurements were removed, reducing the sample size ($n = 86$). See the electronic supplementary material for the list of specimens used.

Of the 86 specimens, 27 were originally collected from a single fossil quarry in Nimaigu Village, Wusha District, Xingyi City, Guizhou Province, China, during scientific excavations led by the Peking University [16]. The specimens occurred in 10 beds between bed nos. 26 and 44, which measured about 2 m in total thickness, near the base of the fossiliferous levels. At least some of these beds may represent mass mortality levels. The remaining 59 were derived from the literature [6], which did not clearly state the origin of the specimens. Given the vintage of the specimens indicated by years contained in their specimen numbers (i.e. 2002–2005), they were probably collected after the main marine reptile fossil locality in the region shifted from Dingxiao to Nimaigu in Wusha District. The stratigraphic distribution of *Keichousaurus* is limited based on our extensive excavation at Nimaigu, so all specimens are expected to have been derived from the aforementioned 2 m interval, representing natural assemblages.

(b) Sex identification

As mentioned earlier, the root of the problem in skeletal-ratio-based sex identification, as traditionally exercised [5,6], is the

assumption that a single ratio can identify sexes regardless of body size, when the threshold ratios should indeed covary with size. We accounted for continuous changes in threshold ratios with body size by using selected components from principal component analysis (PCA). PCA rotates the data into orthogonal principal components while maintaining the information content. Because principal components are independent of each other, some prefer to use them instead of the raw data in multivariate statistical analyses [21]. The first PCA axis (PC1) represents size, unless size has been removed from the data before analysis. In the present data, PC1 is strongly correlated with SVL ($r = 0.964$, $p < 0.001$), unlike other axes (electronic supplementary material). Therefore, by removing the first axis from the rotated data, one would be removing much of the size element from the data while keeping the rest of the information.

The resulting size-independent data were classified into two clusters using k -means. We also tried hierarchical clustering (hcl) based on Ward's method and obtained identical results. The cluster that contained the specimen NMNS-cyn2003-18 was judged to comprise females, given that this specimen is gravid [2].

After this initial sex identification, the result was smoothed using linear discriminant analysis (LDA) in case the clustering methods may have been misled by random similarity between a particular pair of specimens. The sex identification scheme from the initial cluster analysis was used to train LDA, which was then used to reclassify the samples. This secondary sex identifications from LDA were adopted as the final result. For comparative purposes, same multivariate analyses were performed using the three ratios that were traditionally used for sex identification, namely the ratios between distal and mid-shaft widths of humerus,

between lengths of humerus and femur, and between humeral length and SVL [6].

(c) Sex ratio

A χ^2 test for equality of proportions between two samples was used to test if the sex ratios resulting from each method were statistically different between adults and juveniles. A published SVL value of 122 mm was used as the threshold between juveniles and adults based on the size of the smallest gravid female known [2,6]. A previous study suggested 126 mm as the threshold in males. However, there is no male specimen between 63 and 126 mm in SVL, thus this threshold may be overestimated. Because of this sample distribution, there is no practical difference between having one threshold value of 122 mm for both sexes, or employing separate threshold values of 122 and 126 mm for females and males, respectively.

(d) Gompertz allometry

Given the limitation of standard allometric equations in the study of secondary sex characters, as pointed out earlier, we explored an alternative allometric equation that was proposed recently, based on the Gompertz growth equation [20]. The Gompertz equation is one of the expressions of the Richards model of growth [22] and has been used to study the growth of many vertebrate groups, including dinosaurs [23]. The Richards model has other popular forms, such as the von Bertalanffy growth equation, but the analytical solution of the von Bertalanffy equation is complicated [24], and its application to allometry has yet to be established. This leaves the Gompertz allometric equation as the only parametric equation that can accommodate changes of growth rates at this point.

Of the several different expressions of the Gompertz allometric equation, we employed an expression that is most useful for our purpose, which is

$$y = y_{\max} * e^{-b_y * (-\ln x - \ln x_{\max} / b_x)^{d * (t_y / t_x)}},$$

where b_x and b_y are exponential growth rates at $t = 0$, d is relative damping rate, t_x and t_y are growth duration, and x_{\max} and y_{\max} are the maximum values for x and y , respectively.

In a double-logarithmic space, the equation above can be simplified to

$$\ln y = \ln y_{\max} - B * (\ln x_{\max} - \ln x)^D,$$

where B is $b_y / b_x^{d * t_y / t_x}$ and D is $d * t_y / t_x$. Therefore, there are four constants to be estimated, namely x_{\max} , y_{\max} , B and D . In the present case, t_x and t_y can be considered to be approximately equal with each other (i.e. $t_y / t_x \approx 1$; then $D \approx d$).

