ZOOLOGICAL SCIENCE **18**:591–596 (2001)

Thermal Physiology and Reproductive Phenology of *Buergeria japonica* (Rhacophoridae) Breeding in a Stream and a Geothermal Hotspring in Taiwan

Te-Chin Chen[1], Yeong-Choy Kam[2]* and Yao-Sung Lin[1]

[1]*Department of Zoology, National Taiwan University, Taipei, Taiwan, R.O.C.*
[2]*Department of Biology, National Changhua University of Education,*
Changhua 50058, Taiwan, R.O.C.

ABSTRACT—We compared the reproductive phenology and tadpole thermal physiology of two populations of *Buergeria japonica* in Taiwan. The population in Jentse breeds in a geothermal hot spring whose water is a warm, over 35°C year-round, whereas the population in Chukou breeds in a stream whose water temperature is closely correlated with fluctuations in air temperature and averages 23°C. The *B. japonica* population in Jentse breeds year-round, but the Chukou population breeds only from March to October. Tadpoles from Jentse that reared at 32°C attained larger sizes than tadpoles from Chukou that reared at 32°C, whereas tadpoles from both sites attained similar body size when reared at 22°C. Chukou tadpoles reared at 40°C died within 1–2 d, whereas Jentse tadpoles survived for 9 d at 40°C. All tadpoles tolerated heat well, but Jentse tadpoles had higher critical thermal maxima (CTMax) than Chukou tadpoles. Tadpoles from Jentse showed no metabolic compensation but those from Chukou showed an “inverse” metabolic compensation. Results suggest that *B. japonica* that breed in the geothermal hot spring has a prolonged breeding season, high growth rates and the reduction or absence of intra- and inter-specific competition. Evolution of a high level of heat tolerance and, possibly, behavioral temperature selection, enable tadpoles in the hotsprings to offset the thermal stress imposed by warm water.

INTRODUCTION

The rhacophorid tree frog *Buergeria japonica* is common and widely distributed in unforested lowlands and forests in Taiwan up to 1500 m (Zhao and Alder, 1993; Lue *et al.*, 1999). It usually breeds in slow-moving water in ditches and small streams, and there are at least five other anuran species also breed in the similar habitats (Yang, 1998). However, *B. japonica* may also breeds in an extremely unusual habitat, geothermal hotsprings which are carbonate-rich and slightly alkaline. To our knowledge, *B. japonica* is the only known anuran species to breed in such unusual habitats (Ultsch *et al.*, 1999). Although geothermal hotsprings can be found throughout Taiwan, they occur in comparatively low densities. As a result, only certain populations of *B. japonica* have access to hotsprings to breed. One of the most distinct differences between these two breeding sites of *B. japonica* is the thermal environment where tadpoles live. The temperature of a geothermal hotspring is unusually high and rather constant, whereas that of stream is usually low and readily affected by surroundings. Temperature has repeatedly been demonstrated as the most important environmental variable in affecting the physiology, ecology, and behavior of anuran larvae (Rome *et al.*, 1992; Ultsch *et al.*, 1999). Thus, we expect the populations of *B. japonica* tadpoles living in hotsprings should exhibit different physiological adaptation and life history traits than those living in streams and other habitats with cooler and more variable temperature regimes (Kadmon, 1993; Holomuzki, 1997).

In this study, we compared the reproductive phenology and thermal physiology of *B. japonica* populations that breed in geothermal hotsprings and streams and assessed the potential advantages and disadvantages of breeding in geothermal hotsprings.

MATERIALS AND METHODS

Study Sites

We studied and collected tadpoles from a roadside ditch that was not fed by geothermal hot springs at Chukou (elevation 450 m, approximately 23° 27’ 20” N, 120° 36’ 18’’ E). The ditch was about 1 m wide, and from 1 to 30 cm deep, depending on rainfall. There were distinct rainy (January to September) and dry (October to December) seasons. The ditch contained water year round, but the water volume was lower during the dry season. There was no geothermal hotspring nearby. The water temperature ranged from 17 to 28°C annually. The stream’s bed contained a thin layer of sandy substrates, with fallen

---

* Corresponding author: Tel. 886-4-7266816;
FAX.886-4-7211156.
Email: biyckam@cc.ncue.edu.tw

leaves and twigs forming shelters for the tadpoles. We found five other species of anurans, *Rana sauteri*, *Rana kuhlii*, *Rana swinhoana*, *Rana latouchii* and *Rhacophorus moltrechti*, in the ditch during our study period. In October 1997, we observed *R. sauteri* and *B. japonica* tadpoles coexisting. Damselfly larvae, crabs and shrimp were also observed in the water, especially during the summer.

