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Research Article

Physiological Changes of *Eothenomys miletus* under Water Stress Conditions

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CY: Writing-original draft, methodology, software, formal analysis. WZ: Writing review, data curation, investigation, resources, funding acquisition.

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Eothenomys miletus, Water shortage stress, Body mass regulation, Energy metabolism, Digestive tract morphology, Basal metabolic rate

Abstract | This study investigated the physiological responses of body mass regulation to water stress in *Eothenomys miletus* from the Hengduan Mountains, assessing its impact on the species' physiological regulation. *E. miletus* individuals were randomly assigned to either a water-deprived group (experimental) or a group with normal water access (control). Both groups underwent a 7-day acclimation period at (25 ± 1) °C under a 12L:12D photoperiod. Following acclimation, body mass, basal metabolic rate (BMR), organ weights, and digestive tract weights/morphology were measured. After 7 days, the experimental group exhibited significantly lower body mass ($p < 0.05$), reduced whole-body BMR ($p < 0.05$), and significantly larger small intestinal length ($p < 0.05$) compared to those of the control group. These findings indicated that *E. miletus* adjusts energy homeostasis under water stress by modulating metabolic rate and digestive tract morphology. This reflects a physiological adaptation strategy, suggesting the species can enhance its resilience to water-limited environments, potentially relevant in the context of global warming.

Novelty Statement | This study is based on the background of global warming and changes in water resource distribution, and for the first time explores and analyzes the physiological changes of *Eothenomys miletus* under water stress.

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Introduction

How environmental factors such as water, food, temperature, and photoperiod affect the distribution and abundance of animals is one of the important contents of ecological research (Hanya and Chapman, 2013; Guan *et al*., 2018). In order to adapt to their living environment, small rodents in the wild not only regulate their body weight changes, but also use changes in their digestive tract morphology as one of their life history strategies (Wang *et al*., 2009), the phenotypic traits of their digestive organs provide significant insights into the animals' physiological and ecological characteristics, as well as their adaptations to environmental constraints (Pucek, 1965; Zhu *et al*., 2012). The gastrointestinal tract of animals can perform physiological functions, such as nutrient absorption, metabolic regulation, or host defense through complex mechanical, chemical, immune, and neuroendocrine mechanism. Glucose, amino acids, and fatty acids were actively transported or passively diffused

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into the bloodstream or lymphatic system through intestinal epithelial cells (Wright *et al*., 2011), water and electrolytes (such as sodium and potassium) were absorbed through the large intestine (Kunzelmann and Mall, 2002). When facing different environments, the digestive tract morphology of animals also exhibited corresponding physiological adaptation characteristics. Mammals in high-altitude areas may experience changes in digestive tract morphology, such as an increasing in intestinal length, to cope with the challenges of food digestion and energy absorption in low oxygen environments (Hammond and Diamond, 1997), some mammals experience an increase in digestive tract length and capacity during seasons of abundant food, while reducing it during seasons of food scarcity to cope with fluctuations in food supply (Secor, 2009).

