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Original Article

Sexual differences in bite force are not related to testosterone level in the wild-derived red junglefowl

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Abstract

Bite force is an important performance indicator of individual fitness that is closely related to food acquisition, male competition, and mating selection. It is also affected by a variety of factors and different mechanisms. Therefore, it is relatively difficult to understand the evolutionary driving forces of changes in bite force. In this study, the driving factors affecting the bite force of wild-derived red junglefowl (*Gallus gallus jabouillei*) were investigated from the aspects of morphological indicators and physiological characteristics. Results showed that the bite force of wild-derived red junglefowl was directly related to sex, showing obvious sexual differences. However, there was no correlation between the plasma testosterone level and bite force. The bite force of males was significantly greater than that of females, and the body index (i.e., PC1 of five body measures, namely body mass, body length, wing length, tail length, and tarsus length), the grasp index (i.e., tomial length × bill width) of males were significantly greater than those of females. Sexual selection may have played a key role in the evolution of bite force in the red junglefowl. Future studies should examine other key factors affecting changes in bite force to verify the correlation between secondary sexual characteristics and bite force in red junglefowls.

Key words: bite force, evolution, morphometric indices, red junglefowl, testosterone.

In vertebrates, bite force is a performance indicator related to individual fitness and is considered to meet different functional needs, such as feeding, mating, defence, and competition (Anderson et al. 2008). In fact, there is a correlation between morphology, performance, and fitness (Arnold 1983). At the same time, bite force is a major factor in determining the ability to compete at the inter- and intra-specific level (Vanhooydonck et al. 2005; Lailvaux and Irschick 2007). By controlling energy input through shifts in feeding ecology, natural selection, and sexual selection can simultaneously or successively (or even interactively) act on certain traits of organisms (Sagonas et al. 2014). In many animal groups, the tendency of evolution is towards higher bite force and larger individuals (Aguirre et al. 2002; Herrel et al. 2004, 2010a; Chazeau et al. 2013). However, evolutionary trade-offs may also limit the adaptive changes in certain traits of different species (Corbin et al. 2014; Edwards et al. 2016). The bite force of vertebrates is affected by multiple factors, and the mechanisms involved are different. Therefore, elucidating the evolutionary driving force behind changes in bite force is relatively difficult (Wittorski et al. 2016).

At present, there are relatively few studies on the bite force of birds. Previous studies have shown that the main factors affecting bird bite force are morphological and physiological correlations. Among which, the morphological factors include head size (Herrel et al. 2005a; Rao et al. 2018, 2021), head shape (van der Meij and Bout 2008), bill size (Herrel et al. 2005b), and bill shape (Herrel et al. 2010b; Sustaita and Rubega 2014; Soons et al. 2015); other related factors include diet (van der Meij and Bout 2006; Badyaev et al. 2008), sex (Huo et al. 2016), and domestication (Suzuki and Okanoya 2021). The physiologically relevant factors are mainly the size of the masseter muscle group and the size of the adductor mandibulae muscle varies with bite force (Huby et al. 2019). Previous studies pointed out that physiological variation in muscle architecture or jaw biomechanics played an additional role in bite force generation (Bowman 1961; Herrel et al. 2005a). Therefore, theoretically, it is predicted that the more developed an individual's jaw-closing muscles are, the greater their biting force should be. This conclusion has been confirmed in different birds (van der Meij et al. 2004; van der Meij and Bout 2006, 2008; Kamata et al. 2012; Carril et al. 2015). The conclusion is also further supported by previous interspecific comparisons among Darwin's finches, which indicate distinct changes in the position and the degree of pennation in the external jaw adductors (Bowman 1961).

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Measurements of jaw muscle masses, degree of pennation, and orientation are needed to address this further.

Some animals show significant differences in body size and body color between males and females (Hedrick and Temeles 1989; Andersson 1994; Fairbairn et al. 2007). Male and female individuals exhibit sexual differences in morphology (e.g., body size, head size), which often results in sexual differences in bite force (van Damme et al. 2008; Gowan et al. 2010; Noble et al. 2014; Thomas et al. 2015). However, the sexual differences in bite force might have different patterns among different sexual dimorphism species (Cameron et al. 2013; Lailvaux et al. 2019).