The four constants were optimized to the data, which were converted by natural logarithm (not base 10). See the electronic supplementary material for more details.

3. Results

(a) Sex identification and ratio

The resulting sex ratios are summarized in table 1, and sex identifications for specimens are given in the electronic supplementary material. When the traditional ratio-based data were used, all methods resulted in female proportions that are unnaturally high (more than 0.88) in juveniles. This ratio became lower when using the PC-based data, down to about 0.71. The female ratio for adults was about 0.62 with the new method, which is higher than previously suggested (table 1). The juvenile female ratio was significantly higher than that for adults when using the traditional ratios as the data ($p < 0.041$), but the difference was insignificant with PC-based

Table 1. Sex ratios of *K. hui* based on the new and published sex identifications, expressed as the proportion of females, with p -values for significant difference between juveniles and adults.

data	method	juvenile	adult	p -value
PCA	k -means + LDA	0.706	0.623	0.525
ratios	k -means + LDA	0.882	0.623	0.041
	raw ratios [6]	0.882	0.536	0.009
	raw ratios + LDA [16]	0.941	0.58	0.005

data. The highly skewed juvenile sex ratios resulting from the traditional skeletal ratios are unlikely—sauropterygians probably had genetic sex determination [25] that would give offspring sex ratios that are neutral [7], so the juvenile sex ratio is expected to lie between 0.5 and ASR. Therefore, PC-based data performed better than the traditional ratios in sexing *K. hui*.

A post-processing of sex identification by LDA proved effective in objectively screening obvious misidentification in the initial clustering. For example, in the plot of this character against the snout–vent length (SVL), one of the putative males from the raw clustering results (GXD-835002) was clearly separated from other males and instead lay near the curve for females (figure 2*b*). Sexual dimorphism in *Keichousaurus* is most evident in the distal width of the humerus [6,16], so this initial identification by clustering is questionable. LDA reclassified this individual as female, thus preventing an obvious misidentification. It appears that the clustering method was misled by some unusual measurements given for GXD-835002, while LDA was not.

(b) Gompertz allometry

The Gompertz allometric equation (see Material and methods) revealed various degrees of sex-based differentiations in the seven limb characters examined (figure 2*b*). Allometric constants are summarized in table 2. Values of D suggest that lengths of male limb bones exhibited stronger damping of growth rates than SVL. Also, values of B suggest that the initial growth rates were higher for limb bone lengths than for SVL—although the exact values of b_y / b_x are unknown, high B and D values necessitate that $b_y > b_x$, unless b_x has an unlikely value that is smaller than 1. Thus, growth rates for limb bone lengths initially started out faster than those for SVL, and then had steeper accelerations followed by stronger decelerations, giving rise to faster maximum growth rates. Among the limb bones, growth rates were higher for the lengths of forelimb elements than for those of the hindlimb, resulting in relative elongation of the forelimb over the hindlimb during adolescent years.

Growth patterns in females were different from those in males. D in females is approximately 1 across the measurements, suggesting that the damping of growth rates with age was similar among limb bones and SVL, unlike in males. The initial growth rates were higher for limb bones than for SVL (i.e. if $d \approx 1$, then it follows that $B \approx b_y / b_x$), whereas the values of B are all larger than 1. Between the forelimb and hindlimb bone lengths, the initial growth rates were slightly higher for forelimb elements. However, the lack of strong damping in growth rates resulted in length

Table 2. Gompertz allometric constants for seven limb measurements plotted against SVL in *K. hui*.

	female			male		
	y_{\max}	B	D	y_{\max}	B	D
humerus distal width	5.58	1.31	0.89	9.37	1.14	1.11
humerus length	23.26	1.30	1.00	32.52	1.14	1.27
radius length	10.90	1.23	0.99	16.36	1.14	1.27
ulna length	10.44	1.23	1.03	15.38	1.13	1.26
femur length	21.29	1.13	1.03	27.01	1.03	1.14
tibia length	7.74	1.14	1.08	10.54	1.15	1.11
fibula length	9.01	1.13	0.99	11.31	1.04	1.22

ratios between the forelimb and hindlimb that are not as remarkable as in males.

