



# Evolution of sexual dimorphism in the plateau brown frog fails to obey Rensch's rule

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Rensch's rule describes sexual size dimorphism (SSD) that decreases with increasing body size when females are larger than males and SSD that increases when males are larger than females. The plateau brown frog *Rana kukunoris*, a species endemic to the eastern Tibetan Plateau, exhibits female-biased size dimorphism. Using data on body size from 26 populations and age from 21 populations, we demonstrated that SSD did not increase with increasing mean female snout-vent length (SVL) when controlling for sex-specific age structure, failing to support the Rensch's rule. Thus, we suggest that fecundity selection (favouring large female size) balances out sexual selection (favouring large male size), which results in a similar divergence between males and females body size. In addition, sex-specific age differences explained most of the variation of SSD across populations.

*Keywords:* Age difference, Sexual size dimorphism, *Rana kukunoris*, Rensch's rule

## INTRODUCTION

Sexual size dimorphism (SSD) is the intraspecific difference in body size between both sexes, which is a widespread phenomenon in natural populations (Shine, 1989). Rensch's rule states that SSD increases with increasing mean body size among species or populations when males are the larger sex (Rensch, 1950). Interestingly, Rensch's rule is one of the most classic summarisations for the patterns of sexual size dimorphism (Liao et al., 2014). However, the inverse of Rensch's rule postulates that SSD decreases with increasing mean body size when females are larger sex (hypo-allometry; Hedrick & Temeles, 1989).

The evolution of Rensch's rule results from sexual selection, fecundity selection, and ecological divergence all acting concurrently in the same species or population. Sexual selection might favour large male body size because large males have a higher chance of success in male-male competition (Darwin, 1874; Székely et al., 2004; Dale et al., 2007), or smaller male size because of increased mobility or agility (Székely et al., 2004; Kelly et al., 2008), but not in females because reproduction competition is significantly less costly for them (Shine, 1989). In this case, SSD patterns are expected to consistent with Rensch's rule. Thus, Walke et al. (2009) suggested that Rensch's rule may be manifest through the evolution of sex-specific developmental modifiers. Fecundity selection could favour large body size in

females, however, as ecological competition between the sexes could then enlarge this difference. For example, limited resources would result in one sex being smaller to compensate for the larger size of the other sex. Thus, if fecundity selection may mainly act in the different species or same species across populations, which would result in SSD patterns obeying the inverse of Rensch's rule. Liao et al. (2014) suggested that Rensch's rule occurs if intense direct selection favours male adult body sizes in both sexes, while the inverse is expected if intense selection favours female adult body sizes. In addition to these two evolutionary explanations, differences in growth rate and/or age structure between sexes can drive the evolution of SSD (Monnet & Cherry, 2002; Fairbairn et al., 2007). For example, females begin breeding later, live longer but grow more slowly than males, resulting in female-larger patterns of SSD in anuran lineages.

Although a few studies of Rensch's rule have begun to test intraspecific patterns in recent years (e.g., Kupfer, 2007; Herczeg et al., 2010; Kelly et al., 2013; Sutter et al., 2008; Polák & Frynta, 2010; Frynta et al., 2012), most studies have concentrated heavily on interspecific tests of Rensch's rule (reviewed by Liao et al., 2014). Most intraspecific tests have concentrated on taxa with male-biased SSD, while few species with female-biased SSD has been studied. In 90 % of anuran species, females are larger than males (Shine, 1979). However, little attention has been paid to intraspecific patterns of Rensch's rule in amphibians (but see Liao & Chen, 2012; Lu et al., 2014).

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In this study, we examined patterns and possible causes of variation in SSD in the plateau brown frog, *Rana kukunoris*, a species endemic to the eastern Tibetan Plateau (Fei & Ye, 2001). Adult female plateau brown frogs are larger than males in natural populations. Moreover, larger females produce significantly heavier clutches, containing more embryos, indicative of higher fecundity (Chen et al., 2013). Specifically, we tested whether Rensch's rule holds in this species by studying 24 populations. Additionally, we also examined whether there is a correlation between the degree of SSD and operational sex ratio (OSR, the ratio of the sexually competing males to fertilisable females in a breeding aggregation at a given time), sex ratio (SR, the ratio of the number of adult males to the number of adult females in each population), sex-specific age difference (SSAD, the difference between mean male age and mean female age), or elevation.

