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Sexual and natural selection interplay in sexual head shape dimorphism of two sympatric racerunners (Squamata: Lacertidae)

Tao Liang[1,2†], Li Wang[1†] and Lei Shi[1*]

[1]College of Life Sciences, Xinjiang Agricultural University, Ürümqi, China, [2]College of Forestry, Nanjing Forestry University, Nanjing, Jiangsu, China

Both natural and sexual selection can shape sexual dimorphism. However, determination of the contribution of these selection pressures is challenging. In lizards, sexual selection can contribute to the larger head size of males than that of females. However, males and females can also diverge in their head size to prey on different food resources under conditions of limited resources (and/or high competitors). Here, 109 individuals from two sympatric desert racerunners (*Eremias grammica*: 28 males and 30 females; *Eremias velox*: 25 males and 26 females) were studied to determine their sexual head shape (head length, width, and depth). Additionally, 191 and 169 feces samples of *E. grammica* and *E. velox*, respectively, were collected to assess the niche divergence hypothesis (a proxy for natural selection). We found that both species had dimorphic head shapes; male heads (i.e., length, width, and depth) were significantly larger than female heads ($P < 0.05$, in all cases) in *E. grammica*, and male heads of *E. velox* were significantly longer than those of females ($P < 0.05$). Chi-square test revealed that there were significant differences in the proportion (Hymenopteran and Orthopteran) and sizes of prey type between the two sexes of *E. grammica*; conspecific males and females of *E. velox* differed in the proportion of Coleopteran and Hymenopteran prey. Both males and females of these two species had a high niche overlap index (range from ~ 0.78 to 0.99) with each other. There were also significant differences in the sizes of the heads and prey between the two species ($P < 0.05$). However, the interspecific differences were mainly caused by interspecific male–male differences in morphological and prey traits. In summary, we believe that both natural (pressures from resource competition) and sexual selection drive sexual head shape dimorphism in these two sympatric lizards, owing to high food resource competition in arid regions. Therefore, head trait divergence can reduce competition by resulting in a preference for different prey types.

KEYWORDS

arid region, feces, niche divergence hypothesis, niche overlap index, preys, limited resources

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EDITED BY
Guo-Hua Ding,
Lishui University, China

REVIEWED BY
Lin Zhang,
Hubei University of Chinese Medicine, China
Jianli Xiong,
Mianyang Normal University, China

*CORRESPONDENCE
Lei Shi
leis@xjau.edu.cn

†These authors have contributed equally to this work and share first authorship

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Introduction

Both natural and sexual selection can shape sexual dimorphism, which is described as a systematic difference in life-history traits between conspecific males and females (Darwin, 1871; Andersson, 1994). This phenomenon is widespread in reptiles (Cox et al., 2003, 2007; Liang et al., 2021a,b). However, determining the contribution of these selections remains a challenge because head trait variations correspond to differences in bite force (i.e., sexual selection) and prey consumption (i.e., natural selection) (Herrel et al., 2007). Specifically, sexual selection explains that males have larger heads than do females, to increase bite force and competition success during male–male combat (Darwin, 1871; Trivers, 1972). The niche divergence hypothesis (a proxy for natural selection) states that trait divergence between the two sexes (and hence using different microhabitats or food) is the outcome of competition for resources (i.e., larger sizes can eat larger prey, see Schoener, 1967, 1977; Preest, 1994). This hypothesis does not expect male-or female-biased sexual dimorphism but only focuses on trait differences between the sexes. Larger heads may provide access to larger and harder prey, resulting in an enlarged niche. However, we could not easily identify the roles of sexual and natural selection, and the extent of their contribution to males having larger heads. In particular, for some species with pronounced male–male competition, male heads were significantly larger than those of females; however, there was no difference in bite force between the two sexes (e.g., Trapelus sanguinolenta, see Wang et al., 2020). Ecological sexual dimorphisms are therefore thought to result either as a by-product of sexual selection and divergent gamete investment or through competition-driven niche partitioning between the sexes (i.e., ecological character displacement, Dayan and Simberloff, 1998; Lisle, 2019). However, studies on the relationship between head size and the niche divergence hypothesis are lacking (but see Herrel et al., 1999).