Water is a fundamental environmental factor essential for maintaining physiological processes. So far, it had conducted relevant researches on the evaporation and water loss of lung skin in small mammals (Xi and Sun, 1973; Cai and Huang, 1982), the researches on the evaporation and water loss of lung skin in small mammals in China has covered various types of habitats such as desert and semi desert areas (Xiao and Sun, 1988), Qinghai Tibet Plateau areas (Wang *et al*., 1993; Wang and Wang, 2000), and Hengduan Mountains (Zhu *et al*., 2008, 2016; Li *et al*., 2009; Luo *et al*., 2011; Huang *et al*., 2012). When organisms are in a state of water scarcity, their physiological conditions undergo varying degrees of changes. For example, dehydration may reduce the sexual desire of rams in wild conditions, thereby affecting mating behavior (Khnissi *et al*., 2015), the findings demonstrate that water restriction exerts significant adverse effects on nutritional status, blood metabolite profiles, and growth performance in Nguni goats (Mpendulo *et al*., 2020). There was also experimental evidence that different degrees of water stress have different effects on the memory of mice, mild water stress has little effect on the memory of mice, while moderate and severe water stress can cause a decline in the memory of mice (Zhou *et al*., 2013). With global warming, the global water cycle and water resource layout have changed, precipitation has increased in some arid regions while decreasing in humid areas. Research showed that since the 1980s, the overall rainfall in the Sahara region has increased (Nicholson *et al*., 2018), since the 21st century, the northwest region of China has become increasingly humid (Zhang *et al*., 2022), from 1951 to 2012, the southwestern region of China (Yunnan, Guangxi, Guizhou) slightly dried up, with an average decrease of 114mm in precipitation every 10 years (Liu *et al*., 2014). In this context, in addition to the evaporation and dehydration of lung skin, the mechanism of water metabolism regulation in small wild mammals deserves further investigation.

The Hengduan Mountains, situated at the convergence of the Palearctic and Oriental biogeographical realms, form a critical transition zone between the eastern plains/ hills and the Qinghai-Tibet Plateau. Characterized by significant altitudinal gradients and complex topoclimatic diversity, this region harbors exceptionally complex and diverse ecosystems.It is acknowledged as one of the most crucial diversity hubs in China and the world (Zhang *et al*., 2016) and also ranks among the richest regions for mammalian species diversity (Chen *et al*., 2022). *Eothenomys miletus* (Rodentia: Cricetidae: Arvicolinae) is a Chinese endemic species primarily distributed within the Hengduan Mountains region. Its range spans Yunnan, Sichuan, Guizhou, and Hubei provinces, with key populations occurring in Kunming, Dali, Lijiang, Shangri-La, and the Ailao Mountains of Yunnan. This nocturnal rodent inhabits high-altitude montane forests, occupying shallow surface burrows that typically contain two or more distinct grass nests. Its diet consists mainly of succulent vegetation, grass roots, and seeds (Luo *et al*., 2000). Numerous studies have investigated the physiology and ecology of *E. miletus*, including thermoregulation and heat production characteristics (Wang *et al*., 2006; Zhu *et al*., 2014), evaporative water loss (Zhu *et al*., 2008), seasonal variations in thermogenic capacity (Zhu *et al*., 2010a), effects of cold acclimation on body mass, serum leptin levels, and energy metabolism (Zhu *et al*., 2010b), impacts of short photoperiod on energy intake, heat production, and body mass (Zhu *et al*., 2011), and the role of gut microbiota from different Hengduan Mountain altitudes in regulating body mass under high-fat diets (Jia *et al*., 2024). However, physiological regulation of body mass and energy metabolism, along with associated changes in digestive tract morphology, specifically in response to water stress, remains poorly understood in *E. miletus*. This study thus aims to explore the impacts of water stress on the physiological regulation of *E. miletus*, thereby clarifying its adaptive survival strategies under such conditions.

Materials and Methods

Experimental materials

Adult *E. miletus* were captured in shrubland habitats in Xiaguan Town, Dali City (25°34'54"N, 100°14'06"E; elevation 2061.500 m). Following capture, individuals were sanitized and treated for ectoparasites (fleas) before transport to the animal rooms of Yunnan Normal University. Animals were housed individually (260 × 160 × 150 mm^3) without nesting material. Environmental conditions were maintained at 25°C ± 1°C under a 12-hour light/12-hour dark photoperiod (12L:12D). All animals received *ad libitum* access to standard rodent diet (produced by Kunming Medical University) and water for two weeks. Only non-reproductive adult individuals were used in this study. After a 14-day acclimatization period, animals were randomly assigned to two groups: Experimental Group (Water Deprivation): Fed standard diet with *ad libitum* access to food but no access to water (n = 6; 3♀3♂); Control Group: Fed the same standard diet with *ad libitum* access to both food and water (n = 6; 1♀5♂). Body mass between two groups had no significant differences prior to the experiment ($P > 0.05$).