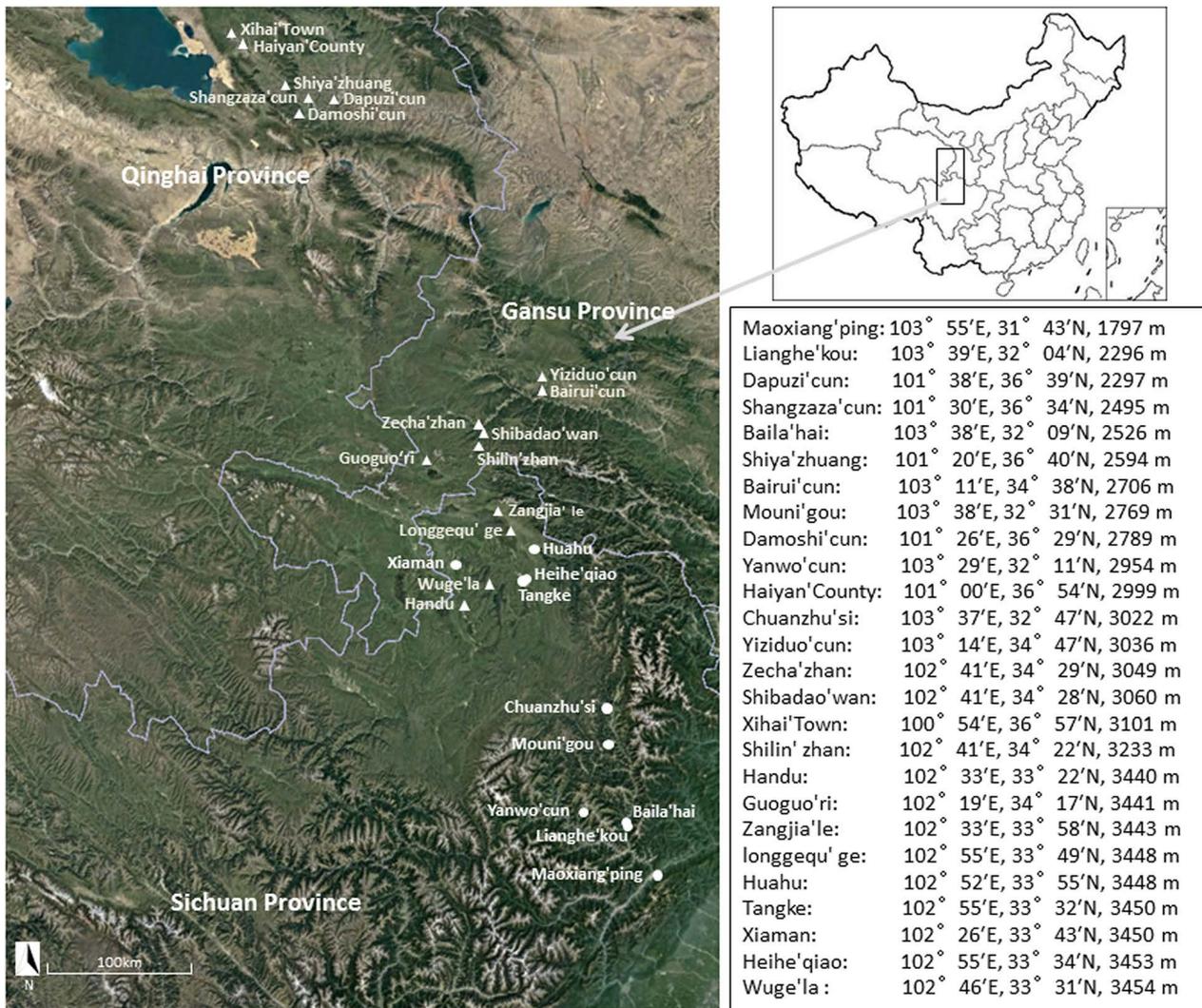
## MATERIALS & METHODS

### Sample collection

A total of 1,868 adult frogs (1,228 males, 640 females, unpublished data) were collected at sixteen localities

with different elevations in the eastern Tibetan Plateau. The body size and age of both sexes in ten different elevations have been surveyed in this species during their breeding seasons (Feng et al., 2015). Thus, from the published literatures and field data we collected for this study, we obtained body size data from 26 male populations and 24 female populations, and age from 21 male populations and 19 female populations (Fig. 1). We recorded population sex ratio and the operational sex ratio in each population.

