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## Altitudinal variation in body size in *Abacarus panticis* Keifer (Acari: Eriophyidae)

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**Abstract** We found that body length of a minute eriophyid mite, *Abacarus panticis* Keifer, increased with elevation and rainfall, decreased with temperature, and exhibited a female-biased dimorphism. There was a negative temperature–body length relation in the female instead of the male, whose size remained constant along temperature gradients. In addition, scaling of body length between sexes is not significantly different from one. We conclude that within-species body length of *A. panticis* conforms to Bergmann’s trend but not Rensch’s rule. Further studies could take advantage of the more rigorous and flexible hierarchical model in the revelation of scale-specific determinants of phenotypic variation.

**Keywords** Body size · Ectotherms · Environment · Sexual size dimorphism · Taiwan

### Introduction

Body size of endotherms within and among species tends to increase with latitudes/altitudes. The so-called Bergmann’s rule dictates that colder climates select for larger animals due to that their smaller surface-to-volume ratio is less prone to heat loss (Watt et al. 2010). While the underlying mechanism for Bergmann’s rule applies solely to endotherms (Watt et al. 2010), an analogous

Bergmann’s trend may manifest in ectotherms owing to other mechanisms. These can include an increase in tolerance of severe climates of bigger animals for their large fat reserves (Watt et al. 2010) or larger body size as a result of slower maturity rate at lower temperatures (Blanckenhorn and Demont 2004). On the contrary, larger body size may prevent ectotherms from gaining heat rapidly for optimal foraging at low temperatures (Pincheira-Donoso et al. 2008); alternatively, shorter growing season in cold environments may restrain body size (Blanckenhorn and Demont 2004); both can lead to a pattern converse to Bergmann’s cline in ectotherms. Indeed, both Bergmann’s and converse Bergmann’s clines have been observed in arthropods (Blanckenhorn and Demont 2004).

Similarly, scaling of sexual size dimorphism (SSD) varies among species (Webb and Freckleton 2007). Rensch’s rule posits that SSD will increase with body size when males are the larger sex (male-biased) while SSD will decrease with body size when females are the larger sex (female-biased) (Rensch 1960). So far, Rensch’s rule has received mixed support and its validity is particularly questioned in female-biased species, including arthropods (Webb and Freckleton 2007). General accordance with Rensch’s rule in male-biased species can largely be accounted for by sexual selection for larger males (Abouheif and Fairbairn 1997; Dale et al. 2007; Walker and McCormick 2009). On the contrary, the occurrence of larger females could involve several mechanisms, acting independently or synergistically, including sexual selection and fecundity selection for larger females, natural selection for reduction of intersexual competition, and sex difference in plasticity to environments (Stephens and Wiens 2009; Chown and Gaston 2010; Stillwell et al. 2010). As such, it is not unexpected that Rensch’s rule is not generally verified in female-biased species due to the many differential influences on body size between sexes. On the other hand, because environmental variation could result in variation in SSD among populations within a species (Teder and Tammaru 2005), investigating how SSD

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varies with environment might help reveal potential ecological processes leading to the observed within-species scaling of SSD. However, studies examining both environmental influences on SSD cline and scaling of body size between sexes remain very limited (but see Stillwell et al. 2007; Jin et al. 2013).

When body size cline was investigated, traits (e.g., body length) of each population were typically represented by the average and then associated with environmental variables (e.g., Ma et al. 2009; Hu et al. 2011). While such averaging has its merit of simplicity, this method could nevertheless lead to misleading conclusions when the discarded within-population variation is so large that including all individual data (instead of considering population mean only) may considerably weaken the association as shown by averaging method (Bryk and Raudenbush 1992). Alternatively, the hierarchical model (also called the multilevel model) takes each individual observation into account and can avoid such bias. Moreover, many study systems are nested in structure. This is especially true for ecological studies because ecological outcomes are often determined by processes involving several spatial and temporal scales (McMahon and Diez 2007; Qian et al. 2010). For example, the composition of European arthropod community is a consequence of synergic forces covering regional, landscape, and local scales (Schweiger et al. 2005). The hierarchical model explicitly considers the nested data structure and can reveal the magnitude of effects of all levels as well as the cross-level interactions (Bryk and Raudenbush 1992), such as the significance of sex (individual level character, commonly named level 1), temperature (population level, level 2), and their interaction on body size (i.e., whether the influence of sex on body size varies with temperature). In comparison, conventional averaging method cannot effectively incorporate nested data structure, especially when the ecological processes involve several scales.