Many research studies showed that species with greater bite force tend to be more aggressive (Lailvaux et al. 2004; Huyghe et al. 2005; Lailvaux and Irschick 2007; Donihue et al. 2016). Simultaneously, testosterone has been linked to aggression across vertebrates (Nelson and Trainor, 2007). For example, the implantation of testosterone remarkably increased the aggressive behaviors of tropical spotted antbirds (*Hylophylax n. naevioides*) in staged male-male encounters (Hau et al. 2000). It was found that the administration of exogenous testosterone resulted in an increase of the mass of jaw closing compared with sham-operated in males of a sexually dimorphic lizard (*Gallotia galloti*). Surprisingly, the dramatic testosterone-induced changes in muscle masses did not result in concordant changes in bite force performance (Huyghe et al. 2010).

The red junglefowl (*Gallus gallus*) is a typical dimorphic species. Therefore, we wanted to determine whether there was sexual difference in bite force in this species. In addition, recent studies on the correlation between bite force and plasma testosterone levels have been reported in several lizards (Husak et al. 2007; Gowan et al. 2010; Huyhe et al. 2010; Noble et al. 2014) and a small primate (Chazeau et al. 2013), however, whether there is a correlation between the bite force of red junglefowls and the plasma testosterone level is not yet known. Therefore, the main objectives of this study were as follows: (1) to investigate whether the morphological indicators and plasma testosterone levels of the red junglefowl are correlated with their bite force and (2) to determine whether red junglefowls exhibited sexual differences in bite force and physical indicators.

Materials and Methods

Study species

The red junglefowl belongs to the order Galliformes, family Phasianidae, and can be divided into five subspecies (del Hoyo et al. 2001). There are two subspecies in China, namely, the southern Yunnan subspecies (*Gallus g. spadiceus*), and the Hainan subspecies (*G. g. jabouillei*) (Figure 1), which are distributed in Yunnan, Guangdong, southwestern Guangxi, and Hainan (Zheng 2023).

Sampling and measurement

In the year of 2012, Hainan Tunchang Xingbang Agricultural Development Co., Ltd. is founded for the artificial domestication and reproduction of wild red junglefowls (the Hainan subspecies). All experimental birds (wild-derived red junglefowls) in this study were purchased from this company and were all from the same age group (see also Hao et al. 2023). In April 2017, the bite force and physical indicators of wild-derived red junglefowl were measured. After blood was collected, the blood samples were subjected to high-speed centrifugation (3,000 rpm for 10 min), and the supernatant was sent for detection of the plasma level of testosterone (Gowan et al. 2010; Huyghe et al. 2010). The testosterone level was determined by the Department of Laboratory Medicine, First Affiliated Hospital of Hainan Medical College, and a test report was issued. In the end, we measured 66 individuals including 34 females and 32 males. It should be noted that testosterone levels in birds are known to rise significantly within a few minutes with capture-handling-restraint operations (van Hout et al. 2010). Both samplings were done within 1~2 min to minimize or standardize the effect according to the handling protocols.

Figure 1. The Hainan subspecies of red junglefowl (*Gallus gallus jabouillei*) (a refers to the male and b refers to the female and juvenile chicks; Photo by Jianhua Wu).

The bite force was measured using a first-generation animal bite force meter (NBIT-DUD-2404A, NBIT Inc., Nanjing, China) with an accuracy of 0.01 N. The instrument is divided into three parts: simulation data acquisition card (NBIT-DUS-2404A), animal bite force sensor, and analysis software (DSU2404A) (Rao et al. 2018). Studies have found that the bite force generated by the front of the bill and the base of the bill are different (Herrel et al. 2010b), and in birds, bite force sensors usually only measure the bite force generated by the front of the bill (van der Meij et al. 2004; van der Meij and Bout 2006). Therefore, a unified standard was used for all experimental individuals, that is, the bite force at the tip of the bill was measured. To ensure the repeatability of the experiments, all birds were biting at equivalent gape angles and were thus tested under mechanically similar conditions (Herrel et al. 2005a). Each individual was measured three times, and the largest bite force among the three measurements was taken as the maximal bite force (Losos et al. 2002; Rao et al. 2018). Notably, when the bite force probe is placed near the beak of birds, they will actively bite the probe. However, some individuals are not easily able to measure biting force. We adopt multiple approaches at different time periods to solve this problem.