Under the niche divergence hypothesis, sexual size dimorphism can arise when males and females compete for limited resources (Dayan and Simberloff, 1998; Bolnick and Doebeli, 2003; Pincheira-Donoso et al., 2018). This can happen when food (MacArthur and Wilson, 1967) is limited and/or the number of potential competitors is high (a proxy of limited resources, see Pincheira-Donoso et al., 2009). However, global island analysis failed to detect a correlation between sexual size dimorphism and competitor number in reptiles (Meiri et al., 2014). The head is the only organ used by lizards to feed; if there is indeed potential resource competition, conspecific males and females would respond with more pronounced head shape divergence than body size (Andrews, 1979).

Phylogenetically correlated species have similar niches, and hence have potentially stronger interspecific competition (Pacala and Roughgarden, 1982; Hawlena and Pérez-Mellado, 2009). In particular, in regions with few resources (e.g., food) but diverse sympatric reptiles (e.g., in desert, see Roll et al., 2017), potential interspecific competition would be high. Therefore, the head divergence between the two sexes could reduce both intraspecific and interspecific competition for food resources (Nel et al., 2015). However, other studies have found that prey size does not correlate with the degree of head dimorphism (Zhao and Liu, 2013; Taverne et al., 2019). Among the several methods used to investigate species' dietary habits, fecal samples are a widely accepted method [see reviewed in Pérez-Mellado et al. (2011)], because it does not require killing the individuals to obtain stomach or gut contents. Therefore, many studies (e.g., Capizzi, 1999; Hawlena and Pérez-Mellado, 2009) have used fecal pellets for dietary studies in lizards (but see Pincheira-Donoso, 2008).

In northwest China, there is a large area of arid desert with poor vegetation but with the second highest lizard richness in China (Liang et al., 2022). For example, there are five sympatric diurnal species in the Tukai Desert: two *Eremias* lizards (*E. grammica* and *Eremias velox*, see **Figure 1**), two *Phrynocephalus* lizards (*P. mystaceus* and *P. guttatus*), and one steppe agama lizard (*Trapelus sanguinolenta*) (Wang et al., 2020). Among these five species, *T. sanguinolenta* is the largest, inhabiting the shrub-ground niche, whereas the other four species are strictly ground-dwelling. For *Phrynocephalus*, these two species have different populations (i.e., *P. mystaceus* is rarely observed, while *P. guttatus* is widespread in the region) and with slight overlap in daily activity time (*P. mystaceus* is active between 12:00 and 16:00; authors' personal observation). *P. mystaceus* is the largest species of this genus, while *P. guttatus* is a medium-sized species, implying potentially weak competition in *Phrynocephalus*. In contrast, both species of *Eremias* were abundant in this desert with similar daily activity times and body sizes. Therefore, coexistence of these phylogenetically related sympatric species is a notable phenomenon; assessing both inter- and intraspecific differences in morphology and prey between these two species may aid in a better understanding. In this study, we examined sexual head dimorphism and its correlation with the niche divergence hypothesis in two *Eremias* lizards. We aimed to address the following questions:

(1) What are the sexual head shape dimorphism patterns in these two species? Both studied species of *Eremias* exhibit pronounced male–male combat in the wild (field observation, also see Liang et al., 2018 for E. arguta); therefore, we predicted that males have larger heads than females because of sexual selection. Sexual selection contributes to larger male heads, which is correlated with male–male competition for mating (Gvozdik and Damme, 2003; Lailvaux and Irschick, 2007; Wang et al., 2020).

