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Elevational Variation in Reproductive and Life History Traits of Sauter's Frog *Rana sauteri* Boulenger, 1909 in Taiwan

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Su-Ju Lai, Yeong-Choy Kam and Yao-Sung Lin (2003) Elevational variation in reproductive and life history traits of Sauter's frog *Rana sauteri* Boulenger, 1909 in Taiwan. *Zoological Studies* **42**(1): 193-202. Sauter's frog, *Rana sauteri* Boulenger, 1909 in the west-central part of the Central Mountain Range of Taiwan at elevations of 300 to 2360 m showed obvious elevational clines in reproductive and life cycle traits. With an increase in elevation, the breeding season and the periods of calling, aggregation, and egg deposition of mature frogs shifted from fall and winter (Oct. to Dec.) to spring (May), while the breeding period decreased but the larval period increased. Also, adult females at high elevations were larger and produced smaller clutch sizes but larger eggs and tadpoles. The temperature experiment showed that low temperatures in winter at high elevations and high temperatures in summer at low elevations are the primary environmental factors that define the breeding success of the species. *Rana sauteri* has experienced long-term selection by environmental factors (e.g., temperature), resulting in populations at high elevations breeding in spring and populations at low elevations breeding in fall and winter to ensure that their tadpoles can grow and complete metamorphosis.
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Key words: Elevation, Reproduction, Life history, Anuran, *Rana sauteri*.

Frogs have a complex life history, consisting of an aquatic larval phase and a terrestrial adult phase. They have moist naked skin, and are sensitive to subtle changes in their surrounding environments. These unique characters under the influences of the environment often result in variations in reproductive and life history traits among different geographical populations. Such phenomena have been observed in many species of frogs with wide ranges of distribution in the Temperate Zone (Pettus and Angleton 1967, Koskela and Pasanen 1975, Berven et al. 1979, Beattie 1985 1987, Berven 1987, Bury and Adams 1999, Miaud et al. 1999).

Temperature varies systematically with elevation (Bervern et al. 1979), causing variations in reproduction (Pettus and Angleton 1967, Berven 1982a, Beattie 1985 1987) and development (Pettus and Angleton 1967, Bervern et al. 1979, Berven 1982b, Beattie 1987, Bervern 1987) among populations at different elevations. Temperature has been recognized as a major factor affecting life history traits of amphibians at different elevations in the Temperate Zone (Pettus and Angleton 1967, Berven et al. 1979, Berven and Gill 1983, Beattie 1985 1987).

Taiwan is an island situated between 21°53'N and 25°37'N. The steep Central Mountain Range largely runs along the N-S longitudinal axis of the island with the highest peak at 3997 m. Based on the floral formations along the elevation gradient, the Central Mountain Range in the central part of the island may be divided into 3 climatic zones: 1) tropical and subtropical climates at elevations of less than 1500 m, 2) temperate climates between 1500 and 3600 m, including warm-temperate, tem-

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perate, cool-temperate, and cold-temperate climates, and 3) subarctic climate above 3600 m (Su 1984).

Sauter's frog *Rana sauteri* Boulenger, 1909 is a common species of brown frog widely distributed in the hills and mountains of Taiwan from 100 to 3500 m in elevation (Kuramoto et al. 1984, Lue et al. 1990, Chou and Lin 1997), a range including tropical to cold-temperate climatic zones (Su 1984). Kuramoto (1978) and Chou and Lin (1997) indicated that Sauter's frog is a species of brown frog which originated in the Temperate Zone and which prefers a cold climate.

Although Sauter's frog is common and widely distributed in Taiwan, its life history has been little studied. It is known that mature frogs aggregate for breeding in lotic habitats such as torrents, riffles, glides, dammed pools, side pools, side channels, seepage areas, edge water, plunge pools, and running water of roadside ditches in montane areas (Chou and Lin 1997) in the breeding season. Eggs are usually found under the downstream side of rocks at depths of 10-15 cm. Tadpoles have an abdominal sucker and an enlarged oral disc, enabling them to hold onto hard substrates in fast-flowing water (Chou and Lin 1997). Its breeding season has been suggested to be from Oct. to Apr. Tadpoles occur almost year round (Kuramoto et al. 1984).

This study attempted to compare the reproductive and life history traits of Sauter's frog in relation to elevation, and to explore the selective mechanisms that govern elevational variations.

MATERIALS AND METHODS

Life history traits

Three life history traits were studied: 1) calling and aggregation of mature adults, 2) mating and egg deposition of mature adults, and 3) occurrence of tadpoles. In general, mating activities, including calling, aggregation, mating, and egg deposition, occur in the same period. The breeding period in this study was defined as the period when egg masses were observed in the water. The larval period was defined as the period when tadpoles were observed in the water.

In order to study the above life history traits in relation to elevation and climatic seasons, we used a field survey with the following survey sites, survey intervals, and survey procedures.