We also studied and collected tadpoles from a ditch that fed by a geothermal hotsprings at Jentse (elevation 510 m, approximately 24° 33' 10 '' N, 121° 30' 01" E). Local people channeled hotspring water to their hotels using pipes. The water fed into large tanks, from which the overflow drained into the ditch via outlet pipes. The water temperature varied from 36 to 40°C annually. The water was slightly alkaline (pH 7–8.4). Because hotspring water was used for bathing only, the water was clean and clear. The ditch was about 35 m long and 0.7 m wide. The water depth varied between 2–10 cm. Water from the hotspring eventually drained into the Bai-Lin River. The ditch's bed contained a thin layer of sandy substrates. Algae (cyanophyta and bacillario-phyta) were common in the bed, particularly from May to November. During this study, we did not find any shrimp, crabs, insect larvae or other species of anurans in the ditch.

The average monthly air temperature at Chukou and Jentse was obtained from the Central Weather Bureau. The temperature of the water in the ditches at Chukou and Jentse was measured once a month, during the second week of the month, between 0800 and 1000. The water temperature was measured at no less than three locations where tadpoles were abundant.

Reproductive Phenology

Each month, from April 1997 to July 1998, we conducted day- and night- surveys of the ditches at Chukou and Jentse. To determine the reproductive phenology of the *B. japonica* populations, we recorded the presence of calling frogs, amplectant pairs, egg clutches and tadpoles. Because the water is rather shallow in both sites, we surveyed tadpoles visually.

Effect of Acclimation Temperature on Tadpole Growth

In August 1997, we collected 90 tadpoles (Gosner stage 26–28) each from the Chukou and Jentse. After capture, tadpoles were maintained at a temperature similar to the water temperature at the time of collection. After transported back to the lab, we changed the water temperature 2–4°C per day until the target temperatures (22, 32, and 40°C) were reached. Tadpoles were randomly assigned, in equal numbers (30 tadpoles), to three temperature regimes. Tadpoles were kept in a plastic container (about 10 l) with circulating water, and the container was put in a temperature-controlled water bath. During the study period, tadpoles were fed boiled spinach *ad libitum* and maintained under a LD 12:12 photoperiod. The tadpoles were counted and photographed with a ruler beneath the petri dish to determine their total length (TL, from snout to tail tip) after 12 d of experiment.

Effect of Acclimation Temperature on Critical Thermal Maxima (CTMax)

Tadpoles at Gosner stages 26-28 (Gosner, 1960) were collected from Chukou and Jentse in May and June 1998. They were acclimated, within ±1° C, to constant temperatures of 22, 32, and 40°C for 7 d. During acclimation, tadpoles were kept in a plastic container (about 10 l) with circulating water, and fed boiled spinach *ad libitum*. All tadpoles were maintained under a LD 12:12 photoperiod. CTMax was determined between 1000 and 1500 to reduce possible influences of daily rhythms on thermal tolerance (Dunlap, 1968; Cupp, 1980).

The procedure used to determine CTMax was similar to that used by Cupp (1980). Tadpoles were placed in 100 ml water, that was within 3°C of the acclimation temperature, in a 150 ml flask. For the CTMax measurement, the flask was placed in a heated water bath set to increase the water temperature about 0.31°C per min. Air was bubbled into the flask for aeration and to distribute the heat evenly in the water. CTMax, taken with a thermocouple, was the water temperature at which tadpoles lost their righting response (LRR). The LRR was defined as the inability of the animal to swim or respond to mechanical stimulation with a probe. Deep body temperatures were not taken. We assumed that, because of the small body size of the tadpoles and the low heating rate employed, there was no measurable lag between changes in water temperature and changes in body temperature (Hutchison, 1961; Dunlap, 1968).

Each specimen was tested in its own flask so that a CTMax was recorded for each individual. We removed tadpoles from the flask soon after CTMax was reached. Before they recovered, which usually took only 5–7 min, we weighed and staged them.

Effect of Acclimation Temperature on Oxygen Consumption ($\dot{V}_{O_2}$)

In March 1998, we collected about 100 tadpoles (Gosner stage 26-28) from Chukou and the same amount of tadpoles from Jentse about two week later. Within 12 h of collection, we measured the $\dot{V}_{O_2}$ of unacclimated tadpoles (30 tadpoles each) from both sites. The remaining tadpoles (70 tadpoles from each site) were divided equally and acclimated in different temperature regimes: Chukou tadpoles were reared in 22° and 30°C water and Jentse tadpoles were reared in 30° and 38°C water. These acclimation temperatures represent the high and low water temperatures experienced in the field. Even though many tadpoles were found in sections of ditches with temperatures ranged from 35–40°C, there were some tadpoles were also found in ditches with lower temperature around 30°C (Kam, Per. Obs.). We reared Jentse tadpoles at 38°C instead of 40°C, because previous experiments had shown that tadpoles survived better at 38°C.

