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Metabolic compensation and behavioral thermoregulation of subtropical rhacophorid (*Polypedates megacephalus*) tadpoles in container habitats

Hua-Jun Wu [a], Chiung-Fen Yen [b], Yeong-Choy Kam [c,*]

[a] *Department of Biology, National Changhua University of Education, Changhua 50058, Taiwan, ROC*
[b] *Department of Ecology, Providence University, Shalu, Taichung, Taiwan, ROC*
[c] *Department of Life Science, Tunghai University, Taichung, 407, Taiwan, ROC*

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Abstract

We examined the relative importance of behavioral thermoregulation and metabolic compensation used by a subtropical rhacophorid (*Polypedates megacephalus*) tadpoles living in man-made container habitats to cope with thermal stress. We collected foam nests of *P. megacephalus* from man-made container habitats, and hatchlings were raised in 150 or 15 L of water (LWB and SWB containers, respectively). Water and air temperatures of containers were monitored using a datalogger. Tadpoles from both types of containers were acclimated at 22 and 32 °C for 10 d before measuring oxygen consumption ($\dot{V}_{O2}$) in a closed-system at 22, 27, and 32 °C. Thermal selection of tadpoles from two containers was determined using an aquatic thermal gradient. We observed daily stratification of temperature in the water column of LWB containers but not SWB containers. Tadpoles from LWB and SWB containers exhibited metabolic compensation so that tadpoles acclimated to 22 °C had significantly higher $\dot{V}_{O2}$ than those acclimated to 32 °C. This was probably related to the variation of environmental temperature experienced by the tadpoles. Tadpoles of LWB and SWB containers selected similar water temperatures with low coefficient of variation, suggesting they are good thermal selectors. Results of this study suggest that *P. megacephalus* tadpoles use both behavioral thermoregulation and metabolic compensation to cope with the environmental temperature fluctuation, and this is, in part, due to the heterogeneity in the thermal regimes of breeding habitats. Even though metabolic compensation of tadpoles incurs a cost, *P. megacephalus* tadpoles that experience no daily thermal gradient in the man-made water bodies and/or seasonal variations in temperature over tadpole period evolve metabolic compensation to maintain physiological homeostasis under different thermal regimes.

Keywords: Anura; Amphibian; Metabolic adaptation; Metabolic acclimation; Thermal physiology; Thermal selectors; Tadpole

1. Introduction

Aquatic ectotherms have evolved various behavioral, biochemical, and physiological strategies to minimize the effect of ambient temperature fluctuations on the rate at which their life functions proceed (Johnston and Bennett, 1996; Willmer et al., 2005). For example, animals living in cold environments remain active by acclimatizing biochemical processes to minimize the effects of ambient temperature fluctuations on physiological homeostasis (Rome et al., 1992; Thibault et al., 1997; St. Pierre et al., 1998; Roger et al., 2004; Berner and Bessay, 2006). In addition, aquatic ectotherms may use behavioral thermoregulation to cope with environmental temperature fluctuations when they often experience a wide range of thermal gradient in their habitats (Hutchison and Hill, 1977; Marshall and Grigg, 1980; Dupre and Petranka, 1985; Wollmuth et al., 1987; Wollmuth and Crawshaw, 1988; Ultsch et al., 1999). By selecting preferred water temperatures at different times of the day or in different developmental stages, animals can maximize their growth and development.

Most amphibians have complex life cycles in which larvae can often be found in varied aquatic habitats such as ponds, streams, road side ditches, ephemeral water puddles, tree holes, bamboo stumps, geothermal hotsprings and others (Kam et al., 1996; Ultsch et al., 1999; Chen et al., 2001). Results of earlier

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* Corresponding author. Tel.: +886 4 23550609; fax: +886 4 23590296.
E-mail address: biyckam@thu.edu.tw (Y.-C. Kam).