Field survey sites

Seven survey sites were selected in the vicinity of the Choushui River along the western slope of the Central Mountain Range at elevations of from 300 to 2360 m in central Taiwan (Table 1; Fig. 1). The Chihchung, Mienyueh, and Haohanpo sites were located at elevations higher than 2000 m on mountain creeks with widths of 0.5-3 m in the breeding period. The creek at Chihchung was dried up from Nov. to the following Apr. At Mienyueh and Haohanpo, the creeks had flowing water from May to Oct., but became a series of pools connected by subterranean flow from Dec. to

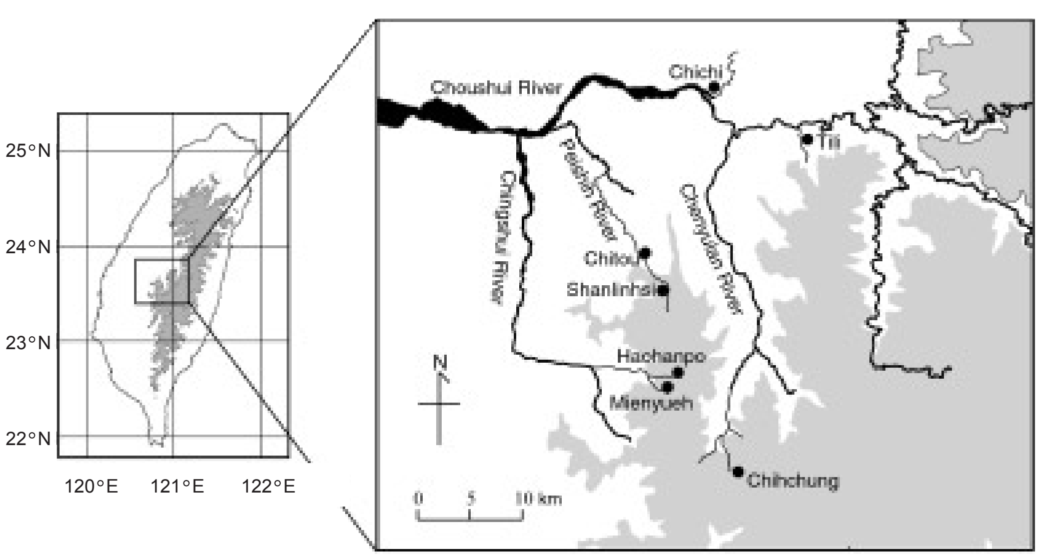

Fig. 1. Survey stations (●) on tributaries of the Choushui River in central Taiwan (shaded area, elevations above 1500 m).

Apr. The remaining 4 sites at elevations lower than 2000 m, namely, Shanlinhsi, Chitou, Tili, and Chichi, had creeks with permanently flowing water with widths of 10-50 m in the breeding period.

The vegetation types were coniferous forests at Chihchung, Mienyueh, and Haohanpo, plantation forests of *Cryptomeria* at Shanlinhsi and Chitou, and orchards at Tili and Chichi. Except for the lowest elevation site of Chichi where stream banks were covered with concrete, the banks of the other 6 sites consisted of natural substrates.

Survey intervals and procedures

At each survey site we made a round trip by walking for about an hour. We went upstream in a 50-m strip along the stream bank, then crossed the stream to go downstream along the other bank. We identified the calls we heard and all of the frogs we encountered irregardless of whether they were *R. sauteri* during this hour. Then we checked the water area within the 50-m strip for about an hour to search for egg masses and tadpoles of *R. sauteri*.

At each of the sites, the survey was first conducted once a month in the daytime. Calls and the appearance of mature male frogs were signs of the beginning of the breeding season. Then, night surveys began, and the frequency of the survey increased to once a week until no egg masses were found for 1 mo. The survey period was from Aug. 1993 to Mar. 1996, except that at Shanlinshi, it was from Aug. 1993 to Aug. 1995. At Chichi where water was highly polluted in the summer of 1994, data collected in 1992 were also used. Accordingly, the survey times differed at each of the sites (Table 1).

Reproductive traits

Reproductive traits studied were 1) snout-vent length and body weight of mature males and females, 2) reproductive investment of breeding females, 3) clutch size of eggs, 4) egg diameter, and 5) total length and body length of newly hatched tadpoles. Because it was difficult to obtain accurate data for the above reproductive traits by field surveys, we collected these data in the laboratory.

Based on the results obtained from early field surveys of 1993 to 1994, we compared the reproductive traits between the spring breeding population from the high elevation sites of Chihchung (2360 m) and Mienyueh (2350 m), and the fall breeding population from the lower-elevation Chitou (1100 m) in 1995. We collected mating pairs from the field: 86 pairs from high-elevation sites and 138 pairs from the low-elevation site. In the field, males and females of the pairs were separated, and the sex of each adult was determined, the weight was taken, and snout-vent length was measured. They were brought back to the laboratory and paired again. Each pair was kept in a Perspex culture vessel (25 x 25 x 16 cm) filled with water to a 10-cm depth. In the center of the vessel, there was a semi-submerged stone which served as a resting and spawning site. The rearing conditions were at room temperature 23 ± 2°C with a daily light regime of a 12-h light period and a 12-h dark period.

Frogs usually deposited eggs within 24 h after being paired. Each of the spent (post-spawning) females was weighed. There were 27 pairs of successful spawning: 9 pairs from high elevations and 18 pairs from the low elevation. The remaining females deposited eggs during transportation, or failed to spawn after being paired.