The morphological indicators measured were body mass, body length, wing length, tail length, tarsus length; head size (head length, width, and height), bill size (bill length, width, and height), and tomial length (measured from the commissural point at the corner of the mouth, diagonally to the tip of the upper mandible, see Rohwer and Spaw 1988). Body mass was measured using an electronic scale (EHA501; Guangdong Senssum Company, Zhongshan, China) with an accuracy of 0.1 g. Other morphological indicators were measured using digital Vernier calipers (Guanglu Measuring Instrument Co., Ltd., Guilin, Guangxi) with an accuracy of 0.01 mm. For indicators that exceeded the range of the Vernier caliper, we uniformly used a tape measure for measurement.

We calculated the body size (or body index) using PCA analysis with the above five traits (i.e., body mass, body length, wing length, tail length, and tarsus length). We took the PC1 of these five traits as the body index. Furthermore, the head size (or head index) was based on the following calculation: head size = 4/3 × π × head length/2 × head width/2 × head height/2 (Møller 2019). Finally, we used the grasp index to represent the size of the bill (Yang et al. 2015). The grasp index of the birds was based on the method recommended by Rohwer and Spaw (1988), i.e., grasp index = tomial length × bill width.

Statistical analysis

Statistical analysis was performed in R 3.2.3 software. Principal component analysis was carried out to investigate the body index affecting the bite force of wild-derived red junglefowl using the "prcomp" function (see Supplementary Figure S1). The PC1 of these 5 body traits explained 71% of the variation, and all these 5 trait loadings positively contributed to the PC1 (i.e., body mass and PC1, Pearson $r = 0.64$; body length and PC1 Pearson $r = 0.91$; tail length and PC1 Pearson $r = 0.88$; wing length and PC1 Pearson $r = 0.86$; tarsus length and PC1 Pearson $r = 0.78$, $n = 66$ individuals). To investigate the sexual dimorphism of bite force, body index, head index, and grasp index (32 males vs. 34 females), we used independent sample T-test to analyze the differences between female and male wild-derived red junglefowls. When the statistical result was $P < 0.05$, the difference is significant, while $P < 0.01$ indicates that the difference is extremely significant, and $P > 0.05$ indicates that the difference is not significant. Unless otherwise specified, the data are expressed as the mean ± standard deviation (SD).

For each individual, we have measured its bite force three times; therefore, we also used a linear mixed-effect model (package "lme4") to investigate sexual differences of bite force and the associations between bite force and testosterone levels, the body index, the head index, and the grasp index. In this model, the individual identity was added as the random effect, which allowed us to estimate the repeatability of bite force in wild-derived red junglefowls. For fixed effects, we included the sex (two levels, male vs. female), testosterone levels, the body index, the head index, and the grasp index. To test the repeatability of bite force, we calculated the Pearson correlation coefficient of the three measurements.

Results

The differences in the maximal bite force, body index (PC1, all those 5 trait loadings positively contributed to the PC1 meaning species with large body sizes have high PC1 scores), head index, and grasp index between female and male wild-derived red junglefowls are shown in Table 1 and Figure 2. Among them, the body index, the grasp index, and the head index of male birds were extremely significantly higher than those the female birds (body index: $t = 17.97$, df = 47.96, $P < 0.0001$; grasp index: $t = 9.58$, df = 57.89, $P < 0.0001$; head index: $t = 6.75$, df = 39.77, $P < 0.0001$, $n = 32$ males vs. 34 females, Table 1). Moreover, the bite force of male birds was higher than that of female birds, and the difference was significant (maximal bite force: $t = 15.15$, df = 63.64, $P < 0.0001$, $n = 32$ males vs. 34 females).

The results of the linear mixed model are shown in Table 2. There was no correlation between bite force and body index ($t = -0.57$, df = 60, $P = 0.569$), head index ($t = -0.19$, df = 60, $P = 0.849$), and grasp index ($t = 1.08$, df = 60, $P = 0.280$). The bite force of wild-derived red junglefowl was significantly correlated with sex, showing sexual differences (sex: $t = 5.48$, df = 60, $P < 0.0001$) but was not correlated with plasma testosterone levels (testosterone: $t = -1.41$, df = 60, $P = 0.158$, see Table 2 and Figure 3 for details). The repetitive force calculation results showed that the bite force had a relatively high repeatability ($\beta = 3.889$, $R = 0.314$).

