Effects of climate warming on the performance of Gynaephora alpherakii (Lepidoptera: Lymantriidae) larvae in a Tibetan alpine meadow

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Abstract

The performance of invertebrate herbivores in grasslands can be influenced by climate warming, but there is a lack of experimental evidence, particularly in high elevation areas. We conducted two complementary experiments to investigate the effect of experimental warming on the performance of the grassland caterpillar Gynaephora alpherakii, a notorious pest species in the alpine Tibetan meadow. The first field experiment examined the effect of warming (non-warmed vs. warmed) on the feeding behavior, growth and development rate of the caterpillars. The second chamber experiment explored the relationship between temperature and caterpillar appetite, excrement mass, respiration rate or change of caterpillar weight. Results show that warming significantly decreased fresh body mass of caterpillars by 27.5%, cocoon volume by 61.1%, and egg production per female moth by 26.9 % at the end of the field experiment. Warming did not affect cocooning time but significantly increased feeding time of caterpillars during the field experimental period. The independent chamber experiment revealed a significant and positive correlation between caterpillar appetite, excrement mass, respiration rate, and temperature. However, except the first examination, there was a significant negative correlation between changes in caterpillar weight and temperature. Stepwise regression analysis indicated that excrement mass had the greatest influence on caterpillar weight. The weight loss of caterpillars to warming might thus be attributed to elevated metabolic rates at higher temperatures, and the behavioral adaptations failed to compensate for the physiological-induced weight loss. These findings suggest that climate warming can modify the performance and thus the fitness of invertebrate herbivores in high elevation areas.

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Abstract

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Key words: body size, feeding activity, grassland caterpillar, invertebrate, Qinghai-Tibet Plateau

Introduction

Climate change poses a significant threat to ecosystems worldwide, with rising temperatures influencing various biological processes and interactions (IPCC, 2021; Harvey et al., 2023). In particular, invertebrate herbivores that play critical roles in ecological dynamics, nutrient cycling, and energy flow within grassland ecosystems, are one of the most vulnerable groups (Hulme, 1994; Katz, 2016; McCary & Schmitz, 2021; Kempel et al., 2023). These organisms are vital for maintaining plant community structure, supporting predator populations, and enhancing soil health through their feeding activities and nutrient excretion (Kempel et al., 2015; Crawley, 2019; Neff et al., 2023). As global temperatures continue to rise, understanding the effects of climate warming on herbivores becomes crucial for predicting changes in community structure and ecosystem functioning.

Previous researches indicate that global warming has profound effects on body size across taxa (Dale & Frank, 2014; Diamond et al., 2014; Chown & Duffy, 2015; Merckx et al., 2018). Body size is expected to decrease in response to climate change due to the inverse relationship between temperature and body size, commonly known as the temperature-size rule for ectotherms (Angilletta et al., 2004; Kingsolver & Huey, 2008). This rule posits that ectotherms exhibit faster growth rates but attain smaller adult sizes under elevated temperatures (Angilletta, 2009), aligning with the intraspecific version of Bergmann's rule (Blackburn et al., 1999). While a decrease in size due to climate change is frequently observed in mammals and birds and is considered a widespread response (Gardner et al., 2011; Sheridan & Bickford, 2011), there are notable exceptions (Meiri et al., 2009; Yom-Tov & Geffen, 2011). Recent studies indicate a growing number of exceptions to the trend of decreasing body size with rising temperatures. For instance, findings show an opposite pattern in species such as the common lizard (*Lacerta vivipara*) in European mountains (Chamaille-Jammes et al., 2006), various taxa on the Tibetan Plateau (Zhao et al., 2014; Xi et al., 2016), as well as other species like the marten (*Martes americana*) in Alaska (Yom-Tov et al., 2008) and the Eurasian otter (*Lutra lutra*) in Norway (Yom-Tov et al., 2006). These exceptional cases challenge the applicability of Bergmann's and James's rules (James, 1970) for endotherms, as well as the temperature-size rule for ectotherms (Ray, 1960; Atkinson, 1994; Atkinson & Sibly, 1997). Consequently, there is no consistent pattern observed between warming and body size, making it crucial to elucidate the underlying mechanisms to fully comprehend the impact of climate warming on body size.