Because egg masses absorbed water immediately after being deposited, we could not measure their absolute weights for calculating the relative reproductive investment of females. Therefore, we used the following formula to calcu-

Table 1. Survey sites along the western slope of the Central Mountain Range of Taiwan

Survey site	Latitude	Longitude	Elevation (m)	Width of stream in breeding period (m)	Range of water temperatures measured in the field (°C)	Number of times surveyed
Chihchung	23°28'34"N	120°50'20"E	2360	3.0	7.2-19.9	45
Mienyueh	23°33'08"N	120°48'07"E	2350	0.5	4.9-19.4	45
Haohanpo	23°33'47"N	120°47'56"E	2050	1.0	5.2-18.5	39
Shanlinhsi	23°38'14"N	120°48'53"E	1600	30.0	10.5-23.2	30
Chitou	23°40'19"N	120°46'49"E	1100	10.0	12.4-25.6	45
Tili	23°47'73"N	120°55'51"E	450	50.0	12.5-25.5	45
Chichi	23°49'57"N	120°48'02"E	300	50.0	13.4-26.3	47

late the relative reproductive investment (R_i) of females:

$$R_i = \frac{W_p - W_s}{W_p} \times 100\%;$$

where W_p is the pre-spawning weight of the females and W_s is the spent weight of the females.

The clutch size, i.e., the number of eggs deposited by a single female, was counted for each pair. When eggs developed to Gosner stages 8 and 9 (Gosner 1960), twenty eggs were randomly sampled from each clutch, and their diameters (vitellus excluding the jelly coat) were measured. When tadpoles grew to Gosner stage 25, then 30 individuals were randomly collected from each clutch. For each tadpole, total length was measured from the snout to tail tip and body length from the snout to the posterior end of the cloacal opening. Measurements were made from 16 clutches: 6 from high-elevation sites and 10 from the low-elevation site.

Effects of temperature on growth and survival of tadpoles

The maximum temperature and the minimum temperature in the field were, respectively, 19.4 and 4.9°C at Mienyueh and 25.6 and 12.4°C at Chitou. To determine the effects of temperature on growth and survival of tadpoles, we used 3 experimental temperatures in reference to the field maximum and minimum monthly temperatures in winter. The 3 experimental temperatures assigned were 20, 15, and 5°C for the high-elevation site, and 25, 15, and 10°C for the low-elevation site.

Instead of using tadpoles raised from the laboratory in the reproductive trait study, we used tadpoles hatched from egg masses collected from the field as the experimental animals. We collected three clutches of eggs, respectively, from Chihchung, Mienyueh, and Chitou. They were hatched in the laboratory at a temperature similar to that used in the reproductive trait study. For each clutch, three groups each with 60 newly hatched tadpoles were randomly collected, and kept, respectively, at the 3 experimental temperatures for each of the 2 elevation sites. In other words, there were 180 tadpoles for each of the experimental temperatures.

When the tadpoles developed to Gonser stage 25 (Gonser 1960) and beganed to feed about a week after hatching, twelve replicates, each with 6 tadpoles, were made, except that 5°C had 6 replicates. Tadpoles of each replica were raised in a Perspex culture vessel (17 x 10 x 10 cm) filled with 1.2 L of dechlorinated tap water at a density of 1 tadpole/200 ml water. The water was continuously aerated. The photoperiod consisted of a 12-h light period and a 12-h dark period. Tadpoles were fed daily with boiled spinach (Kuramoto et al. 1984) and fish pellets (JBL GmbH Joachim Bonme) ad libitum. We found that tadpoles were healthier when fish pellets were added to the food. An excessive amount of food was supplied daily to avoid possible effects of food availability on the experiment. The remnants were removed 8 h after feeding to avoid water contamination. The survival and total length of individuals were recorded every 5 to 7 d for a period of 50 d.

Meteorological data

Meteorological data including monthly maximum, minimum, and mean air temperature, and rainfall for the years 1993 to 1996 were obtained from the Alisan meteorological station (2300 m in elevation) of the Central Weather Bureau of Taiwan, and Chitou (1200 m) and Suili (270 m) sta-

Table 2. Life history traits of *Rana sauteri* at different elevations in Taiwan

Survey site	Elevation (m)	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Chihchung	2360	×	×	×	✧	✧❖✡❍ -----	-----	-----	-----	-----	-----	-----	×
Mienyueh	2350	-----	-----	-----	-----	✧❖✡❍ -----	-----	❍ -----	-----	-----	-----	-----	-----
Haohanpo	2050	-----	-----	-----	-----	✧❖✡❍ -----	-----	-----	-----	-----	-----	-----	-----
Shanlinhsi	1600	-----	-----	-----	-----	×	×	×	✧❖✡❍	✧❖ -----	-----	-----	-----
Chitou	1100	-----	-----	-----	×	×	×	×	✧❖	✧❖✡	✧❖✡❍ -----	✧❖❍ -----	-----
Tili	450	-----	-----	-----	×	×	×	×	✧	✧❖	✧❖✡❍ -----	✧❖✡❍ -----	✧❖❍ -----
Chichi	300	-----	-----	×	×	×	×	×	×	×	✧❖✡❍ -----	✧❖✡❍ -----	-----

✧, breeding call of adults; ❖, aggregation of adults; ✡, pairs in axillary amplexus; ❍, occurrence of egg masses; -----, occurrence of tadpoles; ×, none recorded.

tions of the Experimental Forest of National Taiwan Univ. They were, respectively, located in the vicinity of the 3 survey sites of Mienyueh, Chitou, and Chichi, representing high, middle, and low elevations. Their monthly mean temperature and rainfall profiles were established and compared to the life cycle traits.

