Reciprocal sexual size dimorphism and Rensch's rule in toad-headed lizards, *Phrynocephalus vlangalii*

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Abstract. Rensch's rule describes a pattern of allometry whereby sexual size dimorphism (SSD) increases with body size when males are the larger sex, and whereby SSD decreases with body size when females are larger by intraspecific comparison. In groups of related species or sets of conspecific populations, Rensch's rule has so far largely been confirmed with females being the larger sex in small-sized populations and males the larger sex in large-sized populations. The toad-headed lizard *Phrynocephalus vlangalii* is a small viviparous agamid endemic to China. It exhibits either male- or female-biased SSD depending on the population, and is therefore a good model species to test Rensch's rule relative to SSD direction. Using morphological data from 38 populations across the species' range, we studied whether populations with male- and female-biased SSD both exhibit isometric relationships consistent with Rensch's rule. For populations with male-biased SSD, we reject the hypothesis that SSD consistent with Rensch's rule is driven by allometries in tail length (in this species the tail is used for visual signalling during territory defence). In populations with female-biased SSD we find significant evidence for fecundity selection favouring large females, but Rensch's rule is not supported in this species. Our findings suggest that the underlying evolutionary forces (sexual and fecundity selection) do not promote the direction of SSD consistent with Rensch's rule in both male- and female-biased SSD across populations within a species.

Key words. Squamata, Agamidae, *Phrynocephalus vlangalii*, fecundity selection, Rensch's rule, sexual selection, sexual dimorphism.

Introduction

Conspecific males and females differ significantly in body size in many animal taxa (ANDERSSON 1994). The phenomenon, known as sexual size dimorphism (SSD), continues to attract considerable research efforts (e.g., MONNET & CHERRY 2002, MATĚJŮ & KRATOCHVÍL 2013, LIAO et al. 2013, LIAO et al. 2015, LIAO et al. 2016, JIN et al. 2016). In his seminal work, RENSCH (1960) proposed that SSD increases with overall body size in species where males are the larger sex (hyper-allometry), and SSD decreases with increasing body size in species where females are larger (hypoallometry). Over recent decades, Rensch's rule has been confirmed across a wide range of taxonomic groups with male-biased SSD (insects: FAIRBAIRN 2005, WOLAK 2008, LENGKEEK et al. 2008, WALKER & MCCORMICK 2009; fish: YOUNG 2005; reptiles: IVERSON 1985; turtles: Cox et al. 2007, STUART-FOX 2009, FRÝDLOVÁ & FRYNTA 2010, CEBALLOS et al. 2013; birds: DALE et al. 2007; mammals: CLUTTON- BROCK et al. 1977), and across a small range of taxa with female-biased SSD (STUART-FOX 2009, FAIRBAIRN 1997, TEDER & TAMMARU 2005, STEPHENS & WIENS 2009). In contrast, Rensch's rule is not supported in some taxa with female-biased SSD (JANNOT & KERANS 2003, TUBARO & BERTELLI 2003, WEBB & FRECKLETON 2007, LINDENFORS et al. 2007, LIAO et al. 2013, DE LISLE & ROWE 2013, CABRE-RA et al. 2013). During recent years, intraspecific studies on Rensch's rule have focused on wild (PEARSON et al. 2002, ROITBERG 2007, HERCZEG et al. 2010, LIAO & CHEN 2012, KELLY et al. 2013) and domestic animals (POLÁK & FRYNTA 2009, 2010, REMEŠ & SZÉKELY 2010, FRYNTA et al. 2012). The variations in SSD across populations for most of these do not conform to Rensch's rule (HERCZEG et al. 2010, LIAO 2013).