(2) Does sex-specific divergence in prey composition and size exist in these two species? We predicted that both prey composition and size would differ between the

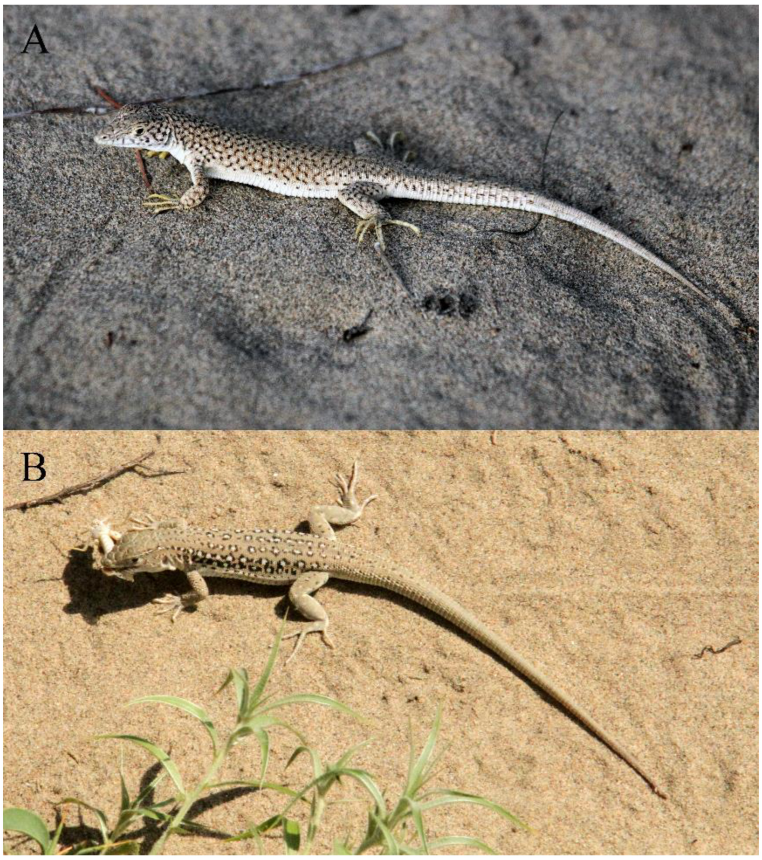

FIGURE 1
Ecological photos of *Eremias grammica* **(A)** and *Eremias velox* **(B)**. (Photos by Lei Shi).

sexes of these two species as it would reduce sexual resource competition within species.

(3) As these two lizards are sympatric and phylogenetically related, the potential food competition between these two species is high. Therefore, we also predicted that there would be differences in prey between the two species to reduce interspecific competition.

Materials and methods

Morphology and feces collection

From July 2018, to August 2019, 61 and 51 *E. grammica* (females: 30, males: 31) and *E. velox* (females: 26, males: 25) individuals were captured from the Tukai Desert (WGS 84, longitude: 80.76°, latitude: 43.97°), Xinjiang, China, respectively. Sexual maturity sizes were 36.17 mm and 42.00 mm for *E. velox* (Wang et al., 2014) and *E. grammica* (Zhao et al., 1999), respectively. We measured the snout-vent length (SVL), head length (HL), head width (HW), and head depth (HD) using digital calipers (Shanggong calipers, 0–150 mm). All measurements were accurate within 0.01 mm.

The lizards were housed in plastic cages (30 × 10 × 15 cm), specifically to collect fecal samples (some individuals had more than one fecal sample). Each cage housed two or three individuals with the same gender, these cages were placed in a room with ambient temperature that varied from 20 to 28°C with a 12-h light/12-h dark cycle. A 250 W light bulb was suspended at one end of each cage, 20 cm above the cage floor, and the lizards could freely move to warmer and cooler places within the cage. No feeding was performed until the fecal sample collection was completed (one to three days). We observed lizards every 4 h (but not at night) to collect the sample. A total of 191 and 169 fecal samples from *E. grammica* (female:111, male:80) and *E. velox* (female:82, male:87), respectively, were collected.

Prey composition and size

Dried fecal sample was placed in petri dishes filled with water for 12–24 h, in order to soften them. Subsequently, we used forceps to separate and collect prey remains (antenna, chelicerae, telson, elytron, etc.). The prey remains were preserved in the same plastic sealing bags of the fecal samples (i.e., the number of plastic sealing bags was equal to the number of feces). One of us (L.S.) used a stereo microscope and identification keys to identify taxa at the order or family level based on the remains of these prey (Xin et al., 1985). Both the left- and right-sided elements were considered effective individuals (see Results section). For Coleoptera, tergites were well maintained in feces, which could be a good proxy for insect intake sizes. As the bigger head has a bigger bite force, it can prey on bigger and harder prey (especially Coleoptera). Therefore, we measured the length and width of the tergites for further purposes (see below).