Determination of weight

Body mass was measured using an analytical balance (Model AB204-S, Mettler Toledo, Switzerland; ±0.01 g accuracy) consistently on experimental days 0, 3, and 7.

Determination of metabolic rate

Basal metabolic rate (BMR) was quantified using an 8-channel FMS portable respirometry system (Sable Systems International). Following a 2-4 h fasting period, animals were acclimated in 1.5-L metabolic chambers for ≥60 min at 25.0 ± 0.5°C (within the thermal neutral zone) within an environmental chamber (SPX-300, Shanghai Boxun). Compressed air flow was maintained at 200 mL/min via mass flow controllers. Oxygen consumption (VO_2) was recorded at 1-min intervals through four consecutive 15-min measurement cycles (total 60 min) using ExpeData software. Post-experiment, BMR was derived from the mean of 10 consecutive minimum VO_2 values during steady-state periods.

Determination of organ and digestive tract weight

The experimental animals were euthanized using CO_2 anesthesia, and the animals were quickly dissected to accurately separate organs (including liver, heart, and kidneys) and digestive tracts (including cecum, large intestine, small intestine, and stomach). The weight of each organ and the weight and length of each digestive tract were measured in a timely manner. All biological samples were frozen in liquid nitrogen and transferred to a -80 °C ultra-low temperature freezer for freezing and storage for future use.

Data analysis

Data analysis and visualization were performed using SPSS 26.0 (IBM Corp.) and OriginPro 2023 (OriginLab). Prior to statistical testing, normality was confirmed for all datasets using the Kolmogorov-Smirnov test ($p > 0.05$). There was no sex-based differences in physiological parameters ($p > 0.05$), data from both sexes were pooled for subsequent analyses. Continuous variables are presented as mean ± SE. Body weight and mass-specific BMR were compared using independent samples t-tests, while all other metrics were analyzed by ANCOVA with body weight as covariate. Statistical significance was defined at $\alpha = 0.05$.

Results

Analysis of differences in body weight and organ weight

Body weight analysis revealed no significant difference in *E. miletus* between experimental and control groups at day 3 (t=-0.732, P=0.481). However, experimental animals exhibited significantly reduced body weight by day 7 (t=-2.871, P=0.017). Post-experimental organ comparisons showed no significant differences in liver ($F_{1,9}$=4.371, P=0.066), kidney ($F_{1,9}$=3.099, P=0.112), or heart mass ($F_{1,9}$<0.001, P=0.995) (Figure 1).

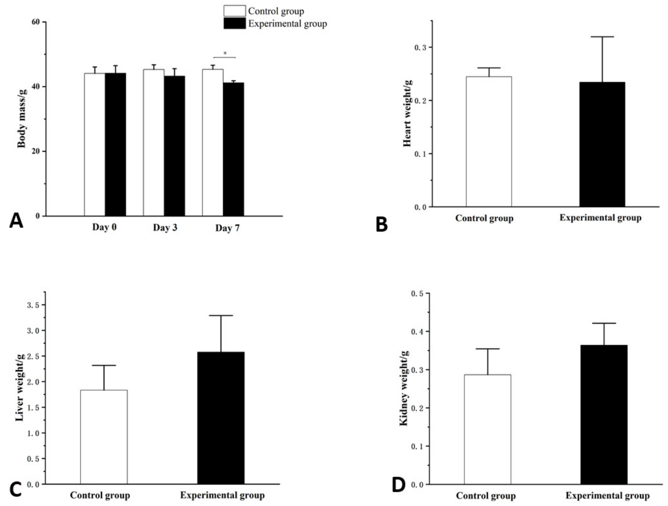

Figure 1: Body mass and organ weight of *Eothenomys miletus* under different water supply conditions. (A) Body mass, (B). Heart weight, (C). Liver weight, (D) Kidney weight; * P<0. 05; the same below.