Sexual dimorphism has attracted considerable attention since DARWIN (1871) proposed the principles of sexual selection (ANDERSSON 1994). Rensch's rule generally implies that the evolution of SSD is mainly driven by selection,

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favouring large males as a consequence of sexual selection stemming from a large-male advantage in male-male competition (Berry & Shine 1980, Fairbairn & Prezio-SI 1994, Abouheif & Fairbairn 1997, Smith & Cheve-RUD 2002, COX et al. 2003, Székely et al. 2004, FAIRBAIRN 2005, DALE et al. 2007, BLANCKENHORN et al. 2007, LISLE-VAND et al. 2009, SERRANO-MENESES et al. 2009). For taxa with male-biased SSD, Rensch's rule results from the action of sexual selection where intense sexual selection fuels the evolution of larger body size in males, accompanied by a weaker correlated selection that favours increased body size in females (FAIRBAIRN 1997, ABOUHEIF & FAIRBAIRN 1997). In species with female-biased SSD, SSD might evolve through different selection pressures on males and females. As proximate causes, sexual selection may favour smaller male size to increase mobility or agility (FAIRBAIRN 1997, SZÉKELY et al. 2004, STUART-FOX 2009). In contrast, fecundity selection favours larger females with increased reproductive potential, and thus has been used to explain SSD patterns consistent with the inverse of Rensch's rule (Cox et al. 2003, LIAO et al. 2013, LU et al. 2014, JIN et al. 2015).

Previous studies on reptiles have confirmed the general pattern of SSD following Rensch's rule applying to taxa with male-biased SSD (Cox et al. 2007, FRÝDLOVÁ & FRYN-TA 2010, CABRERA et al. 2013). In Phrynocephalus lizards, larger male individuals have relatively longer tails so that these individuals have an advantage of improved visibility when engaging in the important behaviour of tail curling and thus stand a better chance of attracting mates. Hence, sexual selection favours an increase in male body size, resulting in an SSD that follows Rensch's rule (Cox et al. 2007). In the present paper, we describe the patterns of SSD in the toad-headed lizard Phrynocephalus vlangalii, a species characterized by an inconsistent SSD (male or female-biased) depending on the population. The aim of this study was to investigate patterns and possible causes of variation in reciprocal SSD found within a single species (P. vlangalii) and in particular, conduct an intraspecific test of Rensch's rule in the species. To this end, we analysed a large dataset of male and female body and tail sizes from 38 populations collected in the Hengduan Mountains, China. In addition to testing for Rensch's rule, we also tested hypotheses regarding whether sexual selection favouring increased body size in males, which was tied to longer tail length, led to variation in SSD consistent with Rensch's rule across male-biased populations. Moreover, we investigated whether fecundity selection favouring increased reproductive investment in larger female size resulted in variation in SSD consistent with the inverse of Rensch's rule across female-biased populations. Temperature can induce substantial phenotypic plasticity in the size of reptiles. In general, SSD can arise when males and females respond differently to temperature at different altitudes (ANGILLETTA & DUNHAM 2003). We therefore analysed the relationship between SSD and altitude. Finally, we discuss why in some populations of P. vlangalii males are larger than females whereas females are larger than males in others.

Materials and methods Study species

The toad-headed lizard P. vlangalii is a small viviparous agamid endemic to China and typically found in arid or semiarid regions. Its distributional range covers Qinghai, Gansu, Xinjiang, and northwestern Sichuan, at altitudes ranging from 2,000 to 4,500 m above sea level (ZHAO & ADLER 1993). The species has an activity season that stretches from May through October. Female reproduction and sexual dimorphism as well as altitudinal variation of morphological characters of P. vlangalii have been described previously (HUANG & LIU 2002, WU et al. 2005, ZHANG et al. 2005, JIN & LIU 2007, JIN et al. 2006, QI et al. 2011). We collected data on average reproductive investments of females in 15 populations (i.e., from 6 male- and 9 female-biased populations). During courtship, males use tail-curling to attract potential mates, with tail length being positively correlated to the frequency of tail-curling as well as territory size (ZHANG et al. 2005, QI et al. 2011). Females will take note of the length of males' tails, the degree of curling, and the frequency of swinging, and then approach a male that advertises himself with a longer tail, intense curling and swinging (QI et al. 2011). As a result, males with longer tails, intense curling and swinging are more likely to mate with females, confirming that a male's tail length plays a more important role than body size and resulting in greater variation in SSD.