Statistical analyses

First, we assessed the normality and homogeneity of the variance of the data. We used the Student's *t*-test to assess the SVL difference between males and females, and further used the analysis of covariance to assess the difference in head sizes (HL, HW, HD), with SVL as the covariance because heads were correlated with lizard body sizes (Liang et al., 2018). Fisher's exact test was used to assess the differences in prey composition between the two sexes. We also performed a Student's *t*-test to assess the difference in tergite size (length and width) between the two sexes for these two species. We used the "space" R-package to assess the niche width of males and females and the niche overlap index (Zhang, 2016). We also repeated all analyses (morphology, prey, and niche) between the two species to assess the potential interspecific competition. We analyzed the differences in: (1) all individuals regardless of sexual dimorphism and (2) sex-specific differences between the two species. Data were log-$_{10}$ transformed to normalize residuals and reduce heteroscedasticity (King, 2000). Graphs were created using "ggplot2" (Wickham, 2016). Descriptive statistics were presented as mean ± standard error (SE).

Results

Sexual dimorphism and allometry of morphology

There was a significant difference in SVL between males (mean: 60.05 ± 0.86 mm) and females (mean: 56.73 ± 0.90 mm) of *E. grammica* (t = 2.69, df = 56, P = 0.009; **Figure 2** and **Table 1**). Males had significantly larger length, width, and depth of the head than did females ($P < 0.05$ in all cases; **Table 1**). In *E. velox*, males were significantly larger than females in the SVL (t = 0.913, df = 48, $P < 0.0001$; **Figure 2**); further, males had significantly longer heads than females ($P < 0.05$, **Table 1**).

We found that sexual head dimorphism was correlated with sex-specific allometric patterns of the head in *E. grammica*; head length (slope: 0.027 ± 0.011, t = 2.42, P = 0.018), width (slope: 0.021 ± 0.009, t = 2.17, P = 0.034), and depth (slope: 0.034 ± 0.01, t = 3.1, P = 0.003) increased more rapidly in males than in females with increasing body size (**Figure 3**). However, *E. velox* exhibited less support for allometric patterns; head length, but not width or depth, increased more quickly in males than in females (slope: – 0.022 ± 0.011, t = –2.03, P = 0.047), with increasing body size (**Figure 3**).

Diet composition, size, and sexual dimorphism

In total, 527 prey items (299 in *E. grammica* and 228 in *E. velox*) belonged to 11 categories, all of which were insects (**Table 2**). The diet of *E. grammica* (299) comprised primarily Coleoptera larvae (30.4%), Acrididae (23.1%), and Formicidae (14.4%), and the remaining nine categories ranged from 0.3 to 10%, whereas *E. velox* comprised primarily Acrididae (41.6%), Coleoptera larvae (14.9%), and Buprestidae (13.5%), with the remaining nine categories ranging from 1.32 to 8.77% (**Figure 4** and **Table 2**).

Fisher's exact test (**Figure 4**) revealed that male and female *E. grammica* were significantly different in prey composition (X^2 = 35.84, P = 0.0005). Males had a higher proportion of Formicidae, Lucanidae, and Cicindelidae (74–80%) in their diet, and females had a higher proportion of Acrididae, Buprestidae, Meloidae, and Scarabaeidae (62–74%). The niche width of males and females was 5.21 and 4.72, respectively; while the overlap index was 0.78 between males and females of *E. grammica*. However, there was no significant difference in the proportion of prey between the two sexes of *E. velox* (X^2 = 16.95, P = 0.097), although females had a high proportion of Apidae, Carabidae, and Diptera (60–67%). Male and female niche widths were 3.99 and 4.52, respectively, with a high niche overlap index of 0.99.