Warming can modify the body size of herbivores through various mechanisms, thereby influencing their response to rising temperatures (Sheridan & Bickford, 2011). One primary mechanism involves changes in metabolic rates; as ambient temperatures rise, ectothermic herbivores often experience elevated metabolic activity, which initially leads to faster growth rates. However, this rapid growth may also result in smaller adult sizes due to accelerated development reducing the available time for growth (Desai & Singh, 2009). Additionally, warming can affect resource availability and induce nutritional stress. Higher temperatures may alter plant phenology, potentially creating mismatches between the timing of herbivore emergence and food availability (Williamson et al., 2002). For instance, if plants mature earlier due to warming, herbivores may encounter reduced access to nutritious foliage, ultimately hindering their growth and resulting in smaller body sizes (Sahin, 2001). Behavioral adaptations also significantly influence changes in body size. As temperatures rise, herbivores may adjust their habitat use and feeding strategies to seek cooler microhabitats or alternative food sources, although these adjustments may not fully counteract the physiological effects of increased temperatures on growth rates (Sheridan & Bickford, 2011). Furthermore, climate-induced stressors, such as intensified competition and altered predator-prey dynamics, can further impact body size. In warmer environments, herbivores may face increased competition for limited resources, leading to suboptimal growth conditions. This interplay of factors underscores the complexity of how warming impacts the size of herbivores. In this end, the mechanisms through which warming affects herbivore body size are multifaceted, involving metabolic, ecological, and behavioral responses. Understanding these interactions is crucial for predicting the ecological implications of climate change on herbivore populations and their roles within ecosystems.

Alpine regions, such as the Tibetan Plateau, are currently experiencing rapid climatic shifts characterized by increasing temperatures and altered precipitation patterns. These changes can significantly impact local biodiversity and ecological interactions (Wu et al., 2011). However, there is a dearth of empirical data regarding the responses of invertebrate herbivores in high-elevation areas, which raises concerns considering the unique adaptations and ecological roles fulfilled by these species in fragile alpine ecosystems.

The grassland caterpillar *Gynaephora alpherakii* exemplifies a pertinent case in this context. This species is a notorious pest in the alpine Tibetan meadows, capable of causing substantial damage to vegetation and disrupting local ecosystems. The life cycle and population dynamics of *G. alpherakii* are closely linked to environmental conditions, making it an ideal model for investigating the impacts of climate change on herbivorous insects (Chen et al., 2015). Previous research has shown that increases in temperature can influence herbivore physiology, behavior, and population dynamics. For instance, higher temperatures have been associated with increased metabolic rates, altered feeding behaviors, and shifts in developmental timing across various insect taxa (Bale et al., 2002; Sheridan & Bickford, 2011). However, most of this research has predominantly focused on lowland ecosystems, thereby highlighting a critical knowledge gap concerning high-elevation species.

To address this gap, we conducted a comprehensive study to examine the effects of experimental warming on the performance of *G. alpherakii* through two complementary experiments. The first field experiment aimed to assess how warming influenced the feeding behavior, growth, and developmental rates of these caterpillars in their natural habitat. The second controlled chamber experiment focused on the relationship between temperature and various physiological metrics, including caterpillar appetite, excrement mass, respiration rate, and changes in body weight. Two specific hypotheses were tested: (1) warming would reduce caterpillar body size, and (2) behavioral adaptations resulting from warming would not fully offset the physiological-induced weight loss.

Material and methods

2.1 Study site and species

This study was conducted in an alpine meadow located in Hongyuan County (32°48'–32deg52'N and 102deg01'–102deg33'E), Sichuan Province, China, within the eastern Tibetan Plateau. Detailed information regarding the climatic conditions and plant community composition can be found in prior studies (Wu et al., 2021).

In this meadow ecosystem, the grassland caterpillar *Gynaephora alpherakii* emerges as one of the most significant and prevalent herbivorous insects. During typical growing seasons, larval densities of this species range from several to tens per square meter, with population outbreaks potentially reaching up to 200 individuals per square meter (Xi et al., 2013). These caterpillars exhibit voracious feeding behavior, primarily targeting sedges while occasionally consuming forbs. Furthermore, their activity patterns are highly sensitive to temperature fluctuations; they are observed crawling to the apices of plant shoots to feed during optimal thermal conditions (e.g., mid-morning and mid-afternoon), while seeking refuge beneath large leaves or on the soil surface during extreme temperatures (e.g., noon or nighttime) (Xi et al., 2013).