Data collection

For the present work, we combined published information (data taken from ZHANG et al. 2005, JIN et al. 2006, JIN & LIU 2007, QI et al. 2011) with our own data based on the measurements of 362 museum specimens at the Zoological Museum in Chengdu Institute of Biology, Chinese Academic of Science, collected between the 1950s and 2000s during the breeding season between July and August (Supplementary table 1). All museum specimens were stored in 10% neutral buffered formalin, which did not result in shrinkage based on the fact that there is no difference in body and tail sizes between data recorded at the time of sampling and the same individuals in preservative (HUANG et al. 2014). Snout-vent length (SVL) and tail length (TL) were measured to the nearest 0.1 mm, and SVL was used as the body size variable to investigate Rensch's rule. Individuals larger than 48 mm in SVL were considered adults, because these males and females have the potential to reproduce (JIN et al. 2006). A total of 362 museum specimens were considered adults because their SVL was > 48 mm (see Table 1). The same threshold was applied to literature data on individuals. We analysed 38 populations of P. vlangalii (Fig. 1). Populations were defined as different field sites of collection. Previously published data on reproductive investment, i.e., the total embryo mass of each female (JIN & LIU 2007), was also considered to test the potential effect of fecundity selection on SSD. The SSD index was

calculated according to LOVICH & GIBBONS (1992) as follows: SSD = $1 \times [(larger sex/smaller sex) - 1]$ if females were larger than males, or SSD = $-1 \times [(larger sex/smaller sex) - 1]$ if males were larger than females. In this manner, positive values indicate female-biased SSD, and negative values indicate male-biased SSD.

Statistical analysis

All SVL and TL data were log₁₀-transformed to correct for allometric effects and achieve data normality (tested with Kolmogorov-Smirnov tests) and linearity. Sex differences in mean body size between populations were tested using a general linear model (GLM) with log₁₀ (SVL) as a dependent variable, and population and sex as fixed factors. We used a reduced major axis regression (RMA) of log, (female size) against log₁₀ (male size) and measured 95% confidence intervals to test the null hypothesis that the slope of the larger sex equals 1 (a pattern consistent with Rensch's rule requires hyper-allometry and therefore a slope significantly > 1; see FAIRBAIRN 1997). The RMA regression was done manually following SOKAL & ROHLF (1981). RMA regression provides more reliable results than least-squares regression in cases such as this one where the potential for error exists in the measurements of both variables. We used a Pearson correlation to test for relationships between SSD and altitude, and a linear regression to test for a correlation between effect size (slope estimate) and sample size per population. To test the effect of sexual selection and fecundity selection on SSD, we estimated the relationships between tail length and SSD, and between reproductive investment and female size, with Pearson correlation coefficients. P values below 0.05 (two-tailed) were considered statistically significant. All values are presented as means \pm 1 SD.

Results



Figure 1. The 38 sampling localities for *Phrynocephalus vlangalii* in Qinghai and adjacent provinces in western China. Black circles – male-biased SSD populations; white circles – female-biased SSD populations.

lations either (male-biased: R = -0.022, n = 18, P = 0.932; female-biased: R = -0.016, n = 20, P = 0.947).

We found that effect size (slope estimate) was not significantly correlated with sample size per population ($R^2 =$ 0.214, P = 0.543), suggesting that sample size itself may not result in a bias in the pattern estimation of SSD to body size. The slope of the generalized least-squares regression of log₁₀ (male SVL) on log. (female SVL) across all populations was not significantly different from 1 in least-squares regression (Fig. 2a; $R^2 = 0.48$, slope = 0.85, 95% CI = 0.55-1.16). A similar pattern emerged when using the RMA regression (slope = 1.23, 95% CI = 0.65-1.36), rejecting Rensch's rule. When treating the reciprocal SSD populations separately we did



not observe any hyper-allometry in populations with malebiased SSD (Fig. 2b; slope = 0.85, 95% CI = 0.66-1.57) or hypo-allometry in populations with female-biased SSD (slope = 0.95, 95% CI = 0.71-1.13; Fig. 2b) either.