A total of 129 tergites belonging to *E. grammica* (21 female and 23 male) and *E. velox* (45 female and 40 male) were collected. We found significant differences in both length (males: 3.61 ± 0.28, females: 2.75 ± 0.16, t = 2.49, df = 42, $P < 0.05$) and width (males: 2.12 ± 0.16, females: 1.7 ± 0.08, t = 2.23, df = 42, $P < 0.05$) of the tergites between both sexes of *E. grammica*. However, differences were only found in the length (males: 3.07 ± 0.1, females: 2.73 ± 0.11, t = 2.64, df = 83, $P < 0.05$) of tergites between male and female *E. velox* (**Figure 5**).

Interspecific variation

We found no significant differences in snout-vent length between *E. grammica* and *E. velox* (t = –0.111, df = 107,

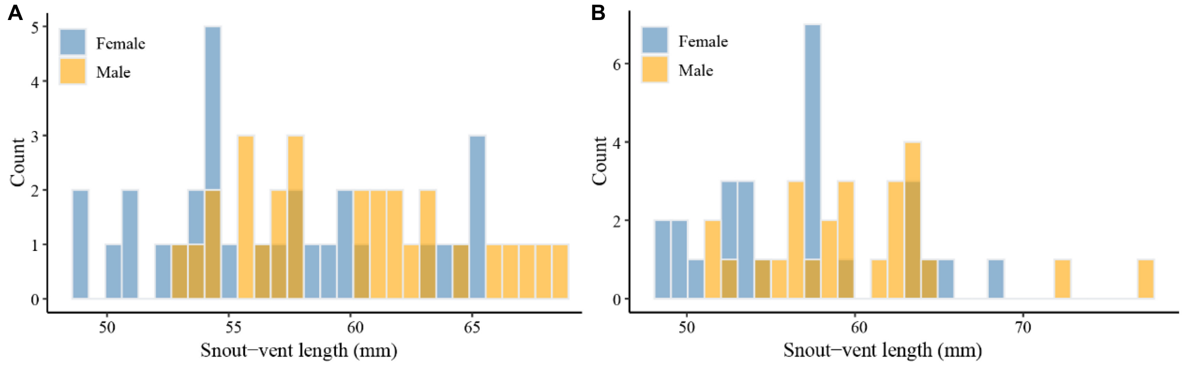

FIGURE 2
Frequency plots of snout-vent length of *Eremias grammica* **(A)** and *Eremias velox* **(B)**.

$P = 0.912$). However, there were significant differences between the heads of these two species: *E. grammica* had a larger head length (slope: $- 0.045 \pm 0.007$, $t = - 5.682$, $P < 0.001$), whereas *E. velox* had a larger head width and depth (width: 0.038 ± 0.007, $t = 5.23$, $P < 0.001$, depth: 0.027 ± 0.008, $t = 3.24$, $P = 0.002$). Variations in interspecific males were similar to the overall results ($P < 0.05$, **Table 1**) within the sexes; however, for females, there was no interspecific variation in head length ($P > 0.05$, **Table 1**).

There was a significant difference in prey composition between the two species ($P = 0.0004$), and the differences between them were significant, with $P = 0.0004$ for males and $P = 0.227$ for females. Niche widths of *E. grammica* and *E. velox* were 5.41 and 4.38, respectively, while the niche overlap index was 0.76 between the two species. Females of these two species had a high niche overlap (0.99) compared to males (0.55). There was no significant difference in prey length between the two species; however, *E. grammica* had significantly wider prey than did *E. volex* ($t = -0.111 \pm 0.021$, $t = -5.31$, $P < 0.001$). The results were still valid when we compared prey sizes, specifically within the sexes (**Figure 5**).

TABLE 1 Sexual dimorphism of *Eremias grammica* and *E. velox* (mm).

Species	Traits	Female	Male	T/F	*P*
E. grammica	SVL	56.73 ± 0.90	60.05 ± 0.86	2.69	0.009
	HL	15.45 ± 0.43	17.90 ± 0.52	59.89	0.018
	HW	8.47 ± 0.12	9.33 ± 0.22	25.06	0.034
	HD	6.89 ± 0.13	7.65 ± 0.14	14.58	0.003
E. velox	SVL	56.54 ± 1.10	60.13 ± 1.17	0.913	0.025
	HL	14.73 ± 0.44	15.11 ± 0.45	49.69	0.048
	HW	9.37 ± 0.31	10.13 ± 0.27	39.54	0.689
	HD	7.35 ± 0.23	8.19 ± 0.27	60.58	0.366

T-values for snout–vent length; F-values for heads. SVL, snout–vent length; HL, head length; HW, head width; HD, head depth.