Discussion

This study explored the driving factors of the bite force of wild-derived red junglefowls from the morphological indicators and physiological characteristics. The results of our study showed that the comprehensive body, head, and bill indices of the wild-derived red junglefowl do not directly determine or affect the bite force. Our study also showed that there was no correlation between bite force and plasma testosterone levels in the wild-derived red junglefowl. The bite force of wild-derived red junglefowl is most directly related to sex, showing sexual differences. In addition, our data analysis showed that the bite force of wild-derived red junglefowls was relatively stable and showed a high repeatability.

Previous studies have shown that the head index, body size, and bill index of some animals are correlated with their bite forces (Herrel et al. 2005a; Anderson et al. 2008; Lappin and Jones 2014; Thomas et al. 2018). Specifically, the larger the head is, the greater the bite force (Aguirre et al. 2002; Herrel et al. 2002; Husak et al. 2006; Chazeau et al. 2013; Lappin et al. 2017). Some studies have also noted that head width and

Table 1. Means and standard deviations of maximal bite force, the body index (PC1), the head index, and the grasp index between male and female wild-derived red junglefowls

	Male	Female	*t* value	*P*
Maximal bite force (N)	26.23 ± 2.66	16.35 ± 2.63	15.15	<0.0001
Body index (PC1)	1.72 ± 0.93	−1.62 ± 0.52	17.97	<0.0001
Head index	35.66 ± 6.07	27.91 ± 2.37	6.75	<0.0001
Grasp index	6.71 ± 0.60	5.45 ± 0.46	9.58	<0.0001
Sample size	32	34		

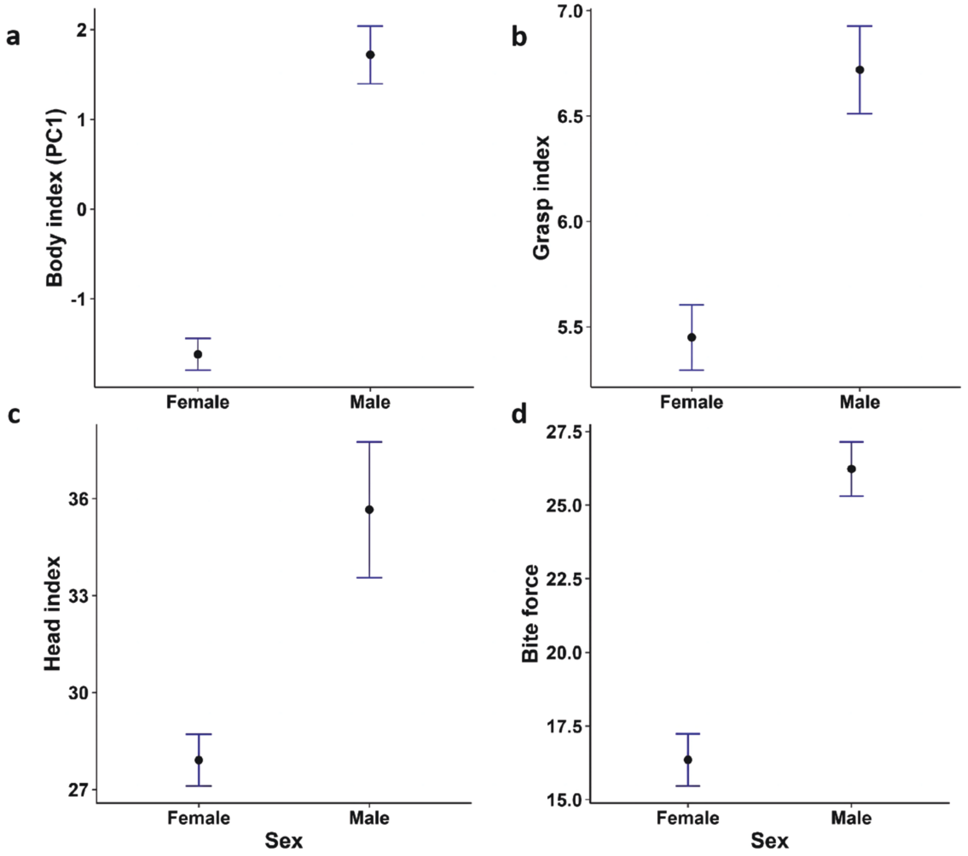

Figure 2. The comparison of three morphometric measures (the body index, the grasp index, and the head index) and bite force between female and male wild-derived red junglefowls.