4. Discussion

The sex identifications given in this study support a male-biased SSD in *K. hui*, although the degree of SSD is smaller than previously suspected [6]—the difference is attributable to the systematic exaggeration of SSD by the ratio-based sex identification scheme employed in the previous study (see Introduction). The male dominance of SSD is evident from the mean adult SVL values between males and females (169 versus 156 mm, respectively), which are significantly different based on ANOVA of log-transformed SVL ($F = 5.278$, $p = 0.0248$), as well as from the maximum SVL values for each sex (238 versus 209 mm). The sexual dimorphism index (SDI) [26], based on the mean SVL following the reptilian convention [9], is -0.087 . Such a value is close to the average in lizards, which have a tendency for male-biased SSD, but is not found among snakes or turtles, which exhibit female-based SSD on average [9]. This provides the first case of statistically tested and unbiased SDI quantified in a Mesozoic reptile. Male-biased SSD is usually correlated with sexual selection of males, rather than fecundity selection of females, in mammals [10], reptiles [9] and birds [11], so it is likely that SSD in *K. hui* was also associated with sexual selection (i.e. larger male phenotypes were selected through higher mating success).

ASR in extant vertebrates is not correlated with offspring sex ratios but with selective mortality of one sex [7,27,28], especially if the sex determination is genetic, as has been inferred for sauropterygian reptiles [25]. In general, female-biased ASR results from high mortality of males as a result of behaviours linked to sexual selection, while male-biased ASR reflects high mortality of females from fecundity selection [27]. Therefore, the female-biased ASR in *K. hui* supports the implication from SSD that sexual selection of males operated in this species. However, it should be noted that the same interpretation may not apply in invertebrates, for which two opposing hypotheses have been proposed concerning the relationships between SSD and ASR. One hypothesis proposes that high mortality in males would lead to female-biased ASR while reducing male–male competition, resulting in female-biased SSD [29]. The other hypothesis states that in

species with male-biased SSD, males need to feed more to gain sufficient nutrients for enhanced growth, leading them to employ more risky feeding habits that would lead to increased mortality, which results in female-biased ASR [30]. The first hypothesis applies to spiders and nematodes [31], whereas the second is favoured in dragonflies [32]. No correlation was found in copepods [33]. Our finding from *K. hui* fits the second hypothesis better—even if the males did not necessarily employ risky feeding habits, increased foraging time to maintain a larger body mass would expose them to higher risks of mortality from predation. However, there may be other mechanisms that are not considered here.

Quantitative tests of sexual selection in extant reptiles involve such metrics as male aggression, territoriality and home ranges [9]. These ecological parameters are usually impossible to quantify in fossils. Given that a direct test of sexual selection is difficult [1], ASR and SSD provide invaluable information from which to infer sexual selection in extinct species. The present sex identification method provides a useful tool to quantify the two metrics based on statistically justified sex sets. A cautionary consideration should be emphasized with regard to applying the new method. As with other morphological sex identification methods, it divides the sample into two size-independent phenotypes whether they exhibit sexual differences or not. It should not be used unless sexual shape dimorphism is suspected. Also, the method fails if size, rather than shape, constitutes the major aspect of sexual dimorphism in the sample. It is sensitive to small or uneven samples, excessive inclusion of non-sexual characters, and measurement errors. The sex of the largest or smallest individuals may be misidentified if the specimens are isolated from the rest of the samples of the same sex in terms of body size.

Other possible biases that could mislead our conclusion include temporal changes and taphonomic selection of phenotypes. Our preliminary observations suggest that the sexual shape dimorphism exists regardless of horizons within this limited stratigraphic segment, so temporal effects are probably negligible. Taphonomic selection of one sex is also unlikely because we observed an approximately even mixture of sexes, and also ASR is not very strongly skewed, suggesting that neither sex is strongly eliminated by taphonomy. Also, the beds yielded a full range of body sizes, including a number of small individuals, so size-based preservation bias is also unlikely.

Concerning the interpretation of sexual shape dimorphism, the advantage of Gompertz allometry [20] is obvious when

comparing the resulting allometric curves between this and the standard allometric equations (figure 2c versus 2f). According to the standard equation, males on average have longer humeri relative to SVL than females already at birth, and the gap widens continuously through life. This interpretation assumes exponential growth of the relevant structures, which is unrealistic. Gompertz allometry provides a more reasonable interpretation. It suggests that males and females have similarly long humeri relative to SVL at birth, but the relative growth rate of the humerus versus SVL is greater in males than in females, resulting in longer humeri relative to SVL in males by the time maturity is reached. Subsequently, the relative growth rate in males exhibits a rapid damping, preventing the sexual gap from widening further. Thus, this and some other secondary sexual characters of *K. hui* (e.g. figure 2d,e) are formed as a result of changing growth rates, rather than an initial sex difference at birth, as previously suggested [16].