Discussion

Sexual dimorphism is a widespread phenomenon in lizards (e.g., body size, Cox et al., 2003; Liang et al., 2021a,b), which is thought to reflect the different reproductive roles between males and females (Orme et al., 2002; Bolnick and Doebeli, 2003). The head is important for feeding, locomotion, defensive behavior, among other vital functions; however, understanding the evolution of head variation is a complex task (Meyer et al., 2019; Wang et al., 2020). In the present study, the body and head sizes of male *Eremias* were larger than those of females (**Table 1**), and male lizards with relatively larger heads exhibited more rapid growth. Additionally, we found that males had different prey compositions and sizes in contrast to those of females. The differences in head traits and prey between these two species were mainly caused by interspecific male–male differences.

Sexual selection drives male-biased dimorphism

Previous studies have revealed that, in reptiles, males generally have relatively larger heads than do females after accounting for body size; this pattern can be found at both global (Scharf and Meiri, 2013) and local regional scales (see Liang et al., 2018 for *E. arguta*). This pattern was also observed in this study. A larger head in males allows for higher bite force than that in females, which is important during intersexual competition (Meyer et al., 2019; Cruz-Elizalde et al., 2020; but see Wang et al., 2020). Additionally, the larger heads of males could also possess larger vomeronasal organs, which is potentially beneficial for detecting females (e.g., Marvin, 2009).

All dimorphic traits of the head were correlated with the growth dynamics between males and females, implying that males exhibit more rapid growth than do females, and consequently larger head sizes (**Figure 3**). Both species (also see

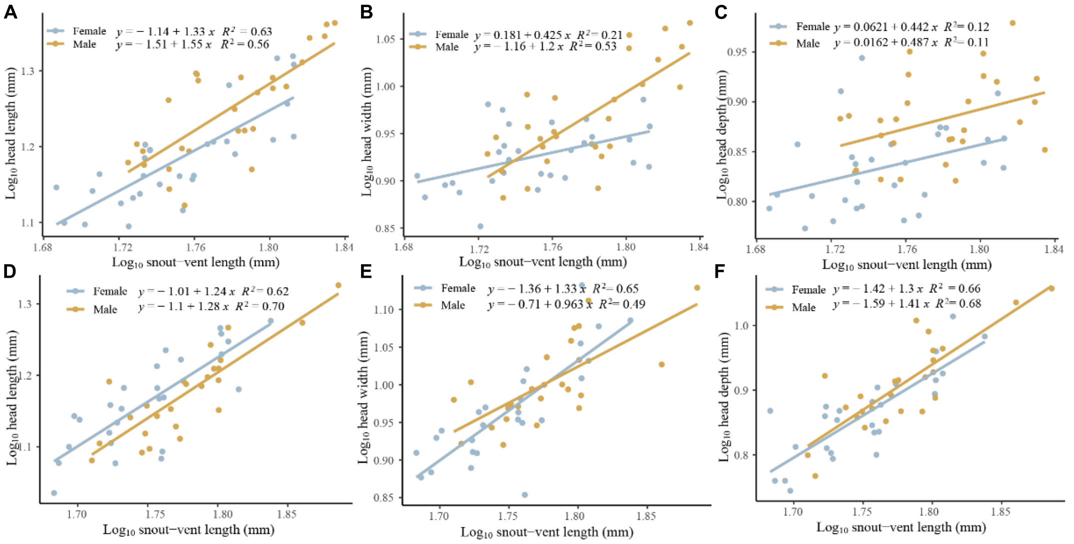

FIGURE 3
Allometric pattern of head length **(A,D)**, width **(B,E)**, and depth **(C,F)** for *Eremias grammica* **(A–C)** and *E. velox* **(D–F)** males and females.

E. arguta, Liang et al., 2018) exhibited territorial behaviors (e.g., male–male competition) during our field observations. Males are aggressive, head and body sizes are likely important traits for signaling the fighting ability of *Eremias* males. Therefore, we suggest that sexual selection may result in sexual head dimorphism in both species.