2.2 Field experiment

We conducted a one-factorial experiment comprising two treatments: 1) Non-warmed and 2) Warmed, with six replicates for each treatment. The field experiment commenced on June 1 and concluded on September 4, 2016.

In late May 2016, twelve cylindrical cages (0.5 m in diameter and height) were systematically deployed in a pasture that was grazed by livestock exclusively during the winter months, maintaining a minimum spacing of 3 m between cages. The vegetation within the study area exhibited homogeneity. Each cage was constructed from a robust steel frame encircled and covered with fine steel mesh (0.1 mm thick, 2 x 2 mm mesh size). Following the initiation of the experiment, the tops of the cages were similarly enclosed with steel mesh, and the bases were embedded 20 cm into the soil to prevent herbivore escape. Additionally, six cages were fitted with transparent plastic film (with sunlight transparency exceeding 95%) to create a warmed microenvironment, while the remaining six served as controls (non-warmed).

Experimental caterpillars were collected from adjacent areas, ensuring that only healthy, medium-sized individuals were selected for the study. Ten individuals of *Gynaephora alpherakii* were introduced into each replicate, reflecting densities observed during both typical and outbreak years. Prior to the initiation of the experiment, larger herbivores (e.g., grasshoppers) and predators (e.g., *Lycosa* sp.) were removed from the cages to eliminate potential confounding effects.

We measured the fresh body mass of each living caterpillar biweekly, carefully collecting individuals from each cage, weighing them using a portable analytical balance (Sartorius, Germany; precision 0.001 g), and then returning them to their respective cages. Additionally, we monitored cocoon production and alive caterpillar number every three days from the emergence of the first cocoon on August 7 until all caterpillars had cocooned by September 7, measuring the length and width of 18 cocoons to calculate their volume using the elliptical volume formula.

We also evaluated the foraging behavior of *Gynaephora alpherakii* following the methodology described by Xi et al. (2013). On sunny days, we recorded the number of feeding individuals—termed "feeding frequency"—on an hourly basis from 08:00 to 18:00 (Beijing time), conducting two observation sessions during the initial 10 days when all caterpillars were alive. This approach ensured that measurements of feeding frequency were independent of density fluctuations (Xi et al., 2013).

Temperature was monitored using thermometers (model DS1921G, Maxim Integrated Products, Sunnyvale, California, USA) in three cages for each treatment. Over the experimental duration, the mean daily temperature in the warmed treatments was observed to be 1.8 degC higher than in the non-warmed controls (Cao et al., 2022).

2.3 Chamber experiment

To determine the influence of temperature on the performance of *G. alpherakii* , i.e., caterpillar appetite, excrement mass, respiration rate and body weight, we conducted a complementary chamber experiment during the period of the field experiment. The chamber was set as a day/night regime of 14/10 h, respectively, and the humidity was set as 45%. The temperature gradient was 2 from 12 to 28, resulting in a temperature gradient of nine levels. Each level repeated four times. Each replicate was a transparent glass box (20, 21, and 17 cm in length, width, and height, respectively). There were 72 boxes in total, each of which contained 0.5 g plant fresh leaves (*Scirpus pumilus*). Five healthy, medium-sized individuals of caterpillars were additionally introduced into each of 36 boxes, and the left 36 ones without caterpillars. The leaves were collected from the field and cleaned up indoor and cut down into 5 cm long fragments. The end of leaves was enfolded by cotton and then inserted into 2 ml centrifuge tube after immersed in water. The chamber experiment lasted for 24 hours. We recorded the weight of leaves, the body weight of each caterpillar, and the weight of excrement before and after the experiment. The caterpillar appetite was calculated following the protocols of Waldbauer (1968):

where W = weight of leaves before the experiment with caterpillars; L = weight of leaves after the experiment with caterpillars; a = (weight of leaves before the experiment without caterpillars - weight of leaves after the experiment without caterpillars)/weight of leaves before experiment without caterpillars; b = (weight of leaves before the experiment without caterpillars - weight of leaves after the experiment without caterpillars)/weight of leaves after experiment without caterpillars

In addition, the respiration rate of caterpillars was also measured using a non-steady-state and automated soil CO_2 flux system (LI-8100, LI-COR Biosciences, Lincoln, NE, USA) with a survey chamber of 10 cm in diameter (835.2 cm^3 for chamber volume). The temperature gradient was 4 from 6 to 28 . Before measuring, 10 caterpillars were placed in experiment chamber with enough food for 24 hours at each treatment (Song et al., 2008). Each treatment contained three replicates.