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studies have showed that metabolic compensation and behavioral thermoregulation are the physiological strategies commonly used by larvae to minimize the temperature effects on physiological homeostasis (Feder, 1985; Wollmuth et al., 1987; Ultsch et al., 1999; Chen et al., 2001; Wu and Kam, 2005). However, amphibian larvae have different larval periods and experience various thermal regimes daily or seasonally, it is unclear whether they use both physiological strategies to cope with thermal stress. Chen et al. (2001) and Wu and Kam (2005) reported that *Buergeria japonica* tadpoles living in geothermal hotsprings thermoregulate behaviorally but do not exhibit metabolic compensation. Marshall and Grigg (1980) contend that the metabolic compensation incurs a cost and confers little advantage to tadpoles with a short larval period that are usually contained within a single season. However, Feder (1982a, 1985) contends that the ability of a species to modify its metabolic rate through thermal acclimation is correlated with variation in environmental temperature experienced over a time scale of weeks to months. Thus, metabolic compensation is beneficial to species experiencing thermal fluctuation regardless of the length of larval period. Furthermore, anuran larvae living in thermally homogenous habitats such as phytotelmata (Kam et al., 2001) experience a narrow range of temperatures in their habitats. Ultsch et al. (1999) speculate that anuran species in these habitats may not behaviorally regulate body temperatures, like some tropical forest-dwelling lizards (Huey and Webster, 1975).

In this study, we examined the prevalence of behavioral thermoregulation and metabolic compensation of a subtropical rhacophorid (*Polypedates megacephalus*) tadpoles living in container habitats i.e., tanks, containers, and rain-collecting reservoirs in the Bagua Terrace in central Taiwan. Specifically, we measured the temperature selection and precision of thermoregulation by tadpoles raised in containers with large and small water volumes. In addition, we measured the oxygen consumption of tadpoles raised in these containers after across three temperatures being acclimated to 22 and 32 °C to assess their ability for metabolic compensation.

2. Materials and methods

2.1. Study animals and collection sites

Polypedates megacephalus is a mid-sized rhacophorid (snout–vent length 4–6 cm) commonly found in the lowland areas of Taiwan, inhabiting woods, orchards, and bamboo groves. Breeding season is from March to September, and foam nests are deposited overhanging ponds, wetlands, rice field, and man-made water containers. Upon hatching, tadpoles drop into the water and continue to grow until metamorphosis.

Bagua Terrace, an elongated tableland (width 4–10 km and length ca. 33 km) running in a south–north direction, is located in the coastal region of Changhua County. This low elevation terrace (100–400 m in elevation) is characterized by orchards and early- and mid-succession woods (Yen et al., 2004). It is the only remaining wooded area in the western coastal plain of Taiwan and surrounded by urban areas and rice fields. The main breeding habitats of *P. megacephalus* in the Bagua Terrace are the man-made water containers such as rain-collecting reservoirs, tanks, and containers of various sizes in orchards.

2.2. Experimental design

We collected four foam nests from the tanks of orchards on the Bagua Terrace in June–August of 2002 and transported them to the woods of Changhua University campus, 2 km away from the collection sites. Upon hatching, we randomly assigned half of the tadpoles of each nest to either a container with 150 L of water (100 cm in depth; LWB container) or a container of same size containing 15 L of water (15 cm in depth; SWB container). We set up two LWB containers, and each contained tadpoles of two egg clutches. We set up four SWB containers each containing tadpoles from a single clutch, to minimize the crowding. This type of container as commonly found in the orchards and was used to collect rain water for irrigation or agrochemical spraying. Throughout the study we added water to maintain water level. We continuously monitored air and water temperatures at different water depths of a LWB and SWB container using a datalogger. Tadpoles were fed *ad libitum* with broiled spinach and tadpole chow which was produced by a local food factory.