The only clear exception to this tendency is the distal width of the humerus (figure 2b), which exhibits a sexual difference since birth.

Data accessibility. All data are included in the electronic supplementary material, or have previously been published.

Authors' contributions. R.M., D.J. and Y.X. conceived the study and discussed it with O.R. and A.T. R.M. drafted the paper. D.J., O.R. and A.T. revised it.

Competing interests. We declare we have no competing interests.

Funding. D.J. was funded by Projects 40920124002 and 41372016 from the National Natural Science Foundation of China, Project 123102 from State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) and Project 20120001110072 from the Research Fund for the Doctoral Program of Higher Education.

Acknowledgements. We thank Geerat J. Vermeij for his suggestions on an earlier version of the manuscript.

References

1. Knell RJ, Naish D, Tomkins JL, Hone DWE. 2013 Sexual selection in prehistoric animals: detection and implications. *Trends Ecol. Evol.* **28**, 38–47. (doi:10.1016/j.tree.2012.07.015)
2. Cheng YN, Wu XC, Ji Q. 2004 Triassic marine reptiles gave birth to live young. *Nature* **432**, 383–386. (doi:10.1038/Nature03050)
3. Caldwell MW, Lee MSY. 2001 Live birth in Cretaceous marine lizards (mosasauroids). *Proc. R. Soc. Lond. B* **268**, 2397–2401. (doi:10.1098/rspb.2001.1796)
4. Motani R, Jiang D, Tintori A, Rieppel O, Chen GB. 2014 Terrestrial origin of viviparity indicated by the oldest embryonic fossil of Mesozoic marine reptiles. *PLoS ONE* **9**, e8B640. (doi:10.1371/journal.pone.0088640)
5. Rieppel O. 1989 A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Phil. Trans. R. Soc. Lond. B* **323**, 1–73. (doi:10.1098/rstb.1989.0001)
6. Cheng YN, Holmes R, Wu XC, Alfonso N. 2009 Sexual dimorphism and life history of *Keichousaurus hui* (Reptilia: Sauropterygia). *J. Vertebrate Paleontol.* **29**, 401–408. (doi:10.1671/039.029.0230)
7. Donald PF. 2007 Adult sex ratios in wild bird populations. *Ibis* **149**, 671–692. (doi:10.1111/j.1474-919X.2007.00724.x)
8. Fairbairn DJ, Blanckenhorn WU, Székely T. 2007 *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford, UK: Oxford University Press.
9. Cox RM, Butler MA, Joh-Alder HB. 2007 The evolution of sexual size dimorphism in reptiles. In *Sex, size and gender roles: evolutionary studies of sexual size dimorphism* (eds DJ Fairbairn, WU Blanckenhorn, T Székely), pp. 38–49. Oxford, UK: Oxford University Press.
10. Lindenfors P, Gittleman JL, Jones KE. 2007 Sexual dimorphism in mammals. In *Sex, size and gender roles: evolutionary studies of sexual size dimorphism* (eds DJ Fairbairn, WU Blanckenhorn, T Székely), pp. 16–26. Oxford, UK: Oxford University Press.
11. Székely T, Lislevand T, Figuerola J. 2007 Sexual size dimorphism in birds. In *Sex, size and gender roles: evolutionary studies of sexual size dimorphism* (eds DJ Fairbairn, WU Blanckenhorn, T Székely), pp. 27–37. Oxford, UK: Oxford University Press.
12. Pincheira-Donoso D, Hunt J. 2015 Fecundity selection theory: concepts and evidence. *bioRxiv* 015586. (doi:10.1101/015586)
13. Young CC. 1958 On the Pachypleurosauroida from keicous, South-west China. *Acta Paleontol. Sin.* **7**, 69–81.
14. Sato T, Cheng Y, Wu X, Shan H. 2013 *Diandongosaurus acutidentatus* Shang, Wu & Li 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauroptrygians. *Geol. Mag.* **151**, 121–133. (doi:10.1017/S0016756813000356)
15. Cheng YN, Wu XC, Sato T, Shan HY. 2012 A new eosauroptrygian (Diapsida, Sauropterygia) from the Triassic of China. *J. Vertebrate Paleontol.* **32**, 1335–1349. (doi:10.1080/02724634.2012.695983)