Frogs were caught by hand from 2008 to 2013 in twelve spawning ponds between March and April, and four feeding sites where frogs may find prey between June and August. We used a caliper to measure snout-to-vent length (snout-to-vent length, SVL, to the nearest 0.1 mm) of both sexes. In *R. kukunoris*, brown-black nuptial pads of front fingers were used to identify males during the breeding season. We randomly removed the longest phalange of the left hindfoot of both sexes in each population which were then preserved in 10 % aqueous solution of formaldehyde for later histological section. All frogs examined were released to original collecting sites. We compiled data on average air temperatures based on data obtained from the Chinese Meteorological



**Figure 1.** Topographic map showing the location of the 26 *Rana kukunoris* study populations in the eastern Tibetan plateau. Triangle, this study; circles, from Feng et al., 2015.

**Table 1.** Study site details, including altitude, latitude, longitude, temperature, sample size (n), mean ( $\pm$ SD) body size and age in males and females of 26 populations of plateau brown frog *Rana kukunoris* in Tibet Plateau.

Sites	Altitude (m)	Latitude (degrees)	Longitude (degrees)	Temperature ( $^{\circ}$ C)	Female SVL (mm)	Male SVL (mm)	Female age (yr)	Male age (yr)	References
Maoliangping	1797	31.71	103.91	10.8	49.50 $\pm$ 5.42 n = 3	43.53 $\pm$ 3.88 n = 34	4.00 $\pm$ 0.00 n = 3	2.97 $\pm$ 1.31 n = 34	Feng et al. 2015
Lianghe'kou	2296	32.07	103.65	9.0	63.77 $\pm$ 7.81 n = 4	50.20 $\pm$ 5.83 n = 17	3.00 $\pm$ 0.00 n = 4	2.65 $\pm$ 0.70 n = 17	Feng et al. 2015
Dapuzi'cun	2297	36.65	101.65	6.2	61.71 $\pm$ 5.19 n = 7	54.70 $\pm$ 3.71 n = 17	4.14 $\pm$ 1.07 n = 7	2.82 $\pm$ 0.53 n = 17	This study
Shangzaza'cun	2495	36.57	101.5	4.1	57.22 $\pm$ 4.81 n = 5	52.96 $\pm$ 6.93 n = 5			This study
Baila'hai	2526	32.09	103.64	8.6		46.99 $\pm$ 5.90 n = 19		3.37 $\pm$ 1.07 n = 19	Feng et al. 2015
Shiya'zhuang	2594	36.68	101.34	3.7	58.45 $\pm$ 4.77 n = 14	51.44 $\pm$ 3.63 n = 39	4.00 $\pm$ 0.91 n = 13	2.49 $\pm$ 0.60 n = 39	This study
Bairui'cun	2706	34.64	103.19	3.9		48.18 $\pm$ 2.89 n = 50		2.68 $\pm$ 0.71 n = 50	This study
Mouni'gou	2769	32.51	103.64	7.6	49.93 $\pm$ 6.45 n = 8	50.44 $\pm$ 6.21 n = 6	3.38 $\pm$ 0.74 n = 8	3.67 $\pm$ 0.82 n = 6	Feng et al. 2015