head height are positively correlated with bite force (Herrel et al. 2005b; Chazeau et al. 2013; Taverne et al. 2020) and that head width plays the most critical role in the evolution of bite force (Herrel et al. 2005b). However, the bite force of wild-derived red junglefowls is not directly related to these key indicators. This is partly consistent with the results of a recent study on turtles, which showed that the modification of turtle skulls did not significantly increase the bite force (Ferreira et al. 2020). Similarly, body size may not be a decisive factor in the development of bite force in wild-derived red junglefowls (but see Dick and Clemente 2017). The relationship between morphological changes and the performance of organisms can be predicted through a complex causal pathway (Arnold 1983; Miles et al. 2007). Androgens, such as testosterone, play a crucial role in regulating the relationship between morphology and performance through their impact on tissue and activity (van Damme et al. 2008). Androgens can indirectly affect performance by altering the growth rate of organisms and controlling the development of morphological characteristics (Adkins-Regan 2005; Ketterson et al. 2005; Hews et al. 2012), and can also regulate behavioral and morphological plasticity changes (Gowan et al. 2010; Huyghe et al. 2010). In a study of green Anole lizards (*Anolis carolinensis*), it was found that bite force was positively correlated with fluctuating plasma testosterone levels (Husak et al. 2007). Another study found that the bite force in the breeding season was greater than that in the non-breeding season, and the seasonal change in the bite force was correlated with the seasonal change in the testosterone level of the six-lined whiptail lizard (*Aspidoscelis sexlineata*) (Gowan et al. 2010). However, the results of our study showed that the plasma testosterone levels of the wild-derived red junglefowl do not directly affect the bite force, which is consistent with the results of studies on the Western Canary Island lizard (*Gallotia galloti*) (Huyhe et al. 2010), the Australian lizard (*Eulamprus quoyii*) (Noble et al. 2014), and the mouse lemur (*Microcebus murinus*) (Chazeau et al. 2013).

Table 2. Linear mixed model explaining proximate determinants of bite force in the wild-derived red junglefowl

	Estimate (β ± SE)	Repeatability	*t* value	*P*
Random effects:				
Individual identity (*n* = 34F; 32 M)	4.082	0.319		
Residual	8.490			
Fixed effects:				
Intercept	10.154 ± 3.868		2.63	-
Sex	9.808 ± 1.789		5.48	<0.0001
Testosterone	−0.641 ± 0.455		−1.41	0.158
Body index	−0.260 ± 0.455		−0.57	0.569
Head index	−0.015 ± 0.078		−0.19	0.849
Grasp index	0.737 ± 0.6833		1.08	0.280

Studies have shown that the shape of the animal's head (Herrel et al. 2006; van der Meij and Bout 2006, 2008) and