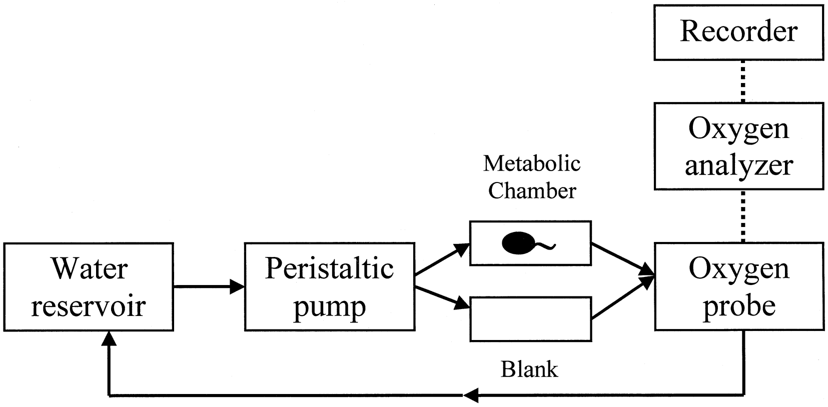

Fig. 1. Schematic drawing of the open system used to measure tadpole oxygen consumption. Water flowed in the direction indicated by arrows.

Tadpoles were acclimated to within ±1°C of the constant, designated temperatures for 10 d before $\dot{V}_{O_2}$ was measured. Tadpoles were kept in a plastic container with circulating water, and the container was put in a temperature-controlled water bath (±1°C). Tadpoles were fed boiled spinach *ad libitum* during acclimation. All tadpoles were maintained under a LD 12:12 photoperiod. Tadpoles were starved for 2 d before the $\dot{V}_{O_2}$ measurements to minimize the confounding effects of feeding on metabolism. We measured 10 tadpoles in each treatment. Each tadpole was weighed and staged after the measurement.

We used an open system to measure the $\dot{V}_{O_2}$ of tadpoles (Fig. 1). We measured the $\dot{V}_{O_2}$ of tadpoles at 24, 30, and 36°C, instead of the acclimated temperatures of 22, 30, and 38°C, to minimize thermal shock to tadpoles at extreme temperatures. Water in the reservoir was aerated during the experiment. Depending on tadpole size, we varied the speed of the peristaltic pump (Cole-Palmer, Masterflex L/S) so that the water tension in the chamber did not fall below 110 mmHg. Water flow was between 48–155 ml per hr. Each specimen was placed in its own chamber so that a $\dot{V}_{O_2}$ was recorded for each individual.

Each tadpole tested was first placed in a metabolic chamber (ca. 5 ml). We set up six metabolic chambers at a time using a peristaltic pump with an empty metabolic chamber as a blank. Over 30–45 min, we gradually raised or lowered the water temperature to the designated temperature. The tadpoles were then allowed to settle and equilibrate at each temperature for 30 min. Most tadpoles settled quietly on the bottom of chamber during the measurements. We waited another 30 min after equilibration before we slowly took a water samples (ca. 1 ml) from the inlet and outlet tubing to measure initial (P_{IO2}) and final (P_{EO2}) oxygen pressure (mmHg) using a Cameron Blood Gas Meter. The Blood Gas Meter was calibrated using air-saturated water and N_2 gas. Oxygen consumption (u mol O2/ h) was calculated using the equation: $\dot{V}_{O_2} = (P_{IO2} - P_{EO2}) \cdot F \cdot \beta$, where F is the water flow (ml/h) and β is oxygen capacitance of water (u mol / mmHg·L) (Dejours, 1981). Determinations of $\dot{V}_{O_2}$ were made between 0900-1800. All $\dot{V}_{O_2}$ measurements for an acclimated temperature were done within 2 d.

Statistical Analyses

We analyzed the data using a SAS program (SAS Institute, 1996). We used analysis of covariance (ANCOVA) to analyze $\dot{V}_{O_2}$ and CTMax. We used initial body mass as a covariate for $\dot{V}_{O_2}$ and CTMax analyses. Body mass was used as a covariate instead of developmental stages, because stepwise regressions on $\dot{V}_{O_2}$ and CTMax found that variation of the measured variables was best explained by the body mass. Feder (1982a) also found that body mass explained most of the variation in the V_{O_2} of anuran larvae. We used analysis of variance (ANOVA) to analyze tadpole growth because the initial TL was statistically similar. If measurements were significantly different between treatments, we used Tukey's studentized range test (HSD) for multimple comparisons. All values are expressed as means ±SD unless otherwise noted. A significant difference was declared when $P \leq 0.05$.