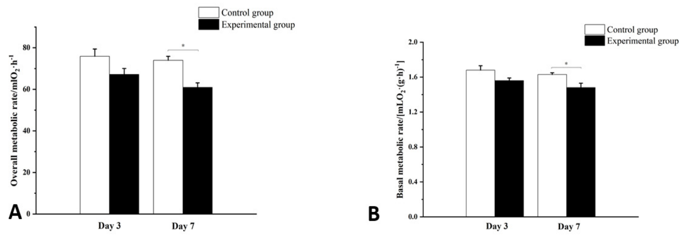

Figure 2: The overall BMR and unit BMR of *Eothenomys miletus* under different water supply conditions. (A) Overall metabolic rate, (B). Basal metabolic rate.

Metabolic rate analysis

No significant difference in overall BMR was observed between experimental and control *E. miletus* at day 3 ($F_{1,9}$=4.260, P=0.069). However, experimental animals exhibited significantly reduced overall metabolic rates by day 7 ($F_{1,9}$=5.980, P=0.037). Mass-specific BMR followed a similar trend: no significant difference at day 3 (t=-1.849, P=0.094) but significant reduction in the experimental group by day 7 (t=-2.749, P=0.021; Figure 2).

Analysis of differences in digestive tract weight

After 7 days of domestication, the stomach weight ($F_{1,9}$= 1.109, P = 0.320), large intestine weight ($F_{1,9}$ =

0.290, P = 0.603), small intestine weight ($F_{1,9}$= 1.963, P= 0.195), and cecum weight ($F_{1,9}$= 1.008, P= 0.342) showed no significant differences between two groups of *E. miletus* (Figure 3).

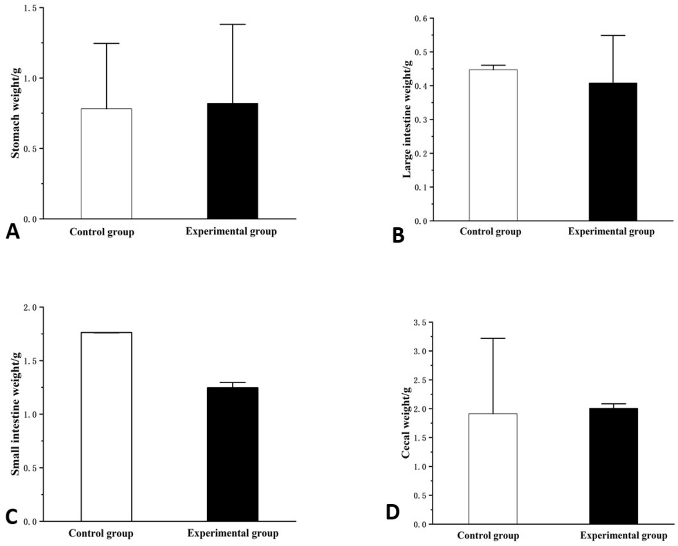

Figure 3: Digestive tract weight of *Eothenomys miletus* under different water supply conditions. (A) Stomach weight, (B) Large intestine weight, (C) Small intestine weight, (D) Cecal weight.

Analysis of differences in digestive tract length

Compared with the control group, a significant increase in the length of the small intestine ($F_{1,9}$= 5.630, P= 0.042; Figure 4) in the experimental group of *E. miletus*. But in the length of the large intestine ($F_{1,9}$= 2.929, P=0.121), cecum ($F_{1,9}$= 4.297, P= 0.068), and stomach ($F_{1,9}$=1.827, P= 0.209) showed no significant differences between the two groups.