Statistical analysis

Each of the reproductive traits was compared between the high elevations and the low elevation, using Student's *t*-test (Sokal and Rohlf 1981). Repeated-measures analysis of variance (ANOVA) was used to compare the percent survival, while repeated-measures analysis of covariance (ANCOVA) was used to compare growth among the 3 experimental temperatures for each of the 2 populations with initial body weight used as a covariate (SAS Institute 1996).

RESULTS

Life history traits

At Chihchung, Mienyueh, and Haohanpo at elevations higher than 2000 m, the breeding season was extremely short, being recorded only in May (Table 2). Most breeding activities occurred in this month, but in July 1995 a single mass of eggs was observed at Mienyueh. This exception might have resulted from the interference of marking frogs which caused all of them disappear in May 1995. At Mienyueh and Haohanpo, tadpoles occurred year round. The larval period was 12 mo. At Chihchung, the stream dried up in winter. We do not know whether tadpoles had metamorphosed to froglets before the stream dried up, or if they died of desiccation.

At Shanlinhsi at an elevation of 1600 m, calling and aggregation of mature adults and egg masses in the stream were observed in Aug. Tadpoles occurred from Sept. to Apr. The larval period was 8 mo. During the late spring to early summer from May to July, water areas of the site were empty of Sauter's frogs, and there were neither tadpoles nor adults in the streams.

At Chitou, Tili, and Chichi at elevations below 1100 m, the breeding seasons were in fall and early winter in Oct. and Nov. at Chitou and Chichi, and in Oct. to Dec. at Tili (Table 2). At Chitou, calling and pairs in axillary amplexus but no egg masses were observed in Aug. and Sept. Tadpoles occurred from Oct. to Mar. at Chitou and Tili and to Feb. at Chichi. The larval periods did not exceed 6 mo. The streams were empty of Sauter's frogs during the late spring to early fall from Apr. to July at Chitou and Tili, and from Mar. to Sept. at Chichi. Like Shanlinhsi, this was a rest period for breeding activity and the aquatic larval phase at Chitou, Tili, and Chichi. Apparently, all tadpoles had metamorphosed to froglets, and all frogs had migrated to the forest floor for feeding.

According to the results obtained above, Sauter's frog in mountain regions of Taiwan might be divided into 3 populations: 1) a spring-breeding population at high elevations above 2000 m, 2) a summer-breeding population around middle elevations of 1600 m, and 3) a fall-breeding population at low elevations of 300 to 1100 m (Table 2). There were obvious clines in life history traits in relation to elevation. With an increase in elevation, breeding seasons shifted from fall to spring, lengths of breeding periods decreased, and lengths of larval periods increased (Table 2).

Table 3. Comparisons of reproductive traits (mean ± SD, sample sizes in parentheses) of *Rana sauteri* between the Chihchung-Mienyueh sites and the Chitou site

	Reproductive trait	Chihchung and Mienyueh	Chitou	*t* value	*p*
Male	Snout-vent length (mm)	38.8 ± 2.42 (86)	38.5 ± 2.00 (138)	0.785	> 0.05
	Body weight (g)	4.4 ± 0.71 (86)	4.5 ± 0.64 (138)	1.796	> 0.05
Female	Snout-vent length (mm)	52.9 ± 2.15 (9)	48.7 ± 2.51 (18)	4.290	< 0.001
	Body weight (g)				
	Pre-spawning	14.0 ± 1.78 (9)	11.9 ± 1.83 (18)	3.014	< 0.05
	Spent	10.9 ± 1.17 (9)	8.8 ± 1.40 (18)	3.743	< 0.001
	Reproductive investment (%)	22.5 ± 3.03 (9)	25.7 ± 2.61 (18)	2.886	< 0.05
Egg	Clutch size	224.9 ± 76.31 (9)	488.1 ± 79.98 (18)	8.178	< 0.001
	Egg diameter (mm)	3.6 ± 0.21 (9)	2.6 ± 0.20 (18)	11.865	< 0.001
Tadpole	Total length (mm)	11.3 ± 0.38 (6)	8.7 ± 0.51 (10)	10.874	< 0.001
	Body length (mm)	4.1 ± 0.11 (6)	3.6 ± 0.16 (10)	7.210	< 0.001

Reproductive traits

Table 3 compares reproductive traits between the high-elevation Chihchung-Mienyueh and the low-elevation Chitou sites. For mature adult males, snout-vent length and body weight were fairly similar between the high-elevation sites and the low-elevation one.

In contrast to males, snout-vent length was much longer and body weight was much heavier for both pre-spawning and spent females at the high elevations than at the low elevation. Despite females being larger at the high elevations, their reproductive investment was lower, and they produced small clutch size, but with larger-sized eggs and newly hatched tadpoles, as compared to those at the low-elevation site.

Like life history traits, there were obvious elevational clines in reproductive traits in relation to elevation. With an increase in elevation, females became larger and heavier, and produced smaller clutches of eggs, but larger eggs and tadpoles.