Damoshi'cun:	2789	36.49	101.44	2.6	56.33 $\pm$ 3.84 n = 43	50.25 $\pm$ 4.19 n = 53	3.67 $\pm$ 0.78 n = 43	2.87 $\pm$ 0.81 n = 53	This study
Yanwo'cun	2954	32.19	103.49	6.9	57.62 $\pm$ 7.77 n = 5	53.38 $\pm$ 3.99 n = 27	3.20 $\pm$ 0.45 n = 5	3.44 $\pm$ 0.58 n = 27	Feng et al. 2015
Haiyan'County	2999	36.90	101.01	1.7	44.76 $\pm$ 4.60 n = 38	43.82 $\pm$ 4.38 n = 150	3.84 $\pm$ 1.11 n = 25	3.27 $\pm$ 0.87 n = 84	This study
Chuanzhu'si	3022	32.78	103.62	6.2	57.42 $\pm$ 2.90 n = 5	51.85 $\pm$ 2.76 n = 21	3.80 $\pm$ 0.84 n = 5	3.19 $\pm$ 0.51 n = 21	Feng et al. 2015
Yiziduo'cun:	3036	34.79	103.23	3.1	59.65 $\pm$ 4.30 n = 51	50.13 $\pm$ 3.44 n = 106	4.90 $\pm$ 0.83 n = 51	3.42 $\pm$ 0.65 n = 71	This study
Zecha'zhan	3049	34.49	102.69	3.1	59.70 $\pm$ 3.43 n = 115	52.03 $\pm$ 3.30 n = 219	4.06 $\pm$ n = 18	3.53 $\pm$ 0.70 n = 19	This study
Shibadao'wan	3060	34.47	102.69	2.9	60.42 $\pm$ 4.28 n = 9	51.23 $\pm$ 2.99 n = 11	4.38 $\pm$ 1.51 n = 8	3.45 $\pm$ 0.52 n = 11	This study
Xiahai'Town	3101	36.96	100.91	1.6	51.20 $\pm$ 0.00 n = 1	43.79 $\pm$ 4.65 n = 8	4.00 $\pm$ 0.00 n = 1	3.38 $\pm$ 0.92 n = 8	This study
Shilin' zhan	3233	34.37	102.68	2.5	58.65 $\pm$ 5.00 n = 40	51.90 $\pm$ 3.96 n = 88	4.07 $\pm$ 0.64 n = 30	2.92 $\pm$ 0.65 n = 24	This study
Handu	3440	33.36	102.55	1.8	46.10 $\pm$ 4.09 n = 10	43.84 $\pm$ 3.40 n = 19			This study
Guoguori	3441	34.29	102.31	1.43	54.84 $\pm$ 3.94 n = 270	47.71 $\pm$ 3.32 n = 399	4.57 $\pm$ 1.17 n = 42	3.95 $\pm$ 0.94 n = 73	This study
Zangjia' le	3443	33.97	102.8	1.5	49.10 $\pm$ 7.22 n = 10	47.00 $\pm$ 2.71 n = 10			This study
longgequ' ge	3448	33.81	102.91	1.5	48.24 $\pm$ 7.86 n = 6	44.85 $\pm$ 4.12 n = 21			This stud
Huahu	3448	33.92	102.87	1.5	52.11 $\pm$ 4.20 n = 7	46.10 $\pm$ 3.38 n = 18	3.71 $\pm$ 0.76 n = 7	3.22 $\pm$ 0.43 n = 18	Feng et al. 2015
Tangke	3450	33.54	102.91	1.8	59.60 $\pm$ 5.98 n = 6	50.40 $\pm$ 3.97 n = 25	3.50 $\pm$ 0.84 n = 6	3.68 $\pm$ 0.85 n = 25	Feng et al. 2015
Xiaman	3450	33.72	102.44	2.0	49.54 $\pm$ 5.88 n = 5	47.34 $\pm$ 3.12 n = 10	3.40 $\pm$ 0.52 n = 5	3.20 $\pm$ 0.45 n = 10	Feng et al. 2015
Heihe'qiao	3453	33.56	102.92	1.8	54.40 $\pm$ 6.61 n = 11	50.78 $\pm$ 3.42 n = 27	3.64 $\pm$ 0.92 n = 11	3.59 $\pm$ 0.89 n = 27	Feng et al. 2015
Wuge'la	3454	33.52	102.76	1.8	42.56 $\pm$ 5.19 n = 21	42.05 $\pm$ 3.80 n = 33			This study