Considering all populations, we found significant relationships existed between male size and tail length (R = 0.730, n = 38, P < 0.001; Fig. 3a.) and between female size and reproductive investment (R = 0.576, n = 15, P = 0.024; Fig. 3b). These relationships remained significant even when discerning between male-biased and female-biased SSD populations (male size and male tail length in malebiased populations, R = 0.580, n = 18, P = 0.012; femalebiased populations, R = 0.822, n = 20, P < 0.001; Fig. 4). However, we only find a positive correlation between female size and reproductive investment in female-biased populations (R = 0.699, n = 9, P = 0.036; Fig. 5), but not in male-biased populations (R = -0.269, n = 6, P = 0.606; Fig. 5)



Figure 2. Relationship between \log_{10} (male size) and \log_{10} (female size) in *Phrynocephalus vlangalii*; a) 38 populations; b) black circle and dotted line - male-biased SSD populations; white circle and grey line - female-biased SSD populations. All data are plotted on a logarithm-transformed scale. The thick grey line represents isometry (slope = 1). Each dot represents a single population based on the mean body sizes of males and females.

Figure 3. Relationships between male size and tail length and between female size and reproductive investment in Phrynocephalus vlangalii across all populations. Each dot represents a single population, n means clutch size.

Discussion

Our results demonstrate that *Phrynocephalus vlangalii* does not display a pattern of SSD increasing with increased body size across populations with male-biased SSD, and/ or decreases with increasing body size across populations with female-biased SSD. In other words, this study shows an inconsistency with Rensch's rule irrespective of SSD bias, and is thus not in line with previous works that most-ly confirmed Rensch's rule when males were the larger sex. Although body size is correlated with tail length in male-biased populations, selection for longer tails cannot explain the variation in SSD that is inconsistent with Rensch's rule. Additionally, fecundity selection favours larger females, which cannot explain isometric relationships consistent with the inverse of Rensch's rule in female-biased populations.

A previous study showed that male *P. vlangalii* perform tail curling and wagging while guarding their territories during the reproductive season, and tail length in *P. vlangalii* is positively correlated with territory size (QI et al. 2011). Territory size in reptiles is generally assumed to reflect access to resources such as food and basking sites as well as mating partners (e.g., MARTINS 1994, HAENEL et al. 2003). For *Phrynocephalus* (Agamidae) lineages, sexual selection also favours larger absolute and relative tail lengths in males (JIN et al. 2013). We therefore hypothesize that the length of a male's tail in *P. vlangalii* might be more important for patterns of sexual selection than body size alone. Although we found a correlation between tail length and body size, this pattern cannot explain the observed deviation from Rensch's rule, however. Meanwhile, the significant relationships between male size and tail length in both male- and female-biased populations also suggest that sexual selection cannot promote SSD by following Rensch's rule. In lizards, variation of SSD can be related to habitat structure (ANDREWS & STAMPS 1994, STUART-FOX 2009), and future studies on SSD in *P. vlangalii* should include detailed descriptions of local habitats as a potential predictor of SSD bias.