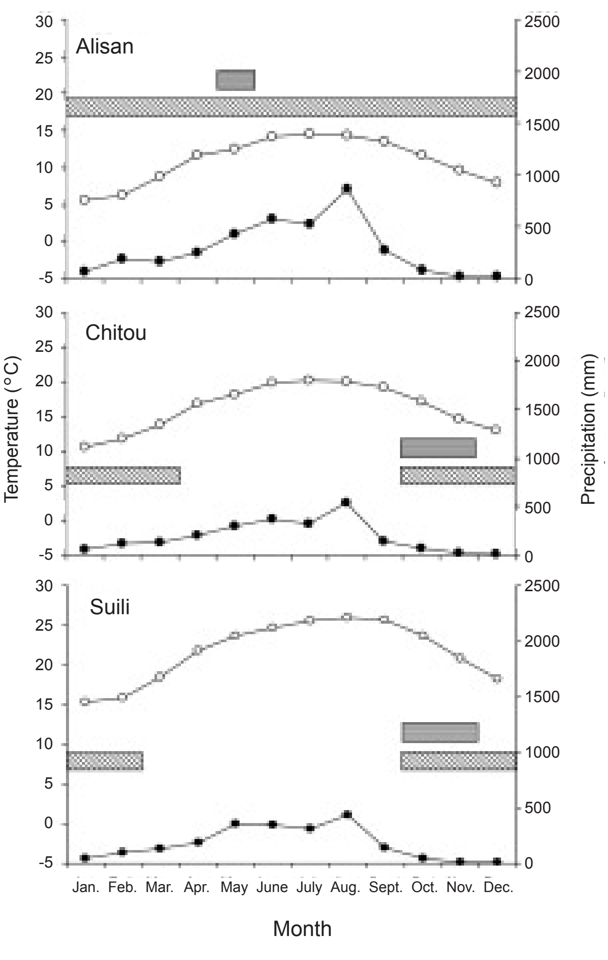

Fig. 2. Breeding periods (▬) and larval periods (▬) of *Rana sauteri* at Mienyueh, Chitou, and Chichi in relation to monthly mean temperature profiles (o—o) and monthly mean precipitation profiles (●—●) of the Alisan, Chitou, and Suili meteorological stations, 1993 to 1996.

Relationships between life history traits and meteorological factors

The breeding periods of Sauter's frog at Mienyueh, Chitou, and Chichi obtained in this study were, respectively, plotted on profiles of monthly average air temperature and rainfall of the Alisan, Chitou, and Suili meteorological stations (Fig. 2). Based on this figure, average monthly air temperatures during the breeding period were estimated to be 12.5°C at Mienyueh, 14.7 to 17.2°C at Chitou, and 20.8 to 23.7°C at Chichi. When these breeding temperatures were plotted against elevation at the 3 sites, there was a significant negatively regressive relationship between breeding temperature and elevation: breeding temperature decreased with an increase in elevation. Also, the breeding period decreased from 2 to 3 mo at low elevations to 1 mo at high elevations (Fig. 3).

In contrast to breeding temperature and breeding period that decreased with an increase in elevation (Fig. 3), the larval period, i.e., the period in which tadpoles were observed, increased significantly from 5 mo at the low elevation to 12 mo at high elevations. The larval period showed a significant positively regressive relationship with elevation (Fig. 4).

The results suggest that Sauter's frog has adapted to a variety of climatic conditions, resulting in a wide distributional range in terms of elevation. It can tolerate a wide range of temperatures for breeding, and also had wide ranges for the

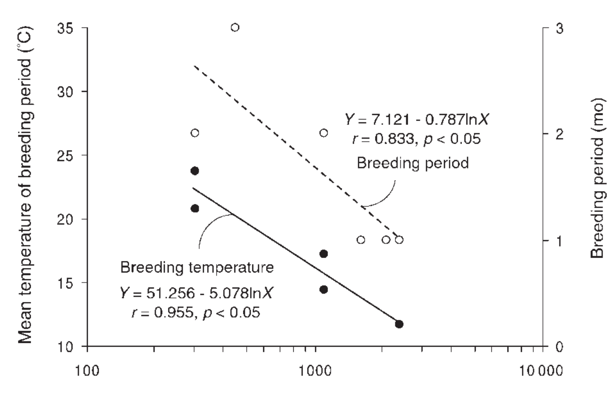

Fig. 3. Relationships of breeding periods (o-----o) and breeding temperature (●—●) of *Rana sauteri* to elevation.

breeding period and larval period.

Effects of temperature on growth and survival

The relationship between body weight and total length is shown as unit growth curves (Figs. 5, 6) for each tadpole as estimated by the following formula:

$$\log(W_b) = -1.244 + 2.435 \log(L_t);$$

where W_b is the body weight of a tadpole, and L_t is the total length of a tadpole (Fig. 5). Tadpoles hatched from egg masses obtained from Mienyueh at a high elevation had significantly faster growth and higher survival at 20°C than at 5°C, while there were no significant difference in survival between 20 and 15°C (Table 4). Although tadpoles survived and grew well and a few tadpoles metamorphosed to froglets at both these temperatures within the 50-d experimental period, the percent survival was only about 50% by the end of the experiment. This reflects that the techniques for raising tadpoles from high elevations need to be improved. At 5°C, the growth almost ceased with high mortality, particularly in the 1st 2 wk of the experiment (Fig. 6). No tadpole reached the metamorphosis stage.