Roles of niche divergence hypothesis in head dimorphism

Head size or shape dimorphism can arise if the sexes evolve appropriate adaptations for different prey: the head is an important organ in obtaining, processing, and ingesting food, and animals with larger (i.e., wider, taller) heads can prey on larger, and harder prey because of larger bite forces (Jiménez-Arcos et al., 2017). This is probably because of the known positive relationship between prey size and hardness (Herrel et al., 1999; Meyer et al., 2019). Consequently, sexual head dimorphism can reduce sexual resource competition by resulting in dietary differences between males and females, as has been reported in many species (Halloy et al., 2006; Losos, 2009). In this study, we found a relationship between the niche divergence hypothesis and male-biased sexual head dimorphism. Specifically: (1) larger-headed males of *E. grammica* had a higher proportion of Cicindelidae, Formicidae, and Lucanidae in the prey composition than did females (**Figure 4**), which was related to sexual head dimorphism; (2) males consumed larger sizes of Coleoptera than did females (measured by tergite sizes, **Figure 5**), suggesting that males could prey on larger insects.

We found weak support for niche divergence in *E. velox* because both prey composition and size showed marginal differences between the two sexes. Males and females had a high niche overlap index (0.99), which was higher than that of *E. grammica* (0.78). This pattern is consistent with that of sexual head dimorphism because neither width nor depth was different between males and females in *E. velox*. Similar results have been reported for other arid lizards (Liu et al., 2011; Zhao and Liu, 2013). This is regardless of the species exhibiting sexual head dimorphism without prey divergence (Zhao and Liu, 2013; Taverne et al., 2019). It is still not easy to determine

TABLE 2 Frequency data of prey consumed by female and male *Eremias* species.

Species	***E. velox***		***E. grammica***	
Gender	**Female**	**Male**	**Female**	**Male**
Formicidae	3	17	11	32
Apidae	2	1	1	1
Carabidae	3	2	7	6
Lucanidae	4	3	2	6
Scarabaeidae	3	3	8	4
Meloidae	5	5	8	5
Buprestidae	18	13	19	11
Tenebrionidae	2	4	4	8
Acrididae	41	54	51	18
Cicindelidae	2	4	1	4
Coleoptera larva	22	12	44	47
Mantidae	0	0	1	0
Diptera	3	2	0	0

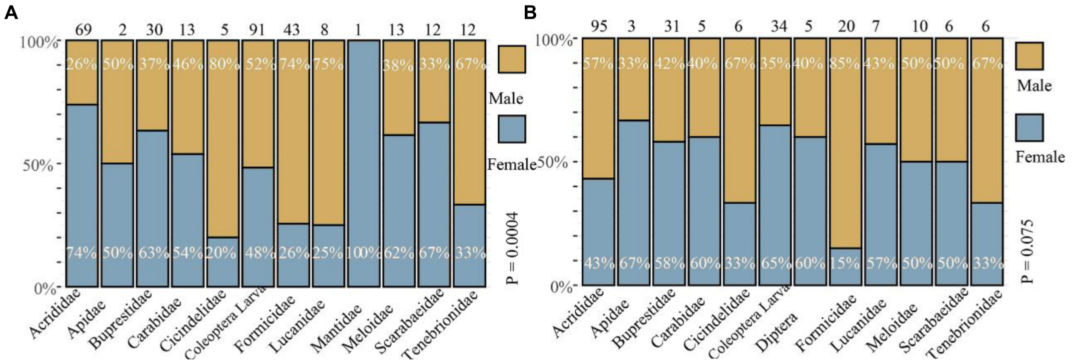

FIGURE 4
Frequency of prey composition (%) between the two sexes of *Eremias grammica* **(A)** and *E. velox* **(B)**. The number in each histogram represents the total number of prey items. The top values indicate the proportion of males, while the bottom values indicate that of females.