Administration (<http://www.cma.gov.cn>), Gansu Gahai-Zecha National Nature Reserve Management Bureau and the published literatures (Feng et al., 2015).

#### Age determination

The paraffin sections and Ehrlich's haematoxylin stain were used to produce histological sections of the phalanges. We counted the number of lines of arrested growth (LAG) in the sections to determine age.

Skeletochronology has been successfully used to age anurans such as *Rana chensinensis* (Lu et al., 2006) and *Bufo minshanicus* (Yu et al., 2019). In this study, 238 females and 449 males were skeletochronologically aged. An index of SSD was calculated with the following equation:  $\log_{10}(\text{mean female SVL}) - \log_{10}(\text{mean male SVL})$  (Smith, 1999). The sex-specific age difference (SSAD) for each population was calculated with the following equation:  $\log_{10}(\text{female age}) - \log_{10}(\text{male age})$ .

### Statistical analyses

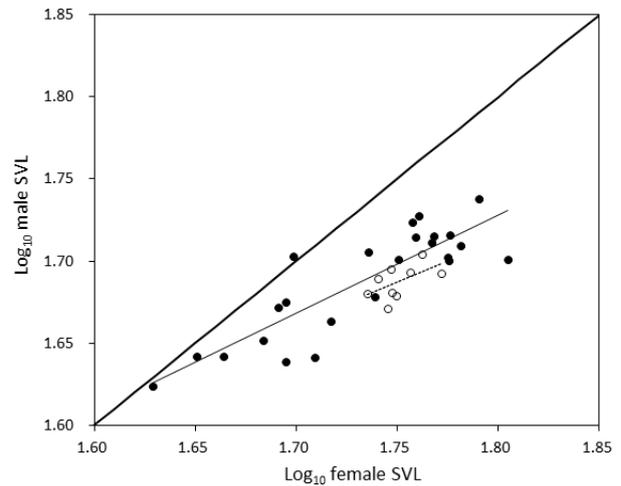
To meet the assumption of normality, we  $\log_{10}$ -transformed body size, age and clutch volume. We fit two generalised linear models (GLMs) to test differences in body size (and age) of sampled individuals between sexes among the 16 (and 11) populations (unpublished data) where population as a random factor and sex as a fixed factor. Then, to investigate variation in SSD among populations, a GLM was used where age was added as covariate together with two interactions between sex and age (fixed effect) and between sex and population (fixed effect). A significant interaction between sex and age would be indicative of differences in growth rates between the sexes, while a significant interaction between sex and population would reveal variation in SSD among-population.

To test Rensch's rule, we regressed mean  $\log_{10}$  (female SVL) on the mean  $\log_{10}$  (male SVL) across 26 or nine populations. The model I regression (ordinary least squares; OLS) may yield misleading results because independent variable (female size) is measured without error (Fairbairn, 1997). Hence, the model II regression (reduced major axis; RMA) was also conducted to test for Rensch's rule and to test the null hypothesis of slope = 1 as judged from the overlap of 95 % confidence intervals with a line of isometry (Fairbairn, 1997; for details, see Sokal & Rohlf [1981, p. 219]).

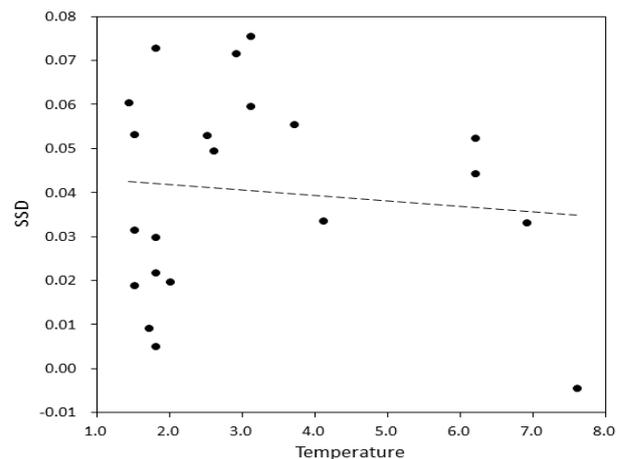
A correlation analysis was used to test the correlation between SSD and SR, OSR, elevation, and temperature, as well as SSAD across populations. Prior to analyses, we removed five populations (1,797 m/asl, 2,296 m/asl and 2,526 m/asl from the published literatures; 2,706 m/asl and 3,101 m/asl from our field studies) because the sample size of one of both sexes was less than five individuals. All analyses were performed with the IBM SPSS Statistics 20.0 (IBM Corp, Armonk, NY, USA).

## RESULTS

The mean body size varied significantly among the 14 populations ( $F_{13, 1794} = 115.179$ ,  $p < 0.001$ ) and between the sexes ( $F_{1, 1794} = 967.377$ ,  $p < 0.001$ ), with females always being larger than males (Table 1). The mean age also varied significantly among the nine populations ( $F_{8, 618} = 20.784$ ,  $p < 0.001$ ; Table 1) and between sexes ( $F_{1, 618} = 189.840$ ,  $p < 0.001$ ). Frogs at higher elevations were significantly older than those at lower elevations ( $p < 0.049$  for 23 of 36 Fisher's LSD post hoc tests); the opposite results occurred ( $p < 0.024$  for 2 post hoc tests), with non-significant differences occurring between neighbouring populations ( $p = 0.089$ – $0.978$  for 4 post hoc tests) or non-neighbouring populations ( $p = 0.105$ – $0.904$  for the 7 post hoc tests). When controlling for the effects of age ( $F_{6, 612} = 155.024$ ,  $p < 0.001$ ), differences in body size among populations ( $F_{8, 612} = 159.759$ ,  $p < 0.001$ ) and between the sexes ( $F_{1, 612} = 127.719$ ,  $p < 0.001$ ) still remained. A non-significant interaction between sex and age indicated that the relationship between body size and age ( $\approx$ growth rate) did not vary between the sexes ( $F_{4, 600} = 1.174$ ,  $p = 0.321$ ). The interaction between population and sex also was statistically significant ( $F_{8,$