Tadpoles hatched from egg masses collected from Chitou at a low elevation grew well at the 3 experimental temperatures of 10, 15, and 25°C, and their growth increased with an increase in temperature (Fig. 7). The growth was faster at 25°C than at 15°C (Table 4), but did not significantly differ between 15 and 10°C. The percent survival did not significantly differ between 15 and 10°C, but it was significantly lower at 25°C than at 15°C.

The above results suggest that there are obvious differences in the responses of tadpoles in the form of growth and survival to temperature regimes at different elevations. Low temperatures represented by the minimum monthly mean temperature in winter seem to be a limiting factor for successful completion of the aquatic larval phase

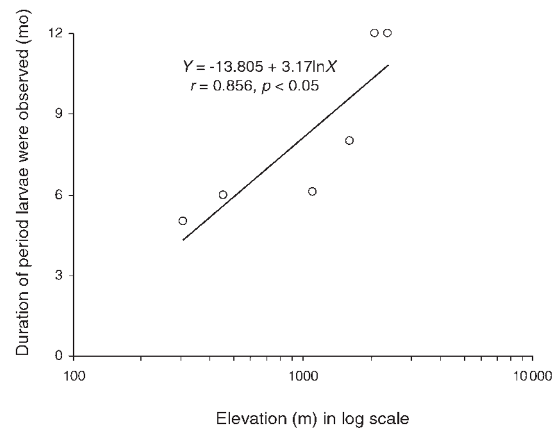

Fig. 4. Relationship of the duration of the period larvae of *Rana sauteri* were observed to elevation.

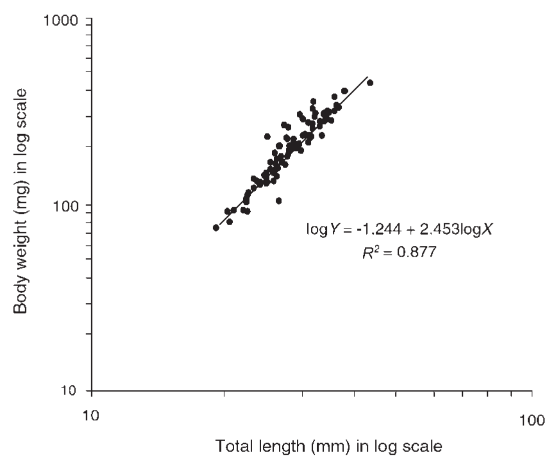

Fig. 5. Relationship between body weight and total length of tadpoles of *Rana sauteri*.

Table 4. *F* values of repeated-measures analysis of covariance (ANCOVA) and repeated-measures analysis of variance (ANOVA), respectively, used to compare the growth and survival curves among experimental temperatures

Site	Experimental temperatures (°C)	Growth curve *F* value	*p*	Survival curve *F* value	*p*
Chihchung and Mienyueh	5 15 20	$F_{2,26}$ = 29.24	< 0.001	$F_{2,27}$ = 19.45	< 0.001
	5 15	$F_{1,15}$ = 10.59	< 0.05	$F_{1,16}$ = 21.55	< 0.001
	15 20	$F_{1,21}$ = 20.15	< 0.001	$F_{1,22}$ = 0.21	> 0.05
	5 20	$F_{1,15}$ = 66.94	< 0.001	$F_{1,16}$ = 19.84	< 0.001
Chitou	10 15 25	$F_{2,32}$ = 9.62	< 0.001	$F_{2,33}$ = 11.96	< 0.001
	10 15	$F_{1,21}$ = 4.00	> 0.05	$F_{1,22}$ = 6.49	> 0.05
	15 25	$F_{1,21}$ = 5.89	< 0.05	$F_{1,22}$ = 21.38	< 0.001
	10 25	$F_{1,21}$ = 20.87	< 0.001	$F_{1,22}$ = 6.35	> 0.05

at high elevations, while high temperatures represented by the maximum temperature in summer are the limiting factor at low elevations.

DISCUSSION

Many frogs in temperate regions breed in early spring when temperatures are increasing, and their breeding time tends to be delayed with an increase in elevation (Berven et al. 1979, Beattie 1985). For example, the breeding time of *Rana temporaria* Linnaeus, 1758 is delayed 53 d by moving from 46 to 838 m in elevation, with an average of 6 d for each increase of 100 m. This phenomenon was explained by the so-called temperature-sum effect expressed by degree-days (Beattie 1985). In other words, adults need to experience a certain number of degree-days to emerge and initiate spawning.

In contrast to *R. temporaria* of the Temperate Zone mentioned above, Sauter's frog in subtropical Taiwan breeds in a wide range of temperatures (Figs. 2, 3) from May in spring to Dec. in winter, and their breeding times are delayed with a decrease in elevation (Table 2; Fig. 2). The temperature-sum effect (Beattie 1985) that explains the elevational clines of the frog in the Temperate Zone is unable to explain the elevational cline of Sauter's frog in the Subtropical Zone.

In the Temperate Zone, temperature determines the breeding season of many frogs. Frogs emerge from hibernation when a particular threshold environmental temperature is reached (Martof 1956, Wells 1976, Berven et al. 1979, Beattie 1985). In this paper, at elevations above 2000 m, the frog bred at 12.5°C in the month of May in spring, but not in the month of Oct. in fall when the same temperature also prevailed. At elevations of less than 1100 m, the frog bred at 20.8-23.7°C in the months of Oct. and Nov. in fall, but not in the months of Apr. and May in spring when the same temperatures also prevailed. Therefore, the breeding temperature requirement is neither a limiting factor for the completion of the aquatic phase of the life cycle, nor a causative factor for the elevational clines in breeding time and the subsequent reproductive and life history traits.