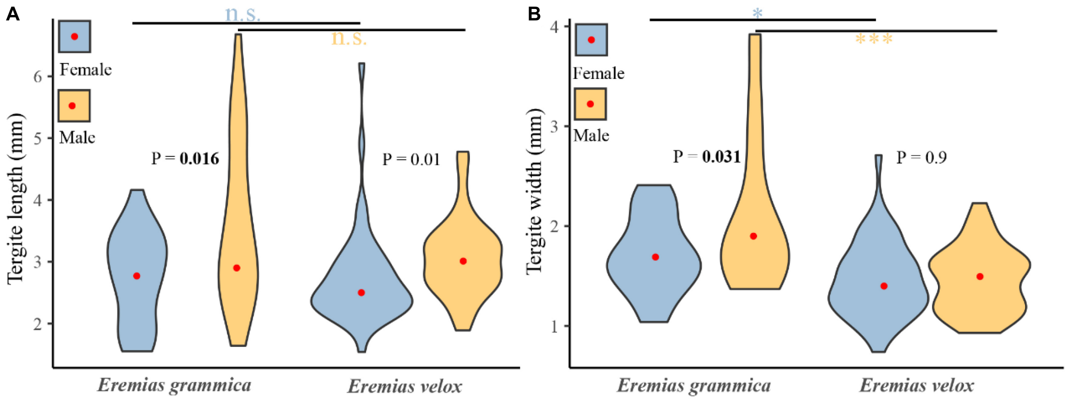

FIGURE 5
Differences of tergite length **(A)** and width **(B)** between males and females for *Eremias grammica* and *E. velox*. The red points are the mean values of size for each group. *P*–values represent the differences in prey sizes between males and females, and the line represents the differences in sizes between two species of the same sex. **P* < 0.05, ****P* < 0.001.

the contribution of sexual and natural selection in this study, because if sexual selection primarily contributes to sexual head dimorphism, males and females differ in their consumption of available prey. Therefore, this would also result in niche segregation between the two sexes (i.e., niche divergence is the result of sexual selection). Males and females can also inhabit different microhabitats to avoid potential competition; however, this was not tested in our study, which should be assessed in the future.

Interspecific variation

Sexual dimorphism can arise when males and females compete for limited resources (Dayan and Simberloff, 1998; Bolnick and Doebeli, 2003; Pincheira-Donoso et al., 2018). Phylogenetically related sympatric species have the same phenotypes in similar ecological circumstances (e.g., anoles, Losos, 2009), and therefore face high interspecific competition for resources. In this study, there was no difference between the body sizes of the two *Eremias* species, but significant differences were observed in both the head and prey between the two species. Moreover, the magnitude and forms of intersexual head trait divergence varied between these two species (e.g., *E. velox* showed less dimorphic head traits). Therefore, a potential explanation would be that, as resources are rare in arid regions, these two sympatric species have evolved different functional traits (head shape) and inhabited different niches to avoid interspecies and intraspecific competition.

Interplay of sexual and natural selections

We acknowledge that we still cannot determine the contribution of sexual and natural selection from the observations of this study, because niche divergence is sometimes a by-product of sexual selection. However, we found that the niche overlap index of the males of these two species (0.55) was much lower than that of the females (0.99), which suggested that interspecific competition was higher in males than in females. When resources are limited, pressures on males are extremely high in these two species; both need resources to meet their fitness requirements, and head divergence could help them inhabit different niches and avoid potential interspecific competition. Sexual head dimorphism and niche divergence may occur simultaneously. Thus, we suggest that both sexual and natural selection resulted in sexual head dimorphism in these two species.

Conclusion

In this study, we found both head shape dimorphism and prey divergence in two sympatric *Eremias* species, with noticeable head differences between the two sexes corresponding to significant differences in prey composition and size in *E. grammica* and vice versa in *E. velox*. Interspecific differences in the heads and preys of these two species were mainly due to male–male variations. We suggest that both sexual and natural selection resulted in sexual head dimorphism in these two sympatric species.

Data availability statement

The data presented in this article can be found online at www.datadryad.org (https://doi.org/10.5061/dryad.ht76hdrk3). Further inquiries can be directed to the corresponding author.

Author contributions

TL, LW, and LS participated in data collection as well as in the conception and writing of the article. TL analyzed the data. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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