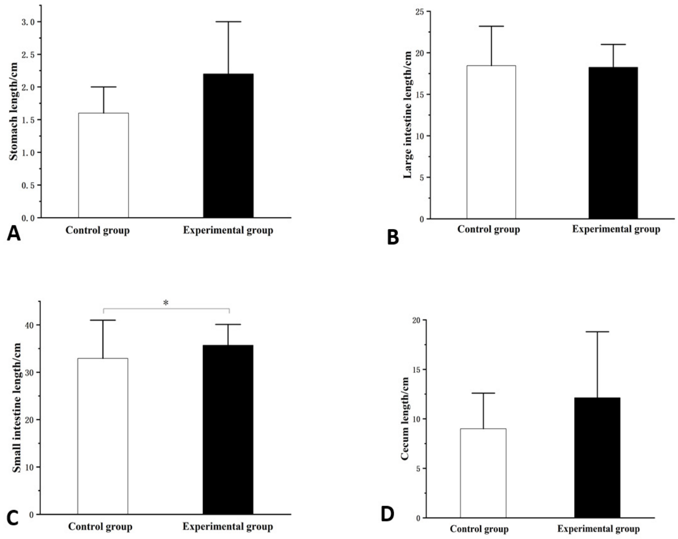

Figure 4: Digestive tract length of *Eothenomys miletus* under different water supply conditions. (A) Stomach length, (B) Large intestine length, (C) Small intestine length, (D) Cecal length.

Discussion

In free-living conditions, animals experience multifaceted ecological constraints including thermal regimes, photic stimuli, and hydric availability. Among these, water constitutes a fundamental environmental parameter, serving as a primary constituent of cellular, tissue, and organ systems. It mediates nutrient transport and metabolic waste elimination, thereby playing a critical physiological role in organismal homeostasis (Lang and Waldegger, 1997; Häussinger, 1996). Rodents' body weight regulation represents a critical physiological adaptation strategy to environmental fluctuations (Miner *et al*., 2005). Water, as an important ecological factor, participates in the weight regulation of organisms. Hydric stress disrupts physiological homeostasis in animals, resulting in significant body mass reduction, compromised reproductive performance, and diminished disease resistance (Barbour *et al*., 2005). Water intake is closely linked to food consumption (Silanikove 1992; Forbes 1997; More *et al*., 1983), adequate hydration is necessary for normal digestive function (Hadjigeorgiou *et al*., 2000), under conditions of dehydration and lack of water, animals may reduce or even stop eating, leading to weight loss. There are also studies showing that under water scarcity conditions, the breakdown of camel hump fat not only provides energy, but also produces about 1.1 mL of metabolic water per gram of fat metabolism, providing a key water source for long-term water scarcity (Schmidt-Nielsen *et al*., 1956). Small rodents in the Australian desert cope with their desert environment by satisfying their water needs through metabolic water (food oxidation) and fat decomposition water (MacMillen and Lee, 1967). This study found that after 7 days, the experimental group of *E. miletus* exhibited significantly lower body weight than the control group, which may be due to reducing food intake and replenishing water through fat oxidation and decomposition under water deficient conditions.

Water serves as an excellent solvent, reaction medium, reactant, and reaction product (J´equier and Constant, 2010), can also have an impact on the metabolism of small mammals. Compared to animals in a normal state, animals in a dehydrated state often have a lower respiratory rate. Some species take deep and slow breaths to obtain more oxygen during each breath, while also reducing the amount of air needed to pass through the lungs, thereby reducing water loss during respiration (Taylor, 1969). Studies have shown that the BMR of birds from desert habitats is lower than that of birds from the Mediterranean region (Tieleman and Williams, 2000). The experimental group of *E. miletus* exhibited significantly reduced overall metabolic rates compared to controls (p < 0.05), demonstrating adaptive downregulation of energy metabolism under hydric stress. This physiological adjustment conserves water by minimizing respiratory losses, thereby maintaining fluid homeostasis in response to water-scarce environments.