Populations with female-biased SSD are also expected to exhibit a hypo-allometric relationship with body size (FAIRBAIRN 1997, CEBALLOS et al. 2013), although empirical data regularly reject this assumption (JANNOT & KERANS 2003, BLANCKENHORN et al. 2007, STEPHENS & WIENS 2009). The processes contributing to the evolution of SSD for taxa with female-biased SSD are generally more diverse than for taxa with male-biased SSD. For example, many birds with female-biased SSD are characterized by paternal care, and it has been proposed that small size may be adaptive for males that provide food to offspring (TUBARO & BERTELLI 2003). BERRY & SHINE (1980) also suggested that small male size may render mate searching more effective and favour agility, and patterns of female-biased SSD have indeed been found to be consistent with this hypothesis (horned lizards: ZAMUDIO 1998; shorebirds: Székely et al. 2004). Comparative studies have furthermore documented evolutionary increases in clutch or litter size associated with shifts toward female-biased SSD (HEAD 1995, Cox et al. 2003), and fecundity selection can result in the inverse of Rensch's rule (FAIRBAIRN 1997, HERCZEG et al. 2010, LIAO & CHEN 2012). Our findings revealed a significant relationship between female size and reproductive investment across all 15 populations and in female-biased SSD



Figure 4. Relationship between male size and tail length in *Phrynocephalus vlangalii* across populations; a) black circle and dotted line – male-biased SSD populations; white circle and grey line – female-biased SSD populations. Each dot represents a single population.

Figure 5. Relationship between female size and reproductive investment in *Phrynocephalus vlangalii* across populations; a) black circle and dotted line – male-biased SSD populations; white circle and grey line – female-biased SSD populations. Each dot represents a single population, n means clutch size.

populations, inconsistent with a slope between male and female body size, which was indiscernible from one slope. Fecundity selection therefore was not powerful enough a factor to reverse Rensch's rule in *P. vlangalii*.

The mechanisms behind SSD allometry across populations within a species can be explained by detailed knowledge of this species' biology (FAIRBAIRN 2005). However, many studies cannot distinguish between local adaptation and phenotypic plasticity behind the observed patterns, because environmental conditions strongly affect the expression of SSD (Fairbairn & Preziosi 1994, Teder & Tam-MARU 2005). In reptiles, individual and populational differences in the most important life-history traits (i.e., age, body size, and growth) can be strongly affected by direct environmental induction (PEARSON et al. 2002, ROITBERG 2007). For example, sex-specific differences in growth rate and/or the time available for growth have the potential of influencing SSD in a given population (KUPFER 2007). In P. vlangalii, the greater variation in SSD that was introduced by our not considering age certainly caused our allometric tests to be less expressive.

Typically for indeterminately growing poikilothermic organisms such as reptiles, ecological factors can impact on ontogeny in sex-specific ways and influence the body size of individuals (CEBALLOS et al. 2011). However, the lack of a correlation between altitude and variation of SSD suggests that altitude-dependent growth and development did not influence our results, even though individual-specific age data are unavailable for our study specimens (differential age and growth has previously been shown to influence SSD; see Wu et al. 2005). Given these considerations, it would be too early to conclude that the patterns of SSD observed are not influenced by direct ecological factors. On the other hand, the combination of field data with measurements from preserved specimens should not have biased any of our inferences, as males and females are assumed to be equally affected.

In conclusion, we have found no evidence that the relationship between SSD and body size in P. vlangalii follows a pattern consistent with Rensch's rule across both male- and female-biased SSD populations. Our evidence suggests that the patterns of sexual and/or fecundity selection cannot explain the variation in SSD between both across male- and female-biased populations that is inconsistent with Rensch's rule despite significant correlations between body size and both tail length and reproductive investment. As the patterns of SSD across populations are expected to show to be insensitive to variation stemming from age structure effects, age-related phenotypic plasticity is a likely explanation for the observed pattern. Future studies on the evolution of SSD in species in which the direction of SSD varies across populations should consider population-specific age and growth rates, identify and consider ecological factors that might impact differentially on sexes and populations, the degree of population isolation, and include the temporal evolutionary stability of population-specific SSD as well.

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Supplementary material

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Supplementary table 1. *Phrynocephalus vlangalii* study populations and their meristic attributes.