2.3. Resting metabolism of tadpoles acclimated at 22 °C and 32 °C

For each container type, a 2 × 3 factorial design with 10 tadpoles in each treatment combination was used, and the factors were acclimation temperature (22 or 32 °C) and test temperatures (22, 27, or 32 °C). We collected 60 tadpoles (Gosner stage 26–28) from each container type and acclimated 30 tadpoles at 22 ± 1 °C and 30 tadpoles at 32 ± 1 °C for 10 d. These acclimation temperatures approximated the minimum and maximum water temperatures experienced in the field. During acclimation, we continued to feed the tadpoles with broiled spinach *ad libitum* but fasted them for a day before the $\dot{V}_{O2}$ measurements. All tadpoles were maintained under a LD 12:12 photoperiod. We measured the $\dot{V}_{O2}$ of 10 tadpoles in each group at each test temperature (22, 27, and 32 °C). Every tadpole was weighed and staged after measurements.

We measured $\dot{V}_{O2}$ of tadpoles by a closed system described in Chen et al. (2001) and Kam et al. (2001). Determination of $\dot{V}_{O2}$ was made between 1200 and 1800 h. At first, each tadpole was placed in a beaker containing water within 3 °C of the tadpole's acclimation temperature, and the beaker was put in a temperature-controlled water bath (±1 °C). Over 20–30 min, we gradually raised or lowered the water temperature to the designated temperature. Then, each tadpole was put in a metabolic chamber containing 20 mL of water. At the same time, we set up an empty metabolic chamber as a blank. Each metabolic chamber was made up of a 20-mL syringe fitted with a three-way stopcock. Just before we closed the chamber, we slowly injected 1 mL of water into an O_2 analyzer (Cameron Blood Gas Meter) to measure initial oxygen pressure (P_{IO2}, mm Hg). The time interval between initial and final gas samples was

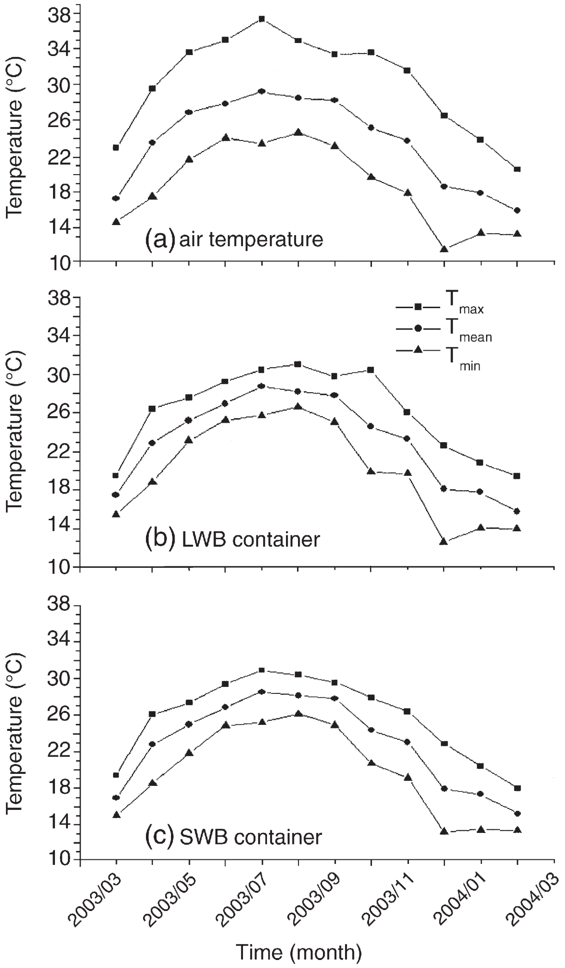

Fig. 1. Maximum, mean, and minimum of (a) air temperature, (b) water temperature of a container with 150 L of water (LWB container), and (c) water temperature of a container with 15 L of water (SWB container). Measurements were taken from March 2003 to March 2004.

dependent on tadpole body size so that oxygen tension in the chamber was not allowed to fall below 110 mm Hg. Most tadpoles settled quietly on the bottom of the chambers during measurements. At the end of incubation, we slowly injected 1 mL of water from the chamber into the O_2 analyzer to measure final oxygen pressure (P_{FO2}, mm Hg). The O_2 analyzer was calibrated using air-saturated water and N_2 gas. Oxygen consumption (μmol O_2/h tadpole) was calculated using the equation:

$$\dot{V}_{O2} = [(P_{IO2}-P_{EO2}) \cdot V \cdot \beta]/t$$

where V is the water volume (L), β is the oxygen capacitance of the water (μmol/mm Hg L) (Dejours, 1981), and t is the duration (h) of incubation.