2.4 Data analysis

Kolmogorov–Smirnov and Levene's tests were used to check for normality of the distribution and variance homogeneity of the sample residuals, respectively. The cocooning rate was arcsine-transformed to achieve normality. One-way analysis of variance (ANOVA) was employed to determine the effects of warming on fresh body mass (per observation day), cocooning rate (per observation day), cocoon volume and egg production per female moth. Once a significant effect was detected, the difference between treatments was determined using *post hoc* Tukey tests. A generalized linear model (GLM with Poisson errors) was used to test the effect of warming on the number of feeding caterpillars (per observation hour). In addition, linear or exponential fittings were used to determine the relationship between temperature and caterpillar appetite, excrement mass, respiration rate or change of caterpillar weight, respectively. A stepwise approach was employed to investigate the significant caterpillar physiological factors influencing caterpillar body size. All the data analyses were conducted in SPSS 22.

Results

Warming significantly decreased fresh body mass of caterpillars by 12.4% in 2014/6/14 (Appendix S1: Table S1: $F = 7.00$, $p = 0.025$), by 27.5 % in 2014/6/23 (Appendix S1: Table S1: $F = 15.69$, $p = 0.003$), by 30.0 % in 2014/7/10 (Appendix S1: Table S1: $F = 15.12$, $p = 0.003$), by 27.5 % in 2014/7/23 (Appendix S1: Table S1: $F = 18.23$, $p = 0.002$) during the observation time (Fig. 1A). Warming did not affect cocooning rate (Fig. 1B) but significantly decreased cocoon volume by 61.1 % (Fig. 1C, Appendix S1: Table S1: $F = 8.59$, $p = 0.015$) and egg production per female moth by 26.9 % (Fig. 1D, Appendix S1: Table S1:$F = 18.22$, $p = 0.002$).

In addition, warming significantly changed the foraging behavior of caterpillars (Appendix S1: Table S2). Specifically, the number of feeding individuals was significantly higher at 9:00 (Appendix S1: Table S2: $Z = 2.35$, $p = 0.019$), 13:00 (Appendix S1: Table S2: $Z = 2.33$,$p = 0.020$) and 14:00 (Appendix S1: Table S2: $Z = 3.32$, $p < 0.001$) during the first examining time (Fig. 2A), and at 10:00 (Appendix S1: Table S2: $Z = 2.01$, $p = 0.044$), 11:00 (Appendix S1: Table S2: $Z = 2.99$, $p = 0.003$), 12:00 (Appendix S1: Table S2: $Z = 2.96$, $p = 0.003$), 13:00 (Appendix S1: Table S2: $Z = 3.71$, $P < 0.001$), 14:00 (Appendix S1: Table S2: $Z = 3.25$, $P = 0.001$), 15:00 (Appendix S1: Table S2: $Z = 2.57$,$P = 0.010$), 16:00 (Appendix S1: Table S2: $Z = 2.40$, $P = 0.016$) and 17:00 (Appendix S1: Table S2: $Z = 3.27$, $p = 0.001$) during the second examining time (Fig. 2B) in the warmed plots than in the non-warmed cages.

Caterpillar appetite, excrement mass and respiration rate increased with temperature (Fig. 3A-I). A negatively linearly relationship was observed between the change of caterpillar weight and temperature (Fig. 3K,L), except the first examining time (Fig. 3J). In addition, results of stepwise regression analysis showed that excrement mass influenced caterpillar weight most (Fig. 4).

Discussion

Our findings demonstrate that climate warming significantly impacted the performance of the grassland caterpillar *Gynaephora alpherakii* in the alpine Tibetan meadow. Elevated temperatures can lead to substantial declines in caterpillar body mass, cocoon volume, and reproductive output. Specifically, the observed reductions of 27.5% in fresh body mass, 61.1% in cocoon volume, and 26.9% in egg production per female moth underscore the potential for warming to adversely affect the population dynamics of this notorious pest species. These present results align with existing literature indicating that climate change can disrupt growth and reproductive strategies across various insect taxa (Desai & Singh, 2009; Sheridan & Bickford, 2011).