Here we use *Abacarus panticis* (Keifer), a phytophagous eriophyoid mite (Acari: Eriophyidae), as a model system to investigate how body size and SSD vary with environments using hierarchical linear models. We also test whether scaling of body size between sexes in *A. panticis* is in accordance with Rensch's rule. Multivoltine *A. panticis* are commonly found on Yushan cane [*Yushania niitakayamensis* (Hayata) Keng f.; Poaceae] in the mountains of Taiwan (Wang and Huang 2011). When eriophyoid mites were collected on *Y. niitakayamensis* (Wang and Huang 2011), we observed sexual dimorphism and an altitudinal variation in the body size of *A. panticis*. Being very minute in size (< 250  $\mu\text{m}$ ) (see "Results"), *A. panticis* should be prone to environmental variation; accordingly, they are ideal for study of ecological determinants of morphological variation. To our knowledge, *A. panticis* is among the smallest organisms to be tested for body size and SSD clines. More broadly, environmental associations were rigorously examined with hierarchical linear models, which should be more adequate for similar studies but remain

infrequently applied. In this study, Bergmann's or converse Bergmann's clines simply dictate an association between body length and elevation or temperature without implicating the mechanism underlying the original Bergmann's rule for endotherms.

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## Materials and methods

### Collection of eriophyoid mites

Between 1991 and 2009, leaves of *Y. niitakayamensis* suspected with eriophyoid mites were collected in the mountains of Taiwan. Sites including low to high elevations were surveyed during each season and most time periods (Supporting information Fig. S1). This prevents the likely confounding influence of seasonal temperature fluctuations and yearly resource variation on body size of mites. Altitude and coordinate of each collection site was obtained with a portable Global Positioning System and verified with a high-resolution contour map (Table 1). Leaves were later preserved in 75 % ethanol with saturated sugar for at least 1 week. Eriophyoid mites were removed from leaves by spinning the preserved liquid in a centrifuge at 1,500 rpm for 3 min and were then transferred to the preparatory medium in a concavity slide. The concavity slide was placed on a hotplate heated to 100 °C and the preparatory medium was stirred continuously using a probe until turning dark brown. Eriophyoid mites were later transferred to another concavity slide filled with wash medium and were left in the wash medium for at least 1 week to clean the mites. Finally, mites were singly slide-mounted in the final medium (formula recipes for the preparatory, wash and final medium are acquired from H.H. Keifer) and were examined under a phase-contrast microscope (Leitz Laborlux S, Leica, Germany; objective: Plan Phaco 2, 40/0.65; eyepiece: 12.5 $\times$ /18 M). Length of body ( $\mu\text{m}$ ) of *A. panticis* was measured with an objective micrometer. Sex was determined based on the existence of genital coverflap on the females.

### Environmental factors

We selected variables for analysis based on the availability of data and our knowledge of the study system. Predictive environmental variables included mean annual temperature (Temp., °C), total annual rainfall (Rainfall, mm), seasonality [Seasonality, °C; difference between the highest (August) and the lowest (January) monthly temperature], and primary productivity (Productivity). Productivity for each locality was represented by the average of the length of 30 randomly selected *Y. niitakayamensis* leaves (cm), which were measured from the tip to the petiole. We compiled a long-term (1991–2009) temperature and rainfall dataset across Taiwan from the Taiwan Central Weather Bureau. The