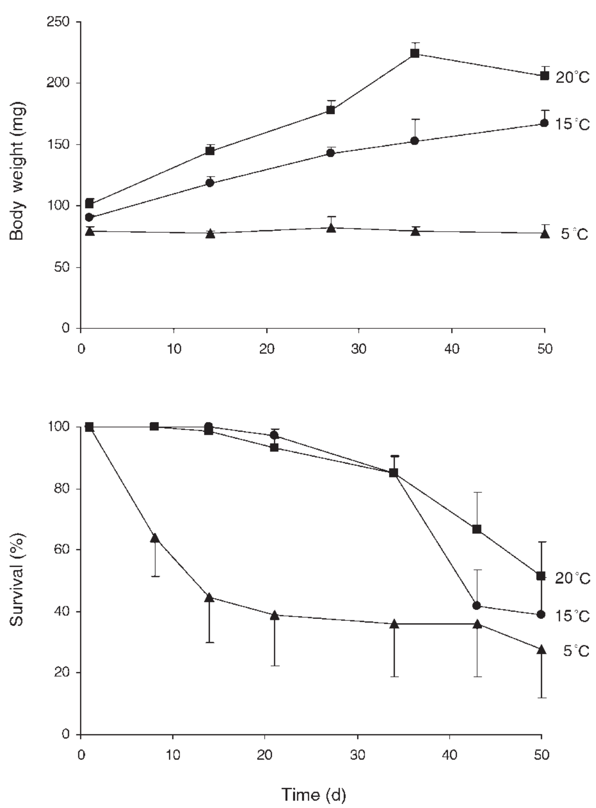

Fig. 6. Growth and survival curves of *Rana sauteri* tadpoles from Chihchung and Mienyueh at the experimental temperatures of 5, 15, and 20°C. Values are the mean ± SE.

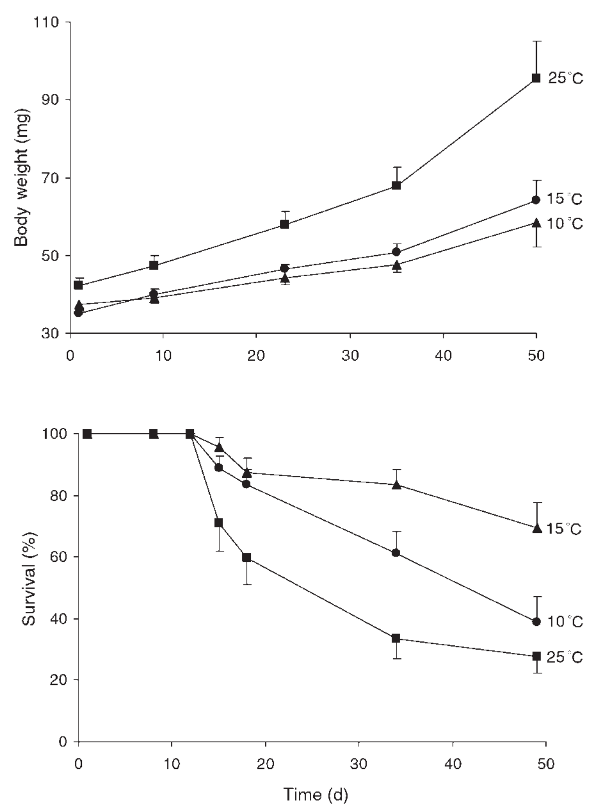

Fig. 7. Growth and survival curves of *Rana sauteri* tadpoles from Chitou at the experimental temperatures of 10, 15, and 25°C. Values are the mean ± SE.

Environmental temperature is a major proximal factor in the growth, development, and overall life-history patterns observed in amphibians (Smith-Gill and Berven 1979, Beattie 1985). According to the results obtained from the laboratory experiment in this study, we found that temperature affected survival and growth of tadpoles at different elevations. This result might be one important factor determining the breeding season of *R. sauteri* at different elevations. At high elevations, the minimum temperature retarded the growth of tadpoles and also caused high mortality (Fig. 6), while at low elevations, the maximum temperature caused high mortality (Fig. 7). In order to complete the aquatic larval phase, tadpoles are required to survive and to grow to the metamorphosis stage. At high elevations where the minimum temperature is a limiting factor for growth and survival, if the breeding season were not in spring but in fall, tadpoles would encounter a hazardously cold winter and die off before reaching the metamorphosis stage. At low elevations where the maximum temperature is a limiting factor for survival, if tadpoles were not born in fall but in spring, they would die off due to hazardous hot temperatures during the summer period.

Therefore, it is hypothesized that the adaptive shift in breeding season with elevation to ensure the best survival and growth of tadpoles in order to complete the aquatic larval phase is the primary adaptive mechanism of the long-term selection of Sauter's frog by environmental temperatures in the Central Mountain Range of subtropical Taiwan. Such an adaptive shift results in formation of an elevational cline of the breeding season as well as of the reproductive and life history traits of this species.