In addition, an important aspect of biodiversity is phenotype plasticity, which is an important mechanism for the formation of ecological species and a key raw material for natural selection and population differentiation (Pigliucci, 2001), and it is related to the behavioral, physiological, morphological, and life history characteristics related to ecology (Miner *et al*., 2005). The digestive system morphology plasticity serves as an adaptive strategy for many small mammals, including rodents, to cope with external environmental changes. As noted by Green and Millar (1987), animals utilize their stomachs to temporarily store food and initiate digestion and absorption. An increase in gastric capacity allows animals to ingest larger food quantities in a single meal while prolonging food retention in the digestive tract, thereby significantly enhancing digestive efficiency (Green and Millar, 1987). The cecum serves as the primary site for microbial cellulose fermentation, functioning as a sensitive indicator of dietary quality variations that drive digestive adaptations (Schieck and Millar, 1985). As the primary site of nutrient assimilation, the small intestine exhibits structural plasticity directly responsive to energetic demands (Wang *et al*., 1995). Elongation of this organ prolongs digesta retention time, thereby potentiating energy acquisition through enhanced digestive efficiency. The small intestine also has a mechanism for absorbing and secreting water and electrolytes (Field, 2003), although intestinal sodium absorption occurs along the entire gastrointestinal tract, the jejunum serves as the predominant site via active co-transport mechanisms coupled with glucose, bicarbonate ions, amino acids, and other nutrients, this sodium flux establishes the osmotic gradient driving passive water absorption, thereby substantiating the small intestine's pivotal role in mediating water absorption dynamics for osmotic balance (Parsons, 1967), it substantiate the pivotal role of the small intestine in mediating water absorption dynamics, a process essential for osmotic balance. The large intestine is the main part that absorbs nutrients after fermentation and decomposition in the cecum and colon, and is an important part for water and ion reabsorption. Its size is closely related to animal water metabolism (Bozinovic and Galland 2006; Liu *et al*., 2007). In this experiment, the length of the small intestine showed a significant increase compared to the control group, under water deficient conditions, *E. miletus* need to prolong the retention time of food in small intestine due to insufficient water intake from the environment, in order to increase their absorption of water from food, indicating that in the face of a water deficient environment, *E. miletus* regulate the morphology of their digestive tract to adapt to the environment.

In conclusion, when facing different environments, small wild mammals undergo a series of physiological and ecological adjustments. Our experiment found that under water deficient conditions, the body weight of *E. miletus* decreased, the length of the small intestine increased, and BMR decreased. This indicated that *E. miletus* maintain their water balance through a series of physiological responses. Reflects that under the background of global warming, changes in the global water cycle and water resource layout, and a slightly drier living environment, *E. miletus* can enhance their adaptation to the water deficient environment in the Hengduan Mountains by changing their body weight, BMR and total digestive tract.

Declarations

Acknowledgement

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IRB approval

All animal procedures were within the rules of Animals Care and Use Committee of School of Life Sciences, Yunnan Normal University. This study was approved by the committee (13-0901-011).

Ethical statement

The method of euthanasia on Eothenomys miletus was performed in accordance with the American Veterinary Medical Association (AVMA) guidelines for the euthanasia of animals (2020). Carbon dioxide have been used as euthanasia methods for *Eothenomys miletus* with low concentrations in AVMA guidelines for euthanasia.

Declaration of competing interest

The authors declare no competing financial interests or personal relationships that could influence this work. All co-authors have reviewed and approved the final manuscript for submission. We affirm that: (i) This work constitutes original research that has not been published previously, (ii) The manuscript is not under consideration for publication elsewhere in any form, (iii) All contributed substantially to the study and accept accountability for its integrity.

Data availability

Physiological data to this submission can be found online at https://figshare.com/articles/dataset/_xls/28801835?file=53688095

Declaration of generative AI and AI-assisted technologies in the writing process

No Generative AI and AI-assisted technologies wer used in the writing process.

Statement of conflict of interest

The authors have declared no conflict of interest.

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Links Researchers