Interestingly, while warming increased feeding time, it did not alter the duration of cocooning. This finding suggests that caterpillars may compensate for the physiological stress induced by higher temperatures through increased feeding efforts (O'Connor, 2009). The increase in feeding duration could indicate a behavioral adaptation aimed at counteracting the metabolic stress resulting from warmer conditions (Reuman et al., 2014). However, despite these increased feeding times, the resultant weight loss and decreased reproductive output highlight the inadequacy of this adaptation to fully mitigate the energy deficits associated with elevated temperatures. This conclusion is consistent with previous studies that have shown similar patterns of increased feeding efforts without corresponding increases in body mass or reproductive success under stress conditions (Sahin, 2001).

The significant negative correlation between weight change and temperature further supports our hypothesis that warmer conditions have detrimental effects on caterpillar performance. The identification of excrement mass as a major influence on caterpillar weight raises critical questions regarding nutrient assimilation and energy allocation in a warming climate (Ohlberger, 2013). Increased metabolic rates may lead to higher energy demands, which, when coupled with potential declines in food quality or availability, could result in reduced growth and fitness (Kingsolver et al., 2004). Such findings are particularly relevant as they resonate with established theories regarding the temperature-size rule, where ectothermic organisms tend to exhibit reduced body sizes at elevated temperatures (Atkinson, 1994).

From an ecological perspective, the implications of our findings are twofold. First, the decrease in body size and reproductive capacity of*G. alpherakii* could lead to a decline in its population density, potentially altering herbivory dynamics in alpine grasslands. Such shifts could have cascading effects on plant communities, particularly if this species serves as a significant herbivore within the ecosystem. Changes in herbivory patterns may affect plant community structure and dynamics, leading to broader ecological consequences (Post et al., 2009; Cao et al., 2022). Second, the potential for warmer temperatures to shift outbreak patterns of this pest could have significant consequences for grassland management and agricultural practices in the region. Understanding these dynamics is critical for developing effective pest management strategies, especially in the face of ongoing climate change. Additionally, the findings of our study may have implications for the conservation of biodiversity in these high-elevation ecosystems, where species interactions are already finely balanced.

While our study offers valuable insights, it also underscores the need for further research to explore the long-term effects of warming on*G. alpherakii* and other herbivorous species in high elevation areas. Future studies should investigate the interactive effects of multiple stressors, such as changes in precipitation patterns and nutrient availability, to better understand the resilience of these herbivores in a warming world. This approach will provide a more comprehensive view of how climate change affects herbivores and their ecosystems, allowing for better-informed management decisions.

In conclusion, our findings provide critical evidence of the detrimental effects of climate warming on the performance of grassland caterpillars. This underscores the urgent need for proactive management approaches to mitigate the impacts of climate change on these vital species and their ecosystems. As climate change continues to pose challenges to biodiversity and ecosystem health, understanding the responses of key species like *G. alpherakii* will be essential for ensuring the sustainability of grassland environments.

AUTHOR CONTRIBUTIONS

Rui Cao: Conceptualization (Lead); Writing - original draft (Lead). Han Chen: Data curation (Equal); Formal analysis (Equal). Kezhi Zheng: Data curation (Equal). Dajie Nong: Data curation (Equal). Menglei Jiang: Data curation (Equal). Ziyu Zhang: Formal analysis (Equal). Xinwei Wu: Supervision (Equal); Writing - review & editing (Equal). Peng Xie: Supervision (Equal); Writing - review & editing (Equal).

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and in Data S1.

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Figure legends

Fig. 1 Variations in fresh body mass of caterpillar (A), cocooning rate (B), cocoon volume (C) and egg production per female month (D) among different treatments during the experiment, which are denoted by solid line with hollow circles (Non-warmed) and solid line with solid squares (Warmed), respectively.

Fig. 2 The number of feeding caterpillars in the treatments, which are denoted by dotted line with hollow circles or (Non-warmed) and solid line with solid squares (Warmed), respectively. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Fig.3 Relationships between temperature and caterpillar appetite (A), excrement mass (B), respiration rate (C) or change of caterpillar weight (D) in the chamber experiment. Sample size (N), regression coefficients (R^2) and statistical test (P values) are provided for the relationships that are statistically significant.