RESULTS

Air and Water Temperatures in Chukou and Jentse

The mean annual air temperatures in Chukou (25.03± 3.72°C) and Jentse (25.84±6.4°C) were not significantly different (ANOVA, $F_{1,22} = 0.34$, $P = 0.57$), but the mean water temperature at Jentse (37.38±2.03°C, range 35.8–40) was significantly higher than at Chukou (23.37±3.02°C, range 17–27 C; ANOVA, $F_{1,22} = 153$, $P = 0.0001$). The water temperature in Jentse was not correlated with air temperature (Spearman rank test, $r = 0.010$, $P = 0.974$, $N = 12$), whereas the water temperature at Chukou was strongly correlated with air temperature ($r = 0.83$, $P = 0.0008$, $N = 11$; Fig. 2). Field observation also found that solar radiation could also raise

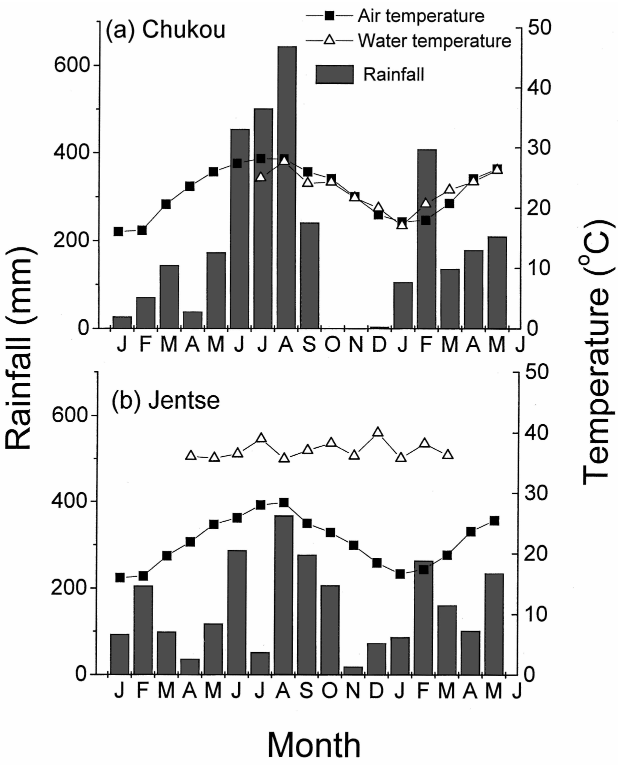

Fig. 2. Air and water temperature, and rainfall at (a) Chukou and (b) Jentse from January 1997 to May 1998.

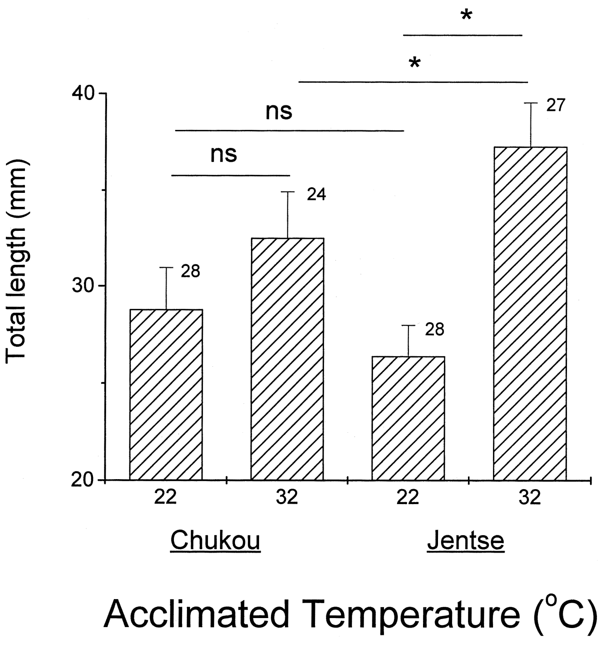

Fig. 3. The total length (mm) of tadpoles from Chukou and Jentse each acclimated at 22 and 32°C. The sample size is next to each bar. * and ns represent significant and insignificant difference at a 0.05 level, respectively. Values are means ± SE.

water temperature in both sites.

Reproductive Phenology

At Chukou, male *B. japonica* aggregated in the ditch and called from early March until October. Amplectant pairs were observed from March to September and tadpoles were seen from April to October, with the greatest numbers present during the summer. The volume of water in the ditch was lowest from October to January, due to reduced precipitation, but the water did not dry up during the study period. In contrast, calling, amplexus, and tadpoles of different sizes were observed year-round in the Jentse ditch.