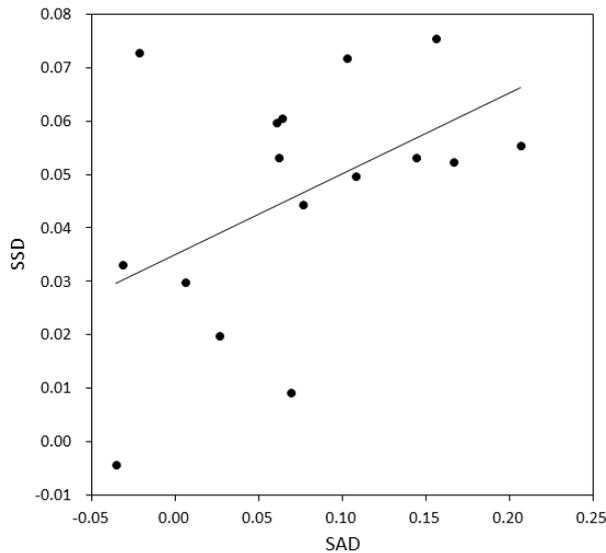
**Figure 2.** Relationship between mean male SVL and female SVL of *Rana kukunoris*. Black circle, relationship based on raw data from 21 populations [linear regression,  $\beta = 0.596 \pm 0.075(\text{SE})$ ]; white circle, relationship based on age-corrected data 9 populations [ $\beta = 0.514 \pm 0.280(\text{SE})$ ]. All data are plotted on logarithm-transformed scale. The thick grey line represents isometry ( $\beta = 1$ ).



**Figure 3.** Relationships between (log) SSD and mean annual air temperature in 16 populations of *Rana kukunoris*. Each dot represents a single population. The dotted line shows a non-significant correlation ( $r = -0.105$ ,  $p = 0.652$ ).

$F_{1, 600} = 19.489$ ,  $p < 0.001$ ), revealing that the degree of SSD vary among the populations.

Model I regression indicated a significant relationship between ( $\log_{10}$ ) male size and ( $\log_{10}$ ) female size among 21 populations ( $F_{1, 20} = 88.80$ , slope = 0.607, 95 % CI = 0.472–0.741,  $p < 0.001$ ; Fig. 2), which conformed to the allometric relationship. Model II regression revealed the same conclusion when RMA regression was used (slope = 0.668, 95 % CI = 0.534–0.803). These results were consistent with the inverse of Rensch's rule. However, there was not a significant allometric relationship (OLS:  $F_{1, 8} = 3.373$ , regression slope = 0.514, 95 % CI = -0.148–1.176,  $p = 0.109$ ; RMA: slope = 0.901, 95 % CI = 0.240–1.563; Fig. 2) between ( $\log_{10}$ ) age-adjusted male size and ( $\log_{10}$ ) age-adjusted female size across nine populations.



**Figure 4.** Relationships between (log) SSD and (log) SSAD in 16 populations of *Rana kukunoris*. Each dot represents a single population. The solid line shows a marginally significant correlation ( $r = 0.481$ ,  $p = 0.059$ ).

The degree of SSD was not related to either OSR ( $r = 0.185$ ,  $n = 17$ ,  $p = 0.477$ ) or SR ( $r_s = 0.800$ ,  $n = 4$ ,  $p = 0.200$ ). Correlations between SSD and elevation ( $r = -0.105$ ,  $n = 21$ ,  $p = 0.650$ ), as well as between SSD and temperature ( $r = -0.105$ ,  $n = 21$ ,  $p = 0.652$ , Fig. 3) were not significant. The degree of SSD was marginally correlated with SSAD ( $r = 0.481$ ,  $n = 16$ ,  $p = 0.059$ ; Fig. 4).