Fig. 4 Results of stepwise general linear regression models showing standardization regression coefficients between change of caterpillar weight and caterpillar appetite, excrement mass or respiration rate, respectively. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

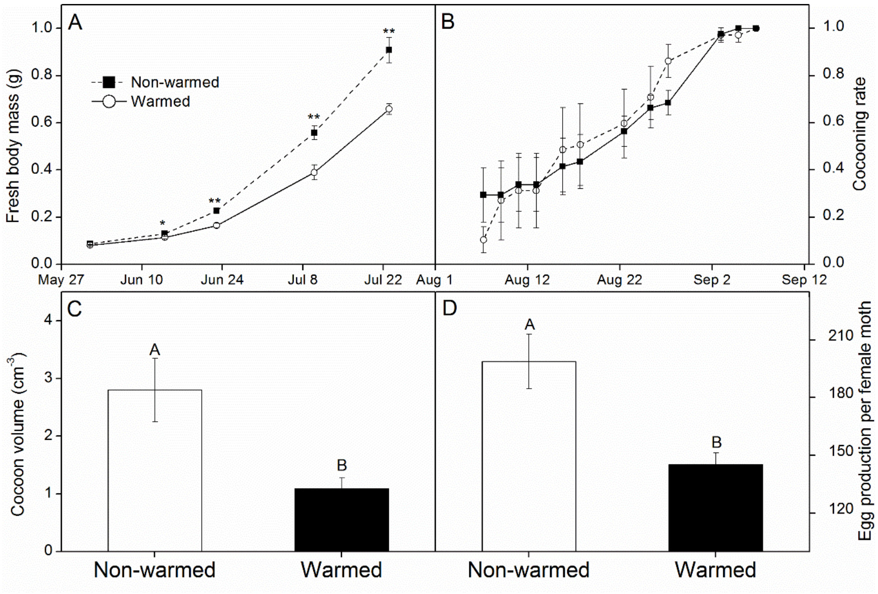

Fig. 1

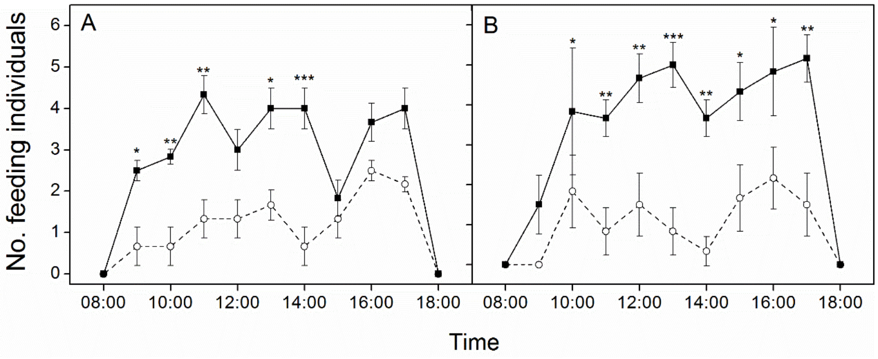

Fig. 2

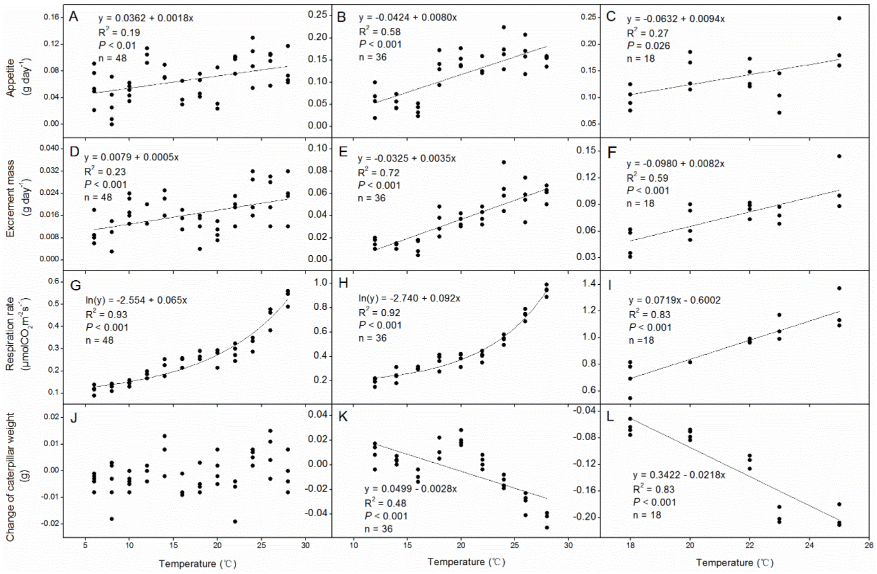

Fig. 3

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Fig. 4