**Table 1** Sites, along with related environmental variables, for the collection of *Abacarus panticis* in Taiwan, and mean body length of *A. panticis* (mean  $\pm$  SE) for both sexes in each site

| Site | Coordinate |         | Altitude (m) | Temperature ( $^{\circ}$ C) | Rainfall (mm) | Seasonality ( $^{\circ}$ C) | Productivity (cm) | Body length (mean $\pm$ SE, $\mu$ m) |                  |
|------|------------|---------|--------------|-----------------------------|---------------|-----------------------------|-------------------|--------------------------------------|------------------|
|      | x          | y       |              |                             |               |                             |                   | Male                                 | Female           |
| 1    | 274200     | 2698800 | 3,400        | 3.0                         | 3,236.0       | 11.0                        | 14.3              | 146.7 $\pm$ 2.2                      | 190.0 $\pm$ 4.5  |
| 2    | 266500     | 2680700 | 3,100        | 4.8                         | 3,240.3       | 11.0                        | 14.3              | 138.1 $\pm$ 4.9                      | 182.4 $\pm$ 24.6 |
| 3    | 239100     | 2573500 | 3,010        | 6.8                         | 3,518.2       | 9.1                         | 10.2              | 174.8 $\pm$ 4.8                      | 185.3 $\pm$ 9.8  |
| 4    | 276800     | 2669000 | 2,800        | 6.0                         | 2,749.4       | 10.6                        | 10.7              | 138.0 $\pm$ 4.1                      | 172.2 $\pm$ 3.6  |
| 5    | 277300     | 2698500 | 2,800        | 6.6                         | 3,263.8       | 10.9                        | 10.2              | 137.8 $\pm$ 4.3                      | 201.6 $\pm$ 9.6  |
| 6    | 288000     | 2696100 | 2,800        | 7.1                         | 2,722.3       | 11.0                        | 9.8               | 133.7 $\pm$ 2.9                      | 155.6 $\pm$ 6.6  |
| 7    | 239100     | 2597200 | 2,800        | 7.3                         | 2,561.2       | 12.0                        | 9.2               | 136.8 $\pm$ 9.0                      | 158.2 $\pm$ 5.0  |
| 8    | 240700     | 2573200 | 2,760        | 8.3                         | 3,455.7       | 9.2                         | 10.7              | 153.2 $\pm$ 3.2                      | 166.7 $\pm$ 8.3  |
| 9    | 273700     | 2668600 | 2,750        | 7.2                         | 2,612.0       | 12.9                        | 8.4               | 146.0 $\pm$ 3.9                      | 155.4 $\pm$ 4.8  |
| 10   | 280400     | 2675200 | 2,600        | 8.3                         | 3,386.4       | 11.8                        | 8.5               | 123.7 $\pm$ 8.2                      | 174.0 $\pm$ 4.3  |
| 11   | 240500     | 2573200 | 2,550        | 9.6                         | 3,463.4       | 9.1                         | 10.4              | 138.6 $\pm$ 2.9                      | 149.3 $\pm$ 4.3  |
| 12   | 278100     | 2697900 | 2,463        | 8.6                         | 3,250.9       | 10.9                        | 12.8              | 128.4 $\pm$ 5.2                      | 170.1 $\pm$ 4.8  |
| 13   | 283700     | 2675800 | 2,350        | 7.7                         | 2,593.7       | 9.7                         | 9.7               | 125.4 $\pm$ 4.4                      | 139.3 $\pm$ 6.1  |
| 14   | 273300     | 2660300 | 2,250        | 10.4                        | 3,155.3       | 11.8                        | 8.1               | 146.8 $\pm$ 8.3                      | 148.8 $\pm$ 4.2  |
| 15   | 287700     | 2674500 | 2,200        | 10.3                        | 3,112.4       | 10.4                        | 13.3              | 134.5 $\pm$ 9.2                      | 161.2 $\pm$ 3.9  |
| 16   | 260300     | 2680800 | 2,200        | 10.6                        | 2,826.5       | 10.8                        | 10.2              | 123.0 $\pm$ 3.1                      | 138.3 $\pm$ 3.3  |
| 17   | 306100     | 2711100 | 1,800        | 10.7                        | 3,509.0       | 10.9                        | 8.2               | 131.7 $\pm$ 7.0                      | 131.4 $\pm$ 14.4 |
| 18   | 290300     | 2719100 | 1,650        | 13.3                        | 3,228.8       | 11.3                        | 9.8               | NA                                   | 135.5 $\pm$ 5.4  |

See text for the definition of environmental variables

two climatic variables were stored in a Geographic Information System dataset with a spatial resolution of  $40 \times 40$  m, from which temperature (including mean temperature and temperature for January and August) and rainfall data for each locality were estimated based on the coordinate of collection locality.