2.4. Selection of temperature by tadpoles in the laboratory

We collected 60 tadpoles (Gosner stage 31–35) from each LWB and SWB container and conducted experiments between 0800 and 1700 h when the effect of diel cycles, if present, was minimal (Wu and Kam, 2005). We determined the thermal selection of tadpoles in an aquatic thermal gradient (Lucas and Reynolds, 1967; Wollmuth et al., 1987; Wu and Kam, 2005). This thermal gradient was achieved by setting up a water lane (length × width × depth: 150 × 20 × 10 cm; water level was 4 cm) with heat exchangers coupled by circulating pumps to either a hot or a cold source. The water lane was divided into 11 chambers by baffles, and each chamber was aerated. About 1.5 to 2 h after the gradient was turned on, a linear thermal gradient from 17 to 36 °C was established.

At the onset of the experiment, we placed a tadpole randomly in a chamber at either the cold end (ca. 17 °C), warm end (ca. 36 °C), or the middle chamber (ca. 28 °C). We then continuously monitored the position of the tadpole and water temperature once every 15 min for 3.5 h. Tadpoles might have moved around at the beginning (Hutchison and Dupre, 1992), but they settled down after 2–2.5 h. We therefore averaged the water temperature of the chambers with tadpoles during the last hour and designated that as the temperature selected by the tadpoles. Every tadpole was tested separately, and temperature selected by each individual was recorded. We terminated the experiment if the tadpoles were in thermal spasm or began to lose their righting response, and the data were excluded from subsequent analyses.

2.5. Statistical analyses

We analyzed the data using SAS software (SAS Institute Inc., 1996). We used t test to compare water temperature selected by tadpoles between treatments. We used an Analysis of Covariance (ANCOVA) to test for temperature effects on $\dot{V}_{O2}$, with body mass as a covariate. Body mass was used as a

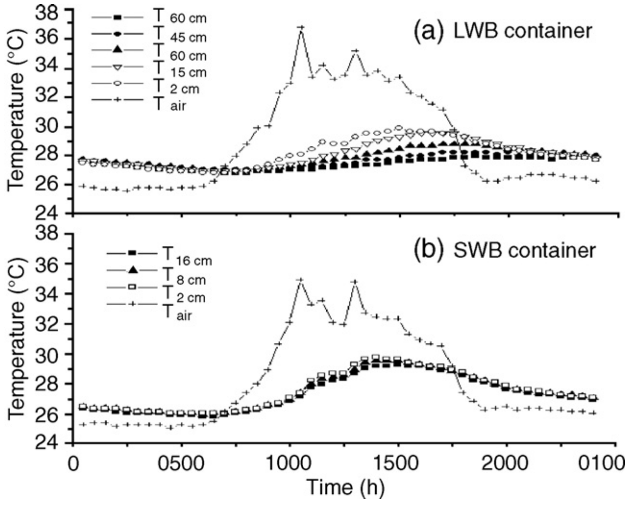

Fig. 2. Water temperature fluctuation in (a) a container with 150 L of water (LWB container) and (b) a container with 15 L of water (SWB container). Air temperature was measured simultaneously. Measurements were taken from 00:00 of July 7, 2002 to 00:00 of July 8, 2002 by a datalogger. In the LWB container, temperature probes were placed at 2, 15, 30, 45, and 60 cm below the water line. In the SWB container, the temperature probes were placed at 2, 8, and 16 cm below the water line.