Effect of Acclimation Temperature on Tadpole Growth

Tadpoles from Chukou died within 1–2 d at 40°C. Although tadpoles from Jentse initially survived and grew to some extent at 40°C (23.51±3.02 mm, $N = 30$), they all died within 9 days. Data of tadpoles reared at 40°C were excluded from statistical analysis. The initial TL of tadpoles from Chukou that reared at 22°C and 32°C were 16.34±1.54 mm and 16.81±2.34 mm, respectively, whereas those from Jentse that reared at 22°C and 32°C were 16.58±2.72 mm and 16.46±1.90 mm, respectively. The initial TL of tadpoles are statistically similar at the onset of the experiments (ANOVA, $F_{3,113} = 0.24$, $P = 0.865$). After 12 d of experiment, the TL of tadpoles are statistically different among acclimated temperatures (ANOVA, $F_{3,104} = 30.91$, $P = 0.0001$; Fig. 3). Within populations, tadpoles from Jentse grew significantly faster and attained longer TL when raised at 32°C than 22°C ($P < 0.05$), but TL of tadpoles from Chukou was similar ($P > 0.05$; Fig. 3). Between populations, Jentse tadpoles at 32°C were significantly larger than Chukou tadpoles at 32°C ($P < 0.05$), whereas there were no differences was found in TL between tadpoles of two populations which reared at 22 ° C ($P > 0.05$; Fig. 3)

Effect of Acclimation Temperature on CTMax

Within populations, an increase in acclimation temperature increased the CTMax of tadpoles from Chukou (ANCOVA, $F_{1,21} = 26.8$, $P = 0.0001$), but had no effect on the CTMax of tadpoles from Jentse (Fig. 4). Chukou tadpoles died within 2 d of being placed in 40°C water, whereas Jentse tadpoles survived up to 9 days at 40°C. Between populations, the CTMax of Jentse tadpoles acclimated at 22°C was significantly higher than that of Chukou tadpoles acclimated at 22°C (ANCOVA, $F_{1,21} = 74.38$, $P = 0.0001$), whereas the CTMax of tadpoles acclimated at 32°C was statistically similar (ANCOVA, $F_{1,21} = 0.09$, $P = 0.771$).

Effect of Acclimation Temperature on $\dot{V}_{O_2}$

The $\dot{V}_{O_2}$ of acclimated and unacclimated tadpoles increased with the increases in ambient temperature (Figs 5 and 6). The $\dot{V}_{O_2}$ of unacclimated Chukou and Jentse tadpoles were not significantly different (ANCOVA, $F_{1,54} = 1.01$, $P = 0.32$; Fig. 5). Chukou tadpoles acclimated at 30°C had significantly higher $\dot{V}_{O_2}$ than those acclimated at 22°C (ANCOVA, $F_{1,55} = 5.39$, $P = 0.024$; Fig. 6a). In contrast, the $\dot{V}_{O_2}$ of Jentse tadpoles acclimated at 38°C was similar to the $\dot{V}_{O_2}$ of those acclimated at 30 ° C (ANCOVA, $F_{1,55} = 0.27$, $P = 0.604$; Fig. 6b).

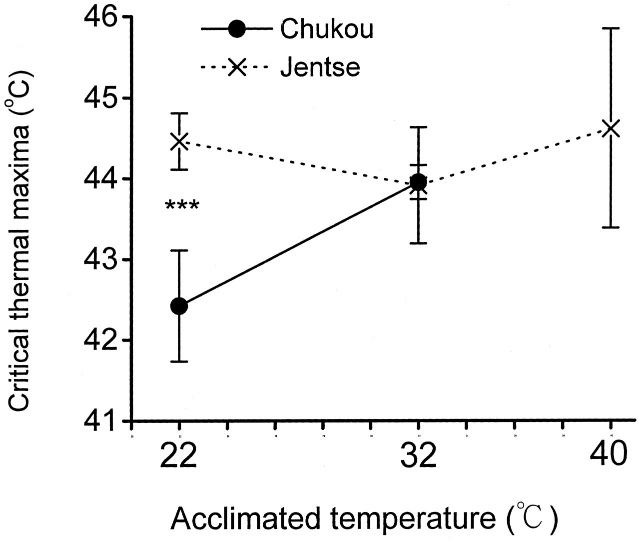

Fig. 4. Critical thermal maxima of tadpoles from Chukou and Jentse acclimated at 22, 32, and 40°C. Critcal thermal maxima was adjusted using body mass as a covariate. *** represents a significant difference at a 0.0001 level. The sample size for each data point was 12 tadpoles. Values are means ± SE.