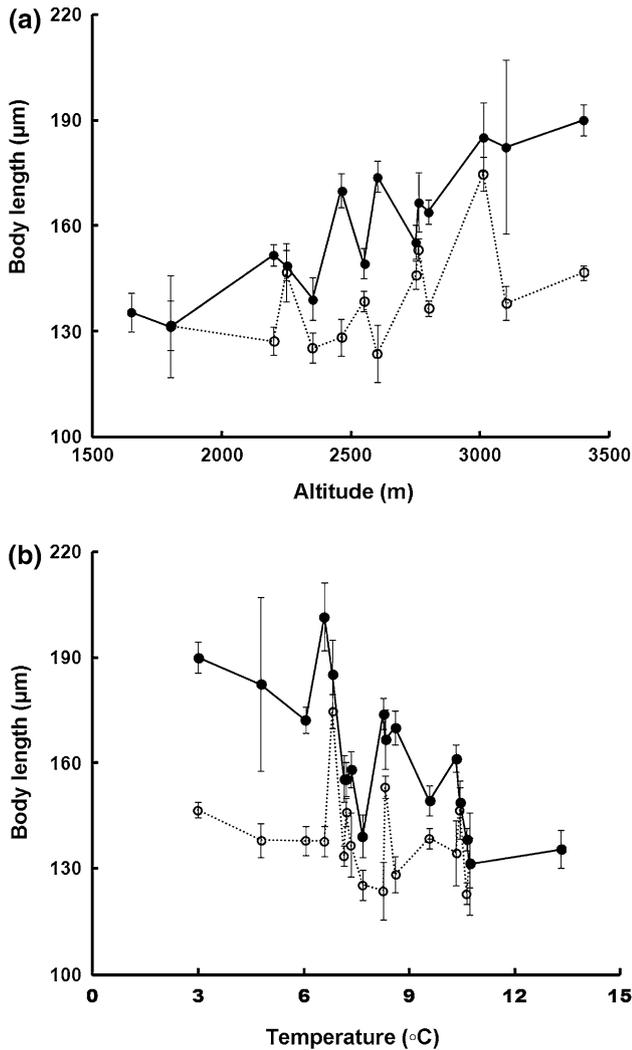
### Statistical analyses

Four separate hierarchical linear models were implemented. Firstly, we assessed the association between body length of *A. panticis* and altitude. Sex of *A. panticis* was also included to reveal sexual difference in body length and sex-by-altitude interaction (that is, whether the degree of SSD varies with altitude). Because SSD is typically represented by the *ratio* of body size between sex (Smith 1999) instead of the *difference* as calculated in hierarchical model, we log transformed the body length so that the conventional definition of SSD (i.e., using the ratio) can be incorporated into the model. That is, we converted body length of (female–male) to  $[\log(\text{female}) - \log(\text{male})]$  so that the latter is equal to  $\log(\text{female}/\text{male})$  and is central around zero. Body length and sex of each *A. panticis* was the level-1 (individual level) variable nested under the locality and was regressed with the altitude (level-2, population level, variable). Locality was treated as the random variable. Such a hierarchical model specifies that characteristics of each *A. panticis* individual (e.g., body length) of the same locality may not be independent of each other, which also helps correct for potential non-independence of repeated sampling of the same site. We then followed Zuur et al. (2009) in the determination of significant factors in the