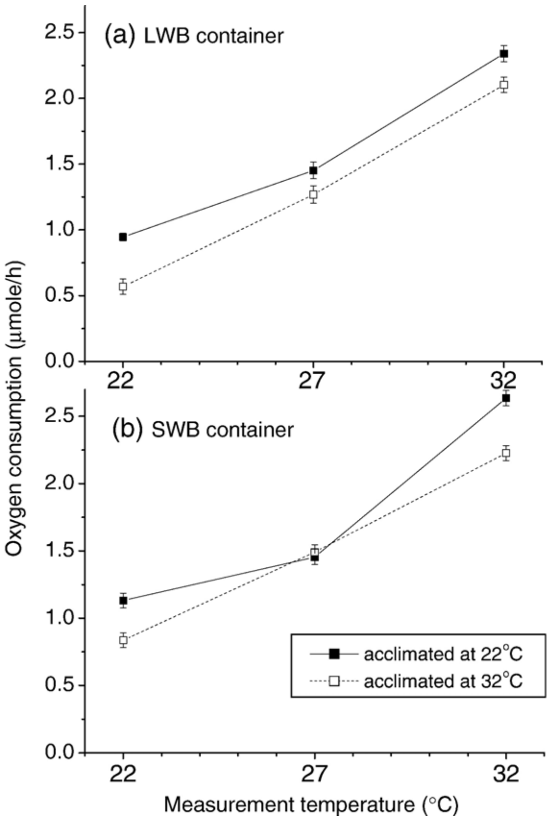

Fig. 3. Oxygen consumption (μmol/h) of *Polypedates megacephalus* tadpoles raised in (a) a container with 150 L of water (LWB container) and (b) a container with 15 L of water (SWB container) which acclimated at 22 and 32 °C and tested at 22, 27, and 32 °C. Values are means ± SD. Sample size for each data point is 10.

covariate instead of developmental stage because a stepwise regression on $\dot{V}_{O2}$ determined that variation in the measured variables was best explained by body mass. Earlier studies also found that body mass explained most of the variation in the $\dot{V}_{O2}$ of anuran larvae (Feder, 1982b). All values are expressed as means ± SD. A significant difference was declared when $P<0.05$.

3. Results

3.1. Seasonal and daily fluctuations of air and water temperatures in containers

Water temperatures of LWB and SWB containers fluctuated seasonally and daily (Figs. 1 and 2). We used the water temperature at the mid water level of containers to calculate mean water temperature. Monthly air and water temperature of LWB and SWB containers showed similar patterns of temperature fluctuation. Water temperature rose rapidly in spring (March to May), reached 31 °C in August, dropped rapidly in the fall, and reached 15 °C in February. The air and water temperatures showed a distinct daily pattern as illustrated by records on July 7, 2002 (Fig. 2). In the LWB container, the air temperature was lowest in the early morning, gradually increased to a peak 1000–1500 h, and dropped rapidly afterward. Water temperature on the surface rose around 0900, as a thermal gradient began to form in the water column. The thermal gradient in the water column lasted during the day, reaching differences as great as 2.3 °C around 1500. In contrast, water temperatures at different levels in SWB containers fluctuated synchronously; no thermal gradient existed.

3.2. Resting metabolism of tadpoles acclimated at 22 °C and 32 °C

Of tadpoles from the LWB container, those acclimated at 22 °C had a significantly higher $\dot{V}_{O2}$ than those acclimated at 32 °C (ANCOVA, $F_{1,53}=21.59$, $P<0.0001$). The $\dot{V}_{O2}$ increased with increased ambient temperatures (ANCOVA, $F_{2,53}=320.46$, $P<0.0001$; Fig. 3a). Results were similar for tadpoles from the SWB container in that those acclimated at 22 °C had a significantly higher $\dot{V}_{O2}$ than those acclimated at 32 °C (ANCOVA, $F_{1,53}=24.39$, $P<0.0001$). The $\dot{V}_{O2}$ of those tadpoles also increased with increased ambient temperature (ANCOVA, $F_{2,53}=324.40$, $P<0.0001$; Fig. 3b)