Supplementary table 1.	Phrynocephalus	vlangalii study	populations ((n = 38) ar	nd their	meristic	attributes.	TL – t	ail length	(mm);
SVL - snout-vent length	(mm); TOM - t	otal offspring n	nass (g). All v	variables are	e shown	as mean	± SE.			

Sites	Location	Altitude (m a.s.l.)	Sample size males\ females	Males SVL	Females SVL	Males TL	Females TOM	Data sources
Heidaban	39.44°N, 95.11°E	2289	10/10	57.3±1.4	60.8±1.5	66.0±1.7		JIN et al. (2006)
Lenghu	38.75°N, 93.35°E	2751	9/7	63.3±1.1	64.0±1.5	65.0±1.2		JIN et al. (2006)
Lenghu	38.74°N, 93.36°E	2756	9/6	55.6±2.0	57.3±1.1	53.0±2.7	1.45±0.13	JIN et al. (2006); JIN & LIU (2007)
Nomhon	36.38°N, 96.45°E	2857	6/6	62.6±3.3	59.0±2.0	70.3±3.3	1.77±0.24	JIN et al. (2006); JIN & LIU (2007)
Delingha	37.22°N, 97.40°E	2873	17/17	67.3±1.0	68.8±1.8	73.0±1.2	3.27±0.46	JIN et al. (2006); JIN & LIU (2007)
Urt Moron	36.82°N, 93.16°E	2894	11/9	56.2±1.5	53.6±0.7	62.1±1.6	1.61±0.15	JIN et al. (2006); JIN & LIU (2007)
Maqu	34.95°N, 102.08°E	2926	14/25	57.5±0.6	59.7±0.7	56.6±0.7	2.41±0.19	JIN et al. (2006); JIN & LIU (2007)
Ulan	36.93°N, 98.47°E	2929	47/21	55.7±1.3	51.1±0.8	59.3±0.7	2.85±0.28	JIN et al. (2006); JIN & LIU (2007)
Xingride	36.01°N, 97.88°E	3074	27/9	59.0±0.7	61.2±1.0	63.9±1.7	3.26±0.29	JIN et al. (2006); JIN & LIU (2007)
Mangya	38.35°N, 90.15°E	3174	8/7	60.5±1.2	56.4±1.5	62.2±1.9	2.81±0.31	JIN et al. (2006); JIN & LIU (2007)
Qagan Us	36.30°N, 98.08°E	3190	20/17	54.1±1.0	59.0±1.1	56.8±1.4	3.68±0.26	JIN et al. (2006); JIN & LIU (2007)
Da Qaidam	37.85°N, 95.42°E	3200	8/8	59.3±1.7	55.3±1.9	64.0±2.6	2.19±0.35	JIN et al. (2006); JIN & LIU (2007)
Dulan	36.23°N, 98.11°E	3242	7/14	57.3±1.3	57.0±1.2	54.5±2.0	2.55±0.60	JIN et al. (2006); JIN & LIU (2007)
Zoige	33.89°N, 98.11°E	3370	19/18	60.3±1.7	54.6±1.1	62.8±2.4		JIN et al. (2006)
Zoige	33.89°N, 98.13°E	3470	14/10	58.5±0.8	61.2±0.8	63.2±0.8	2.62±0.40	JIN et al. (2006); JIN & LIU (2007)
Maduo	34.75°N, 98.11°E	4250	23/19	54.1±0.8	54.5±1.3	56.6±0.8	2.32±0.24	JIN et al. (2006); JIN & LIU (2007)
Maduo	34.75°N, 98.11°E	4565	36/33	52.0±0.5	53.8±0.5	52.4±0.6	1.78±0.11	JIN et al. (2006); JIN & LIU (2007)
Zoige		3350	8/12	58.7±1.2	52.0 ± 1.6	64.3 ± 1.4		Wu et al. (2005)
Daotanghe	36.58°N, 101.82°E	3400	58/34	61.0±1.1 48.1–70.2	68.5±0.7 61.2-74.6	62.3±1.4 44.0-74.0	3.70±0.20	Zhang et al. (2005)
Hongyuan		3500	11/26	53.9 50.2–66.9	55.2 48.6–57.7	56.5 50.2–66.9		JIANG et al. (1980)
Dulan	36.21°N, 98.16°E	3150	15/17	56.4±1.1 49.4–60.4	53.9±0.8 48.6-58.3	62.6±1.0 56.3–66.5		Own data
Da Qaidam	37.61°N, 95.37°E	3100	10/14	53.2±0.6 49.3–55.6	50.3±0.5 49.2–54.4	59.9±0.9 55.4–64.3		Own data
Xiaman	33.88°N, 102.54°E	3450	9/6	59.2±1.1 54.1-62.7	61.5±0.8 58.9–65.0	62.1±1.4 60.4–68.8		Own data
Xiaman	33.87°N, 102.56°E	3400	17/6	54.9±2.3 48.2-61.5	55.9±0.8 49.3-61.7	59.8±2.2 51.7-64.5		Own data
Chaka	36.65°N, 99.37°E	3200	18/11	55.1±1.0 48.6-59.2	54.0±0.8 48.2-61.1	57.5±1.1 51.2-63.2		Own data
Kunlunshan	35.88°N, 94.37°E	3700	8/7	51.2±0.8 48.7–53.8	50.9±0.7 48.2–54.8	56.9±0.6 55.6–59.0		Own data
Geermu	36.38°N, 94.97°E	2800	10/9	51.1±1.2 48.7–52.4	51.4±0.9 48.3-53.2	55.8±1.2 58.3-60.5		Own data
Shugan Lake	38.90°N, 93.90°E	2800	11/11	59.1±1.1 51.8-65.2	57.2±1.3 49.5-63.3	65.5±1.2 55.4–70.9		Own data