16. Xue Y, Jiang D, Motani R, Rieppel O, Sun Y, Sun Z, Ji C, Yang P. 2015 New information on sexual dimorphism and allometric growth in *Keichousaurus hui*, a pachypleurosaur from the Middle Triassic of Guizhou, South China. *Acta Paleontol. Pol.* **60**, 681–687. (doi:10.4202/app.00006.2013)
17. Zhang X, Xiong JL, Lv YY, Zhang L, Sun YY. 2014 Sexual size and shape dimorphism in the Wushan salamander, *Liuia shihi* (Liu, 1950) (Urodela: Hynobiidae). *Ital. J. Zool.* **81**, 368–373. (doi:10.1080/11250003.2014.920927)
18. Reinhard S, Renner S, Kupfer A. 2015 Sexual dimorphism and age of Mediterranean salamanders. *Zoology* **118**, 19–26. (doi:10.1016/j.zool.2014.08.002)
19. Reinhard S, Kupfer A. 2015 Sexual dimorphism in a French population of the marbled newt, *Triturus marmoratus* (Urodela: Salamandridae). *Salamandra* **51**, 121–128.
20. Nijhout HF, German RZ. 2012 Developmental causes of allometry: new models and implications for phenotypic plasticity and evolution. *Integr. Comp. Biol.* **52**, 43–52. (doi:10.1093/icb/lcs068)
21. Ma ZL, Cardinal-Stakenas A, Park Y, Trosset MW, Priebe CE. 2010 Dimensionality reduction on the Cartesian product of embeddings of multiple dissimilarity matrices. *J. Classif.* **27**, 307–321. (doi:10.1007/s00357-010-9059-3)
22. Tjørve E, Tjørve KMC. 2010 A unified approach to the Richards-model family for use in growth analyses: why we need only two model forms. *J. Theor. Biol.* **267**, 417–425. (doi:10.1016/j.jtbi.2010.09.008)
23. Cooper LN, Lee AH, Taper ML, Horner JR. 2008 Relative growth rates of predator and prey dinosaurs reflect effects of predation. *Proc. R. Soc. B* **275**, 2609–2615. (doi:10.1098/rspb.2008.0912)
24. Ohnishi S, Yamakawa T, Akamine T. 2014 On the analytical solution for the Pütter–Bertalanffy growth equation. *J. Theor. Biol.* **343**, 174–177. (doi:10.1016/j.jtbi.2013.10.017)
25. Organ CL, Janes DE, Meade A, Pagel M. 2009 Genotypic sex determination enabled adaptive radiations of extinct marine reptiles. *Nature* **461**, 389–392. (doi:10.1038/Nature08350)
26. Lovich JE, Gibbons JW. 1992 A review of techniques for quantifying sexual size dimorphism. *Growth Dev. Aging* **56**, 269–281.
27. Székely T, Liker A, Freckleton RP, Fichtel C, Kappeler PM. 2014 Sex-biased survival predicts adult sex ratio variation in wild birds. *Proc. R. Soc. B* **281**, 20140342. (doi:10.1098/rspb.2014.0342)
28. Arendt JD, Reznick DN, Lopez-Sepulcre A. 2014 Replicated origin of female-biased adult sex ratio in introduced populations of the Trinidadian guppy (*Poecilia reticulata*). *Evolution* **68**, 2343–2356. (doi:10.1111/Evo.12445)

29. Vollrath F, Parker GA. 1992 Sexual dimorphism and distorted sex-ratios in spiders. *Nature* **360**, 156–159. (doi:10.1038/360156a0)
30. Crowley PH, Johansson F. 2002 Sexual dimorphism in Odonata: age, size, and sex ratio at emergence. *Oikos* **96**, 364–378. (doi:10.1034/j.1600-0706.2002.960218.x)
31. Poulin R. 1997 Covariation of sexual size dimorphism and adult sex ratio in parasitic nematodes. *Biol. J. Linn. Soc.* **62**, 567–580. (doi:10.1111/j.1095-8312.1997.tb00322.x)
32. Johansson F, Crowley PH, Brodin T. 2005 Sexual size dimorphism and sex ratios in dragonflies (Odonata). *Biol. J. Linn. Soc.* **86**, 507–513. (doi:10.1111/j.1095-8312.2005.00549.x)
33. Hirst AG, Kjørboe T. 2014 Macroevolutionary patterns of sexual size dimorphism in copepods. *Proc. R. Soc. B* **281**, 20140739. (doi:10.1098/rspb.2014.0739)