3.3. Thermal selection of tadpoles in the laboratory

Tadpoles from LWB and SWB containers selected 28.3 ± 3.4 °C (range: 21.2–34.3 °C, $n=30$) and 27.9 ± 2.8 °C (range: 22.1–31.7 °C, $n=30$), respectively, and the selected temperature did not differ statistically between container types ($t=0.48$,

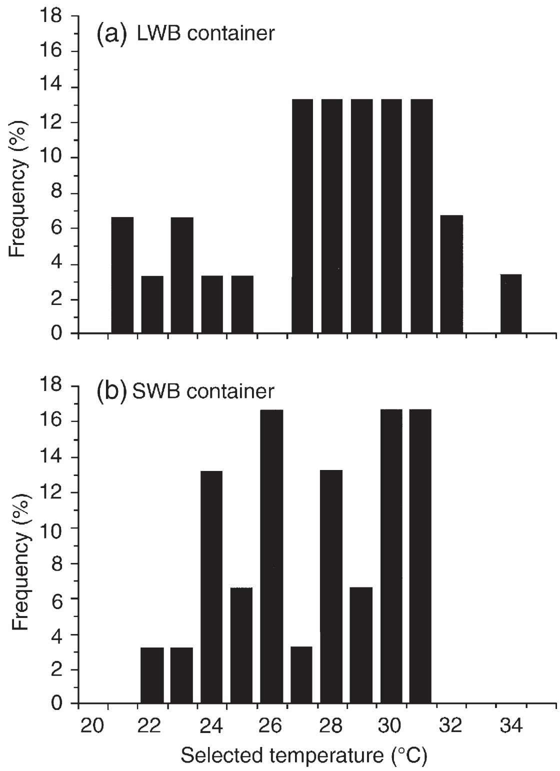

Fig. 4. Frequency distribution of water temperature selected by *Polypedates megacephalus* tadpoles raised in (a) a container with 150 L of water (LWB) and (b) a container with 15 L of water (SWB). Sample size from each container is 30.

$P = 0.632$). In addition, the coefficient of variation of temperatures selected by tadpoles of the LWB containers (12.14%; Fig. 4a) was larger than those from the SWB containers (9.93%; Fig. 4b).

4. Discussion

In Bagua Terrace, *P. megacephalus* breeds in man-made containers, tanks, and rain-collecting reservoirs. All these containers receive water from rainfall, and they probably function like arboreal pools (Laessle, 1961; Kam et al., 1996; Caldwell and Olivéra, 1999; Lehtinen et al., 2004) with water level synchronized the rainfall pattern. Arboreal pools are characterized by having a small volume of water, ranging from 15 mL to 250 mL (Kam et al., 1996; Caldwell and Olivéra, 1999). Since heat exchange between arboreal pools and the environment is very rapid, the water temperature of arboreal pool is not constant, fluctuating simultaneously with the air temperature and showing no stratification of water temperature within the pools (Kam et al., 2001). This probably also explains the lack of stratification of water temperature in the SWB containers. In contrast, the LWB containers contained 10 times more water than SWB containers and the rate of heat exchange is slower, which facilitates the development of a thermal gradient in the water column for most of the day.

Polypedates megacephalus tadpoles from SWB and LWB containers exhibited metabolic compensation which is probably related to the amount of variation experienced in environmental temperature (Feder, 1985; Rome et al., 1992; Ultsch et al., 1999). The larval period of *P. megacephalus* ranges from 35 to 60 days depending on environmental temperature. A tadpole could experience relatively large fluctuations in body temperature (up to 10 °C) during development. As a result, *P. megacephalus* tadpoles most likely evolved metabolic compensation to maintain activity levels under different thermal regimes. Another possible explanation for the existence of metabolic compensation is that *P. megacephalus* tadpoles are confined in containers with homogenous habitats that offer very little thermal heterogeneity for behavioral thermoregulation, and this is particularly true for tadpoles in the SWB containers. These two explanations for the existence of metabolic compensation in *P. megacephalus* tadpoles are not necessarily mutually exclusive. Our results support the hypothesis (Feder, 1985; Kam et al., 2001) that the beneficial effects of metabolic compensation outweigh the cost for anuran species living in thermally homogenous habitats and experiencing thermal fluctuation; even for those with a short larval period.