hierarchical linear models. Firstly, homogeneity of variance between the two sexes was confirmed with Levene's tests, and if violated, followed by including a weighing variable to adjust for sexual difference in variation of body length. Secondly, we assessed whether sex should be included in the random component of the model (i.e., whether SSD varies with locality) by estimating the likelihood ratio (LR). Thirdly, starting with the fixed part of the hierarchical model containing all explanatory variables (sex, altitude, and the interaction), the least significant variable (beginning with interaction) was sequentially removed from the model until all remaining variables were significant based on a series of LR tests (S2 for an exemplary statistical procedure). Lastly, normality of residuals of the final hierarchical linear model was confirmed with Shapiro–Wilk's test.

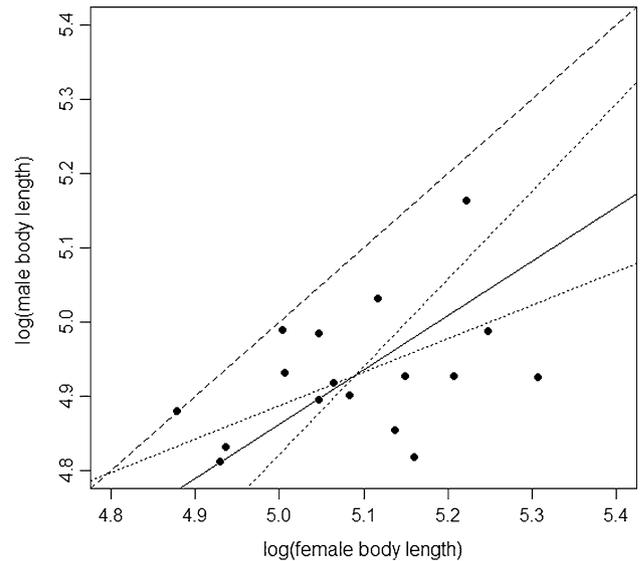
Altitudinal variation in body size may actually reflect the influence of other environmental factors correlated with altitude, such as temperature. We therefore built another hierarchical linear model to investigate the determinants of body length using four environmental factors: temperature, rainfall, seasonality, and productivity, and following the same statistical procedure as mentioned above. Sex of *A. panticis* was also included to reveal any sex-by-environment interaction. Analogously, the association between body length and four ecological variables was assessed for males and females, respectively, following the same method (Zuur et al. 2009).

Based on Fairbairn (1997), allometry for SSD was tested by regressing log-transformed mean body length of males on log-transformed mean body length of females (Fig. 2). A slope statistically larger than 1 means that SSD increases with body length for male-biased



**Fig. 1** Environmental associations of body length of *Abacarus panticis* in Taiwan; **a** altitudes, **b** mean temperature. Females (filled circles and solid lines); males (open circles and broken lines). For easy inspection, body length is shown using original value and is represented with population mean  $\pm$  SE

SSD or SSD decreases with body length for female-biased SSD; that is, such scaling of SSD is accordant with Rensch's rule. Otherwise, Rensch's rule is concluded to be invalid. When regressing body length between sexes, model II regression is more appropriate than model I regression (e.g., ordinary least square) because the former method accounts for measurement uncertainty in the  $x$  variable (in this case, body length of females) while model I regression assumes no measurement error in the  $x$  variable (Fairbairn 1997). We used reduced major axis regression, a commonly used model II regression technique, to estimate the slope and 95 % confidence interval (CI) of this parameter. Because hierarchical models have not been developed for model II regression, we adopt the conventional method (i.e., using population mean instead of individual body size) for this part of the analysis. All the procedures were



**Fig. 2** Slope and 95 % confidence interval (CI) of the regression of log (mean body length of males) on log (mean body length of females) of *Abacarus panticis* in Taiwan by reduced major axis regression. Slope (black line), 95 % CI (dotted lines), and the referenced isometric line (dashed line). Dots show data for the sites

implemented in the nlme and lmodel2 packages in R-2.14.2 (R Development Core Team 2012).