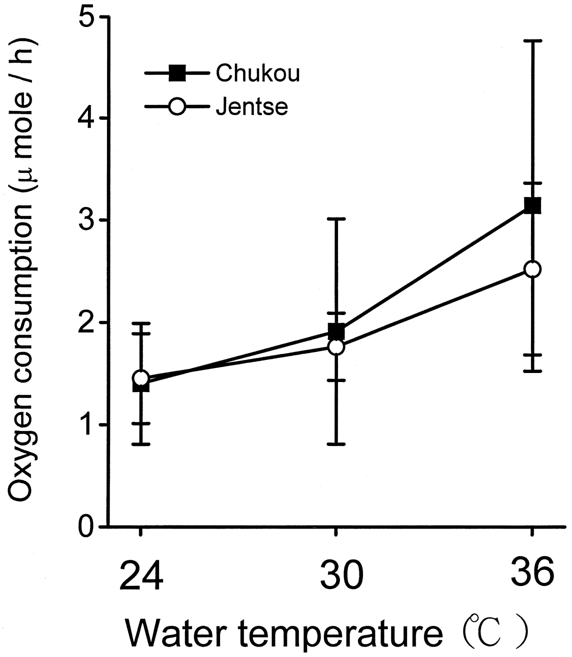

Fig. 5. Oxygen consumption, at different temperatures, of unacclimated tadpoles from Chukou and Jentse. Oxygen consumption were adjusted using body mass as a covariate. The sample size for each data point was 10 tadpoles. Values are means ± SE.

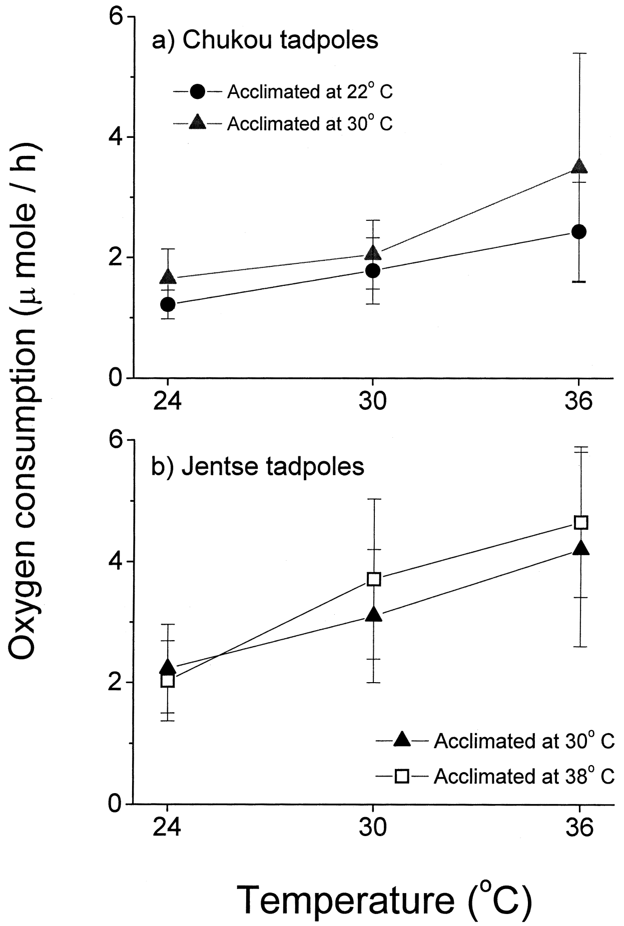

Fig. 6. Oxygen consumption of tadpoles from (a) Chukou and (b) Jentse acclimated to different temperatures. Oxygen consumption was adjusted using body mass as a covariate. The acclimation temperatures for were 22 and 30°C for Chukuo tadpoles, and 30 and 38°C for Jentse tadpoles. The sample size for each data point was 10 tadpoles. Values are means ± SE.

DISCUSSION

The population of *B. japonica* in Jentse breeds year-round whereas that those in Chukou breeds probably from March to October. Chukou experienced a dry season (October to December) when water volume in the ditches was reduced, nevertheless, the ditches contained water year round. In addition, the water temperature in Chukou varied as much as 12°C between summer and winter and the winter water temperature dropped to 16–17°C. In contrast, the ditches in Jentse contained year-round warm water that fed by geothermal springs. It is possible that the warm and stable temperature of the geothermal hotspring water allows *B. japonica* to prolong the breeding season. On the other hand, the low temperature is likely to inhibit *B. japonica* from breeding in Chukou during the winter. This may also be true for all other species of rhacophorid frogs except *Rhacophorus taipeianus* in subtropical Taiwan that do not breed during the winter (Yang, 1998; Lue *et al.*, 1999). Rainfall has been considered as an important extrinsic factor to initiate the breeding activity of anurans in the tropical and subtropical regions (Duellman and Trueb, 1986). However, the *B. japonica* population in Chukou did not breed until March, even though it received rain since January and February. This finding suggests that rainfall is not the primary factor in controlling the breeding cycle of *B. japonica*.