Sites	Location	Altitude (m a.s.l.)	Sample size males\ females	Males SVL	Females SVL	Males TL	Females TOM	Data sources
Qinghai Lake	32.88°N, 97.53°E	3190	16/9	55.4±1.8 48.1-61.3	59.7±1.1 55.5-70.0	55.5±4.9 45.3-62.8		Own data
Maduo	35.20°N, 98.97°E	4200	12/7	55.8±0.8 53.5–59.0	57.1±0.7 53.7-62.3	57.4±1.3 49.9–60.2		Own data
Xinghai	35.92°N, 100.03°E	3300	10/7	58.1±1.0 53.3-60.5	56.3±1.5 48.8-63.0	58.5±1.3 53.2-61.2		Own data
Gonghe	36.17°N, 99.13°E	2850	16/20	55.9±0.7 49.5-61.0	55.2±0.7 48.1–60.0	59.2±1.0 51.0-63.2		Own data
Taka	36.28°N, 99.44°E	3100	12/6	60.5±3.7 48.2–74.3	61.4±3.3 48.5-71.8	60.7±4.0 47.7–77.8		Own data
Dulan	36.26°N, 98.15°E	3200	5/7	60.1±1.5 52.4–67.7	58.7±1.1 50.2-60.6	67.1±1.4 58.9–70.2		Own data
Yintan	36.54°N, 100.28°E	3400	8/7	56.0±1.2 51.5-60.3	59.2±1.1 54.0-64.3	54.9±2.1 45.9–61.7		Own data
Chaka Lake	36.46°N, 99.02°E	3670	7/8	53.7±0.4 50.2–57.7	59.0±2.3 53.9-66.7	59.4±0.6 58.6-61.5		Own data
Delingha	37.26°N, 97.20°E	3200	7/5	53.5±1.2 50.2–55.4	51.9±0.9 48.0-53.7	55.6±2.7 47.8–60.0		Own data
Maqu	33.95°N, 102.09°E	3430	6/8	61.0±1.5 59.5-63.5	58.2±1.1 55.7-62.3	55.6±1.2 59.5–70.7		Own data

Online Supplementary data – LI ZHAO et al.