That tadpoles of LWB and SWB containers selected similar water temperatures was expected because the thermal regimes in both containers were similar. The low coefficient of variation (CV) of the selected temperatures indicated that tadpoles could precisely select temperature. Dupre and Petranka (1985) used the coefficient of variation of selected temperature as a measure of the ability of larvae of four amphibian species to choose temperature. They concluded that larvae are considered strong thermal selectors if the CV of the selected temperature is less than 16.3% whereas larvae are considered weak thermal selectors if the CV of the selected temperature is greater than 22.5%. Even though interspecific comparison on the precision of thermoregulation may not be adequate, the low CV of temperature selected by *P. megacephalus* tadpoles from both LWB and SWB containers, indicates they should be considered good thermal selectors. The tadpoles from LWB containers were good thermal selectors partly because of the thermal gradient present in the LWB container, even though the gradient was small. It is unclear, however, why the tadpoles of the SWB container were good thermal selectors even though the thermal environment was virtually homogenous, offering no opportunity for behavioral thermoregulation, as proposed by Ultsch et al. (1999). One possible explanation may relate to the breeding sites of *P. megacephalus*. The frog population in Bagua Terrace all breeds in man-made water bodies. Even though many of the breeding sites are small-sized containers, larger rainwater reservoirs are also used by frogs as oviposition sites. During the field survey, we noted that a large reservoir (diameter 1.8 m, depth 1.7 m) was used as an oviposition site. On June 22, 2003, we measured the water temperature profile for 24 h using a datalogger and found that the temperature was clearly stratified among water column all day. The surface water temperature fluctuated but temperatures 55 cm below the water surface remained unchanged throughout the day. The thermal gradient in the water column varied from 2.5 °C (at 0600 h) to 4.8 °C (at 1630 h). Thus, for *P. megacephalus* tadpoles of Bagua Terrace living in different containers that vary in thermal profiles, they may evolve both thermoregulatory mechanisms to cope with thermal stress (Noland and Ultsch, 1981; Wollmuth et al., 1987; Nie et al., 1999; Wu and Kam, 2005).

In conclusion, results of this study demonstrated that *P. megacephalus* tadpoles would use both behavioral thermoregulation and metabolic compensation to cope with the environmental temperature fluctuation, and this is, in part, due to the heterogeneity of breeding habitats in Bagua Terrace. However, metabolic compensation of tadpoles incurs a cost, thus, whether a species would routinely use both physiological mechanisms remains unclear. Chen et al. (2001) and Wu and Kam (2005) reported that *B. japonica* tadpoles exhibit behavioral thermoregulation but not thermal metabolic compensation. *Buergeria japonica* tadpoles live in geothermal hotspring with distinct thermal gradient daily and seasonally, and tadpoles could routinely select temperatures that are optimal for the growth and development; this may explain a lack of metabolic compensation because its cost may overweigh the benefit. It appears that behavioral thermoregulation is principally used by amphibian larvae which experience thermal gradient in their environments (Hutchison and Hill, 1977; Noland and Ultsch, 1981; Wollmuth et al., 1987; Wu and Kam, 2005). On the other hand, amphibian larvae that experience no thermal gradient in their environments would use metabolic compensation more often than originally thought (Feder, 1982a,b, 1985; Rome et al., 1992; Ultsch et al., 1999; Kam et al., 2001). This may be the case for *Chirixalus eiffingeri* tadpoles that live in small, thermally unstratified, arboreal pools where behavioral thermoregulation is not possible. As a result, metabolic compensation becomes an important mechanism to maintain physiological homeostasis of tadpoles (Kam et al., 2001).

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