Based on growth data from the laboratory, tadpoles living in the warm, geothermal hotspring in Jentse should grow faster and have a shorter tadpole period than tadpoles in the cooler water in the Chukuo ditch. Rapid growth enables tadpoles to escape crowded conditions, and presumably reduces intraspecific competition (Semlitsch and Caldwell, 1982; Holomuzki, 1997; Wilbur, 1997; Alford, 1999). In addition, because no other anurans breed in the geothermal hotspring, the *B. japonica* population breeding there experiences no interspecific competition. Predation pressure is probably low because we did not find any predacious invertebrates, such as insect larvae, crabs, and shrimp, in the geothermal hotspring during the study period (Kam, Per. Obs.).

The disadvantage of breeding in the geothermal hotspring is that the frogs, and particularly the tadpoles, must cope with the high temperatures. *B. japonica* tadpoles that live in hotsprings are trapped in a warm aquatic environment and may be exposed to lethal, high temperatures, thus, tadpoles with a high thermal tolerance would be at a selective advantage in such an environment (Ultsch *et al.*, 1999). The CTMax measurements indicate that *B. japonica* tadpoles tolerate heat well, and the *B. japonica* tadpoles in Jentse tolerate heat better than those in Chukou. It is worthwhile mentioning that the CTMax of *B. japonica* tadpoles from the hotspring stayed high at around 43–44 C (Fig. 4), suggesting that the heat tolerance of tadpoles is probably set at the physiological upper limit at all times. Earlier studies have demonstrated that the thermal tolerance of amphibian larvae is correlated with their geographical distribution and breeding habits (Herreid II and Kinney, 1967; Brown, 1969; Miller and Packard, 1977; Hoppe, 1978; Cupp, 1980; Ultsch *et al.*, 1999). Larvae that live in desert habitats, temporary ponds or shallow pools, in which high temperatures are common, usually have a high thermal tolerance. In this study, between population differences in heat tolerance could result from genetic differences or differing early thermal histories (Brown, 1969; Miller and Packard, 1977; Cupp, 1980). Because experimental tadpoles were collected from the field, it is unclear whether differences in between population heat tolerance have a genetic basis or result from different early thermal histories. Tadpoles from Chukou and Jentse were exposed to different thermal regimes during a critical developmental period, which may have caused significant, irreversible changes in their respective thermal tolerances (Gibson, 1954; Fry, 1958; Cupp, 1980).

Ectothermic animals reared at cool temperatures may have higher metabolic rates at a given temperature than animals with a warmer thermal history (Bullock, 1955; Fry, 1958; Feder, 1982b; Rome *et al.*, 1992; Ultsch *et al.*, 1999). Metabolic compensation is one of the physiological strategies commonly used by fishes and invertebrates to minimize the effect of varying ambient temperature on physiological homeostasis. However, in this study, the metabolic rate of tadpoles with a cool thermal history (Chukou population) was similar to that of tadpoles with a warm thermal history (Jentse population) (Fig. 5). In addition, acclimation of tadpoles to a higher and a lower temperature did not induce thermal compensation in Jentse tadpoles (Fig. 6b), and even a “inverse” thermal compensation was detected in Chukou tadpoles (Fig. 6a). Other studies on anuran tadpoles also found that tadpoles do not undergo thermal metabolic compensation (Parker, 1967; Marshall and Grigg, 1980). Marshall and Grigg (1980) contend that metabolic acclimatory abilities confer little advantage to tadpoles whose larval life span is short and usually contained within a single season. As a result, behavioral changes may be the principal means for minimizing the effects of environmental temperature fluctuations on metabolic processes (Hutchison and Hill, 1977; Dupre and Petranka, 1985; Wollmuth *et al*., 1987; Wollmuth *et al*., 1988). In the field, hotspring water seeping from the rocks can be as hot as 60–70°C (Kam, Per Obs). As the water flows into ditches or depressions, it cools gradually. As a result, the temperature of the water in the ditch should vary depending on distance from the source, ranging from 42°C to 30°C (Wu C.-S., unpublished data). Although we did not address temperature selection by tadpoles in this study, we contend that tadpoles would actively select water at the temperatures they prefer at different developmental stages in order to maximize their growth and development (Dupre and Petranka, 1985; Hutchison and Hill, 1977; Wollmuth and Crawshaw, 1988).

ACKNOWLEDGEMENTS

This study was supported, in part, by a National Science Council Grant (NSC 88-2621-B-018-002-A10) to YCK. We would like to thank C.-F. Yen, C.-S. Wu, P.-I. Lin, P.-F. Yeh, I.-R. Tsai, W. H. Chou, I.-R. Yang, T.-E. Lin, S.-P. Wu, P.-J. Shieh, S.-W. Fann and many others for field and laboratory assistance. Comments and suggestions on an earlier draft of this manuscript by A. F. Warneke are appreciated.