Mature females had significantly larger body sizes than did mature males (Table 3). Both differential growth and differences in age structures might cause sexual size dimorphism (Ryser 1996). With an increase in elevation, female Sauter's frogs increased in body size, but the breeding period decreased, and they produced a smaller clutch size which decreases a female's reproductive investment. Modification of these reproductive traits might provide higher energy reserves for Sauter's frog to survive and to grow in order to complete the terrestrial phase in hazardous cold environments (Pettus and Angleton 1967, Berven 1982a, Miaud et al. 1999). Because extremely low temperatures might slow down development and growth (Berven et al. 1979, Smith-Gill and Berven 1979, Bury and Adams 1999) or cause cessation of the response to the hormone for metamorphosis (Norris and Platt 1974, Lofts 1976), the larval phase should lengthen with increasing elevation. Furthermore, large egg sizes increase the yolk contents to increase energy reserves for higher embryonic development rates (Pettus and Angleton 1967, Ryser 1996). Larger egg sizes also produce larger tadpoles (Crump 1984, Blaustein et al. 1999) for better survival in shorter growing seasons of cooler environments (Berven and Gill 1983, Ryser 1996). These partially compensate for the adverse effects of low temperatures on physiological processes of tadpoles (Pettus and Angleton 1967, Koskela and Pasanen 1975).

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REFERENCES

Beattie RC. 1985. The date of spawning in populations of the common frog (*Rana temporaria*) from different altitudes in northern England. J. Zool. (Lond.) **205:** 137-154.

Beattie RC. 1987. The reproductive biology of common frog (*Rana temporaria*) populations from different altitudes in northern England. J. Zool. (Lond.) **211:** 387-398.

Berven KA. 1982a. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. Evolution **36:** 962-983.

Berven KA. 1982b. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. II. An experimental analysis of larval traits. Oecologia **52:** 360-369.

Berven KA. 1987. The heritable basis of variation in larval developmental patterns within populations of the wood frog (*Rana sylvatica*). Evolution **41:** 1088-1097.

Berven KA, DE Gill. 1983. Interpreting geographic variation in life-history traits. Am. Zool. **23:** 85-97.

Berven KA, DE Gill, SJ Smith-Gill. 1979. Countergradient selection in the green frog, *Rana clamitans*. Evolution **33:** 609-623.

Blaustein L, JE Garb, D Shebitz, E Nevo. 1999. Microclimate, developmental plasticity and community structure in artificial temporary pools. Hydrobiologia **392:** 187-196.

Bury RB, MJ Adams. 1999. Variation in age at metamorphosis across a latitudinal gradient for the tailed frog, *Ascaphus truei*. Herpetologica **55:** 283-291.

Chou WH, IY Lin. 1997. Geographical variations of *Rana sauteri* (Anura: Ranidae) in Taiwan. Zool. Stud. **36:** 201-221.

Crump ML. 1984. Intraclutch egg size variability in *Hyla crucifer* (Anura: Hylidae). Copeia **1984:** 302-308.

Gosner KL. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16:** 183-190.

Koskela P, S Pasanen. 1975. The reproductive biology of the female common frog, *Rana temporaria* L., in northern Finland. Aquilo Ser. Zool. **16:** 1-12.

Kuramoto M. 1978. Thermal tolerance of frog embyros as a function of developmental stage. Herptologica **34:** 417-422.

Kuramoto M, CS Wang, HT Yu. 1984. Breeding, larval morphology and experimental hybridization of Taiwanese brown frogs, *Rana longicrus* and *R. sauteri*. J. Herpetol. **18:** 387-395.

Lofts B. 1976. Physiology of the amphibian. Vol. 3. New York: Academic Press.

Lue KY, CY Lin, KS Jung. 1990. Wildlife data bank of Taiwan, (1) Amphibians (II). Taipei: Ecological Research of the Council of Agriculture No. 8. (in Chinese)

Martof B. 1956. Growth and development of the green frog, *Rana clamitans,* under natural conditions. Am. Midl. Nat. **55:** 101-117.

Miaud C, R Guyetant, J Elmberg. 1999. Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): a literature review and new data from the French Alps. J. Zool. (Lond.) **249:** 61-73.

Norris DO, JE Platt. 1974. T_3- and T_4-induced rates of metamorphosis in immature and sexually mature larvae of *Ambystoma tigrinum* (Amphibia: Caudata). J. Exp. Zool. **189:** 303-310.

Pettus D, GM Angleton. 1967. Comparative reproductive biology of montane and piedmont chorus frog. Evolution **21:** 500-507.

Ryser J. 1996. Comparative life histories of low- and high-elevation population of the common frog *Rana temporaria*. Amphibia-Reptilia **17:** 183-195.

SAS Institute. 1996. SAS/STAT user's guide. Gary, IN: SAS Inst.

Smith-Gill SJ, KA Berven. 1979. Predicting amphibian metamorphosis. Am. Nat. **113:** 563-585.

Sokal RR, FJ Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. San Francisco: Freeman.

Su HJ. 1984. Studies on the climate and vegetation types of the natural forests in Taiwan. (II) Altitudinal vegetation zones in relation to temperature gradient. Q. J. Chin. For. **17:** 57-73. (in Chinese with English abstract)

Wells KD. 1976. Multiple egg clutches in the green frog (*Rana clamitans*). Herpetologica **32:** 85-87.