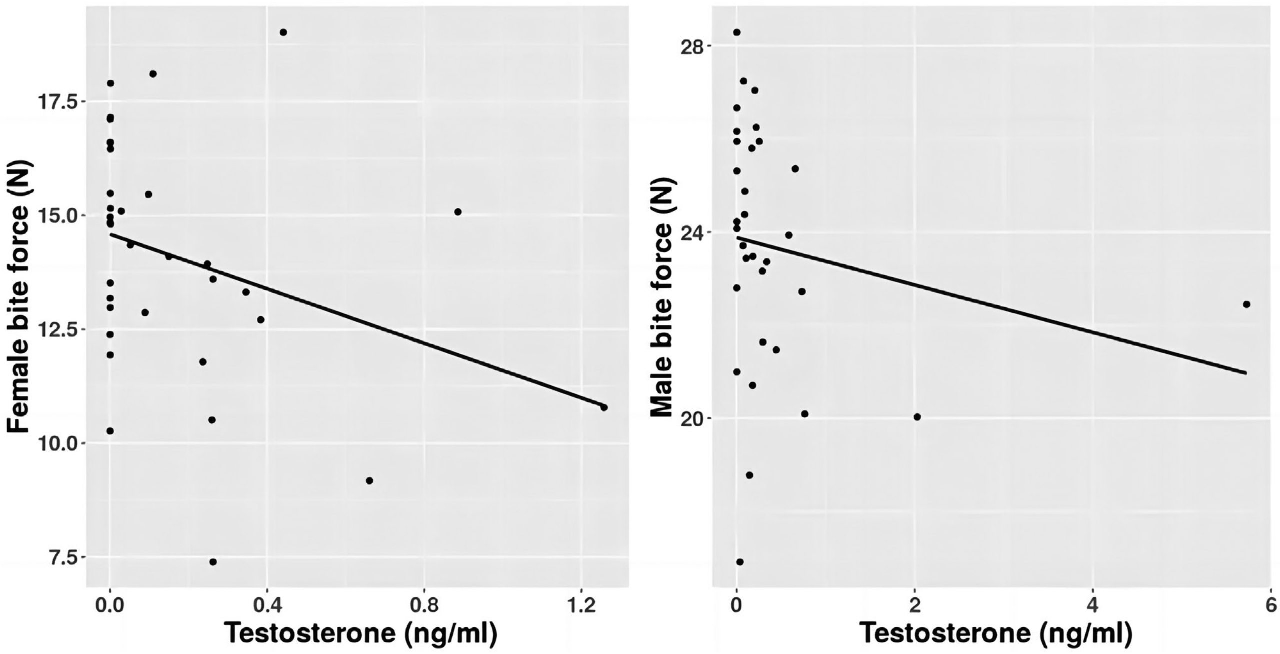

Figure 3. The relationship between circulating plasma testosterone and bite force for female and male wild-derived red junglefowls (there were no significant correlations for both sex and regression lines have been added for visualization).

the shape of the bird's bill (Herrel et al. 2005a; Badyaev et al. 2008) also affected the bite force to some extent. The evolution of bite force can take many different forms. For example, bite force can be increased with the body size or the size of the head, and bite force can also be affected by changing the shape of the head (Herrel et al. 2002; Harmon et al. 2005). The morphological indicators of the wild-derived red junglefowl do not directly determine the bite force. However, we do not explore the correlation between the shape of the head and bill and their bite force. In this study, the body index, the grasp index, and the head index of males were significantly greater than those of females. Moreover, the bite force of male birds was far greater than that of female birds. To reveal the proximate determinants of bite force in red junglefowls is not easy, needing for systematic and in-depth research.

It is interesting to note that testosterone targets muscles directly (reviewed in Tobiansky and Fuxjager 2020), and can also directly target the musculoskeletal systems underlying different behaviors (Adkins-Regan 2005; Tobiansky and Fuxjager 2020). Therefore, physiological properties of the muscles that could vary between red junglefowl of males and females, which may lead the differences in bite force. In addition, sexual selection may play an important role in the evolution of bite force in these birds, which need to be confirmed in future work. In addition, androgens, such as testosterone, can regulate behavioral and morphological plasticity changes (Gowan et al. 2010; Huyghe et al. 2010) and indirectly affect performance by changing the growth rate of organisms and controlling the development of morphological characteristics (Adkins-Regan 2005; Ketterson et al. 2005; Hews et al. 2012). Therefore, the relationship between animal bite force and plasma testosterone level needs more investigations because morphological changes and the performance of organisms may also be a complex causal relationship (Miles et al. 2007).

In summary, this study explored the factors affecting the bite force of wild-derived red junglefowls and revealed sexual differences in bite force between males and females. In birds, the shape and size of the bill show variability (Cooney et al. 2017), and the variability of avian bills leads to differences in bite force to cope with the needs for foraging (Herrel et al. 2005a,b). Further studies are needed to confirm whether the size of the mandibular muscle and dietary differentiation are the key factors affecting the bite force of red junglefowls and/or whether the bite force of male birds is largely driven by sexual selection.

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Authors' Contributions

W.L. designed the study; X.R. carried out experiments and performed laboratory, X.R. and D.W. completed the statistical analyses. X.R. wrote the draft manuscript, D.W. and W.L. improved the manuscript. All authors approved the final submission.

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Ethics Statement

The experiments reported here comply with the current laws of China. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2011-006).

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data and all R codes used in this study are provided as electronic supplementary material (file1_data, file2_R codes and additional files).

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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