## Results

A total of 362 *A. panticis*, including 245 females and 117 males, collected from 18 sites across Taiwan were measured (Table 1). Each site was sampled with an average of 2.0 $\times$  (range, 1–4) and was recovered with a mean of 20.1 *A. panticis* specimens (range, 6–44). Body length of *A. panticis* ranged 94.6–223.6  $\mu\text{m}$ . The values of explanatory variables varied among the localities; altitude 1,650–3,400 m, temp. 3.0–13.3  $^{\circ}\text{C}$ , rainfall 2,561.2–3,518.2 mm, seasonality 9.1–12.9  $^{\circ}\text{C}$ , and productivity 8.1–14.3 cm (Table 1).

Because of the sexual difference in variance of body length (Levene's homogeneity test,  $p < 0.001$ ), a variable accounting for heteroscedasticity was included in the hierarchical linear model associating altitude and sex with body length of *A. panticis*. LR test revealed that sex should be included in the random component (LR = 10.66,  $df = 1$ ,  $p < 0.001$ ). Sequential removal of the least significant factor in fixed component of the model showed that body length of *A. panticis* increased with altitude ( $t = 5.82$ ,  $df = 16$ ,  $p < 0.001$ , Fig. 1a), differed between sex ( $t = 5.81$ ,  $df = 343$ ,  $p < 0.001$ , females larger than males), but there was no sex-by-altitude interaction (S2 for detailed statistical procedures).

Investigation of association between sex and four environmental factors with body length of *A. panticis*, following the same procedure, showed that body length of *A. panticis* decreased with temp. ( $t = -2.42$ ,  $df = 15$ ,

$p < 0.05$ ), increased with Rainfall ( $t = 3.26$ ,  $df = 15$ ,  $p < 0.01$ ), and differed between sex ( $t = 3.99$ ,  $df = 342$ ,  $p < 0.0005$ ). A significant sex-by-temp. interaction was also observed ( $t = -2.21$ ,  $df = 342$ ,  $p < 0.05$ ) (Fig. 1 b). Seasonality and primary productivity had no significant influence on body length (both  $p > 0.05$ ); neither did their interactions with sex (both  $p > 0.05$ ).

Similarly, body length of female *A. panticis* decreased with temp. ( $t = -7.14$ ,  $df = 15$ ,  $p < 0.0001$ ), increased with rainfall ( $t = 3.11$ ,  $df = 15$ ,  $p < 0.01$ ), but had no association with seasonality or productivity (both  $p > 0.05$ ). However, all four environmental variables had no influence on the male body length (all  $p > 0.05$ ).

We excluded one site containing only female *A. panticis* (Table 1). Reduced major axis regression analysis of the remaining 17 sites shows that the slope of regression line for body length of males on body length of females was not significant different from one ( $b = 0.73$ , 95 % CI 0.45–1.18) (Fig. 2).

## Discussion

However opposite in responses, Blanckenhorn and Demont (2004) maintained that Bergmann's and converse Bergmann's clines may actually be two ends of a continuum of body size patterns determined by an interaction of temperature and season length. It is expected that smaller arthropods should conform to Bergmann's trend due to their rapid acclimation to temperature and a short development time (Blanckenhorn and Demont 2004). As predicted, minute multivoltine *A. panticis* conforms to Bergmann's cline and are larger at higher elevations or lower temperatures. Such altitudinal increase in phenotypic body length may have a genetic basis, being simply a result of phenotypic plasticity, or a combination of both (Stillwell 2010), and could probably be discerned by common-garden or reciprocal transplant experiments. Because the current study did not disentangle the relative role of adaptation and plasticity, the proximate mechanism underlying the observed Bergmann's cline remains to be investigated. Lower temperatures may select for larger animals due to their better resistance to starvation (Pincheira-Donoso et al. 2008). Alternatively, the required development period of *A. panticis* may be short relative to the limited growth season at high altitudes such that a plastic physiological response to low temperature is still allowed to be fully attained (Blanckenhorn and Demont 2004). Only experimental studies can partially disentangle these non-mutually exclusive mechanisms. The observed Bergmann's cline could, nevertheless, be a result of sampling artifact if body length of *A. panticis* is mainly a plastic response and certain elevations are merely surveyed during specific periods. For example, high altitudes sampled only in winter and low altitudes solely in summer could lead to the same body size cline. Because low- to high-altitudinal sites were sampled during each season and most time periods, the observed

Bergmann's cline is unlikely to be owing to the sampling bias.