REFERENCES

Alford RA (1999) Ecology: resource use, competition, and predation. In “Tadpoles: The Biology of Anuran Larvae” ed by RW McDiarmid, R Altig, The University of Chicago Press, Chicago, pp 240–278

Brown HA (1969) The heat resistance of some anuran tadpoles (Hylidae and Pelobatidae). Copeia 1969: 138–147

Bullock TH (1955) Compensation for temperature in the metabolism and activity of poikilotherms. Biol Rev 30: 311–342

Cupp PV (1980) Thermal tolerance of five salientian amphibians during development and metamorphosis. Herpetologica 36: 234–244

Dejours P (1981) Principles of comparative respiratory physiology. 2nd ed, Elsevier North-Holland, Amsterdam

Duellman WE, Trueb L (1986) Biology of amphibians. McGraw-Hill Book Company, New York

Dunlap DG (1968). Critical thermal maximum as a function of temperature of acclimation in two species of hylid frogs. Physiological Zoology 41: 432–439

Dupre PK, Petranka JW (1985) Ontogeny of temperature selection in larval amphibians. Copeia 1985: 462–467

Feder ME (1982a) Effects of developmental stage and body size on oxygen consumption of anuran larvae: a reappraisal. J Exp Zool 220: 33–42

Feder ME (1982b) Environmental variability and thermal acclimation of metabolism in tropical anurans. J Thermal Biol 7: 23–28

Fry FEJ (1958) Temperature compensation. Ann Rev Physiol 20: 207–224

Gibson MB (1954) Upper lethal temperature relation of the guppy, *Lebistes reticulatus*. Can J Zool 32: 393–407

Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 18: 183–190

Herreid II CF, Kinney S (1967) Temperature and development of the wood frog, *Rana sylvatica*, in Alaska. Ecology 48: 579–590

Holomuzki JR (1997) Habitat-specific life-histories and foraging by stream-dwelling American toads. Herpetologica 53: 445–453

Hoppe DM (1978) Thermal tolerance in tadpoles of the chorus frog *Pseudacris triseriata*. Herpetologica 34: 318–321

Hutchison VH (1961) Critical thermal maxima of salamanders. Physiol Zool 43: 92–125

Hutchison VH, Hill LG (1977) Thermal selection of bullfrog tadpoles (*Rana catesbeiana*) at different stages of development and acclimation temperatures. J Thermal Biol 3: 57–60

Kadmon R (1993) Population dynamic consequences of habitat heterogeneity: An experimental study. Ecology 74: 816–825

Lue CY, Tu MC, Shian GS (1999) A field guide to the amphibians and reptiles of Taiwan. Great Nature Magazine Publisher, Taipei, Taiwan

Marshall E, Grigg GC (1980) Lack of metabolic acclimation to different thermal histories by tadpoles of *Limnodynastes peroni* (Anura: Leptodactylidae). Physiol Zool 53: 1–7

Miller K, Packard GC (1977) Critical thermal maximum: ecotypic variation between montane and piedmont chorus frogs (*Pseudacris triseriata*, Hylidae). Experientia 30: 355–356

Parker GE (1967) The influence of temperature and thyroxine on oxygen consumption in *Rana pipiens* tadpoles. Copeia 1967: 610–617

Rome LC, Stevens ED, John-Alder HB (1992) The influence of temperature and thermal acclimation on physiological function. In “Environmental Physiology of the Amphibians” Ed by ME Feder, WW Burggren, University of Chicago Press, Chicago, pp 183–205

SAS Institute, Inc (1996) SAS/STAT User’s guide. SAS Inst. Inc., Gary

Semlitsch RD, Caldwell JP (1982) Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. Ecology 63: 905–911

Ultsch GR, Bradford DF, Freda J. (1999) Physiology: coping with the environment. In “Tadpoles: The Biology of Anuran Larvae” ed by RW McDiarmid, R Altig, The University of Chicago Press, Chicago, 189–214

Wilbur HM (1997) Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78: 2279–2302

Wollmuth LP, Crawshaw LI (1988) The effect of development and season on temperature selection in bullfrog tadpoles. Physiol Zool 61: 461–469

Wollmuth LP, Crawshaw LI, Forbes RB, Grahn DA (1987) Temperature selection during development in a montane anuran species, Rana cascadae. Physiol Zool 60: 472–480

Yang ER (1998) A field guide to the frogs and toads of Taiwan. Chinese Photography Association, Taipei

Zhao EM, Alder K (1993) Herpetology of China. Society for the Study of Amphibians and Reptiles

(Received October 10, 2000 / Accepted December 28, 2000)