## DISCUSSION

Several hypotheses, including sexual selection, fecundity selection, and sex differences in age have been proposed to explain the evolution of SSD (Shine, 1979; Monnet & Cherry, 2002; Herczeg et al., 2010). In the present study, our results showed that the degree of SSD of *R. kukunoris* varied across different populations, and the degree of female-biased SSD displayed an allometric relationship (slopes  $< 1.0$ ) with mean female body size when ignoring the influence of age structure, conforming to the inverse of Rensch's rule. This result was consistent with previous studies in owls (Abouheif & Fairbairn, 1997), fish (Herczeg et al., 2010) and amphibians (Liao, 2013; Liao et al., 2014).

The majority of studies suggest that sexual selection in favour of large male size is the primary cause of Rensch's rule because large males are more likely to succeed in male-male competition (Fairbairn, 1997). Conversely, to date a few earlier amphibian studies found evidence for the inverse of Rensch's rule (Fairbairn, 1997; Herczeg et al., 2010; Liao & Chen, 2012; Liao, 2013). The fecundity selection on females favouring large size has been proposed as a hypothesis to explain the inverse of Rensch's rule (Fairbairn & Preziosi, 1994). In this study, we did not find a significant relationship between SSD and OSR or SR, suggesting variation in SSD was not associated with the variation in the strength of male-male competition. Moreover, the allometric relationship

was not significant when adjusting for sex-specific age in the analysis, thus our result showed that SSD size relationships in *R. kukunoris* was inconsistent with Rensch's rule and the inverse of it. This pattern has been found exclusively in taxa with female-biased SSD (by reviewed in Liao et al., 2013). Thus, we suggest that fecundity selection (favouring large female size) balances out sexual selection (favouring large male size) and generates a similar divergence between males and females body size, thus the lack of association between SSD and size.

In indeterminately growing ectotherms, environmental factors (e.g., temperature) are likely to play an important role across ontogeny by sex-specific ways to decide final body size (Ceballos & Valenzuela, 2011; Zhang & Lu, 2013). In this study, we found no significant correlation between the degree of SSD and temperature, as well as SSD and elevation, revealing that temperature and elevation are unlikely to explain part of variation in SSD for *R. kukunoris*. For example, males and females may be exposed to similar temperatures, or similar habitat utilisation in natural populations.

Differences in growth rate and age between the sexes have potential effects on the variation in SSD (Fairbairn et al., 2007; Monnet & Cherry, 2002). For instance, anurans living in low temperatures obtain maturity later and grow slower than those exposed to warm temperatures (Morrison & Hero, 2003). In this study, a non-significant interaction between sex and age across populations suggested that differences in growth rates between the sexes may not explain variation in SSD. However, a relationship between SSD and SSAD was marginally significant. Similarly, previous studies showed that a significant correlation between SSD and SSAD by means of comparisons across species or populations (Monnet & Cherry, 2002; Liao & Chen, 2012; Zhang & Lu, 2012; Liao, 2013; Liao et al., 2013). We also found that variation in SSD across populations and the allometric relationship between sexes across populations were not significant when removing the effects of age. Thus, those results suggested that sex differences in the age structure are likely to explain the variation in SSD in *R. kukunoris*. Similarly, Liao and Chen (2012) suggests that the variation of SSD in Chinese wood frog *Rana chensinensis* can be explained by sex differences in age among populations. Therefore, sex difference in the age structure is one of the mechanisms that most likely contributes to the extent of SSD among populations (Liao & Chen, 2012). In the latest studies, however, variation in SSD of *R. kukunoris* resulted from sex differences in growth rates (Feng et al., 2015). This finding is not consistent with our findings from intraspecific comparisons of the same species because the limited sample size in the latest study may have an effect on the insignificant results.

In conclusion, our results showed hyperallometry in SSD in *R. kukunoris* when females are larger, indicating a pattern consistent with the inverse of Rensch's rule. Fecundity selection is the more likely to explain this pattern because reproductive output increases significantly with increasing female body size within and among populations. However, the allometric relationship

was not significant when adjusting for sex-specific age in the analyses, thus our result showed that SSD size relationships in *R. kukunoris* was inconsistent with Rensch's rule and the inverse of it. We suggest that the interplay between natural and sexual selection on females and males have generated a similar divergence between male and female body size, thus the lack of association between SSD and size. Additionally, sex differences in age for populations are a likely explanation for the variation of SSD in *R. kukunoris*.

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