Contrary to the prediction that body size increases with aridity (i.e., decreases with rainfall) due to the higher desiccation-resistant capability of larger animals (Remmert 1981), body length of *A. panticis* increases with rainfall. This might be owing to that Taiwanese mountains are typically so moist that desiccation is less a limiting factor. Although an association between body size and primary productivity (represented with leave length) is not detected in this study, it is likely due to that plant quality is more important in determining body size (Ho et al. 2010) than plant quantity. Higher rainfall may lead to more frequent growth of Yushan cane and increase the availability of grass of better quality, thus leading to larger *A. panticis*. A common-garden experiment on body size provided with low- versus high-elevation leaves of Yushan cane could verify this hypothesis.

The slope of regression line between male and female body length is not statistically different from 1 and is largely within the  $<1$  range (Fig. 2), indicating that within-species scaling of SSD in *A. panticis* is not accordant with Rensch's rule. Moreover, there is a trend that SSD (female/male) increases with body size for this female-biased species (Fig. 2), a pattern more similar to inverse of Rensch's rule. Violation of Rensch's rule is commonly observed among female-biased species (Webb and Freckleton 2007). Several processes could potentially lead to a disagreement with Rensch's rule in female-biased species. In this study, SSD in *A. panticis* varies with temperature and this is mainly caused by the change in the female instead of the male (Fig. 1b). That is, females are much larger at lower temperatures whereas body length of the male is less varied, thus leading to the negative SSD–temperature association. A general agreement in pattern between intraspecific scaling of body length between sexes and a trend of larger females in colder environment suggests that temperature, or factor(s) associated with it, may be one of the driving forces leading to the observed scaling of SSD in this study. Namely, body lengths of females but not males are affected by temperature, and the intersexual difference in response to temperature might result in the noticed SSD scaling that body lengths of females increase faster than those of males.

Larger females at lower temperature is consistent with the parental investment hypothesis (Ficetola et al. 2010), which posits that larger females reproduce larger progeny to increase their survivorship in cold environments. This could be achieved through a delayed maturation at a larger size (Angilletta et al. 2004) and should be plausible considering the less cost for a longer development time under low predation risks at high latitudes/altitudes (McKinnon et al. 2010). Nevertheless, given that the magnitude of SSD also decreased with latitudes (e.g., Blanckenhorn et al. 2006; Stillwell et al. 2007), and converse Bergmann's clines are not uncommon in arthropods (Blanckenhorn and Demont 2004),

selection for larger progeny at cold climates should not be the only mechanism determining the direction and magnitude of SSD cline.

Conventionally, environmental associations of phenotype and SSD clines are investigated by firstly calculating population and sex-specific population means (to derive SSD), followed by associating each outcome with ecological factors (e.g., Ma et al. 2009; Hu et al. 2011). In this study, we demonstrate that body length and SSD clines can readily be incorporated into a single hierarchical linear model. Besides, unlike the averaging method that disregards within-population variation outright without considering any potential resultant bias, the hierarchical linear model includes all individual measurements and should therefore be a more rigorous method. Moreover, relative to the averaging method, the hierarchical linear model is capable of explicitly modeling ecological processes operating across multiple spatial scales, such as the interactive effects of sex, an individual-level factor, and temperature, a population-level variable, on body length. In light of these advantages, hierarchical model has gained much attention in recent years among ecologists (McMahon and Diez 2007; Zuur et al. 2009; Qian et al. 2010) but its application on environmental association of phenotype and SSD clines of arthropods remains limited. Accordingly, further studies could take advantage of the more rigorous and flexible hierarchical model in the revelation of scale-specific ecological determinants of phenotypic traits.

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