

Reproductive ecology of the stream-dwelling frog *Feirana taihangnicus* in central China

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We studied the breeding ecology of *Feirana taihangnicus*, a stream-dwelling frog endemic to central China, in a forest-covered mountainous area in north Henan. Frogs emerged from hibernation in mid March and oviposition took place between late April and early May. About one week before the oviposition period, both sexes had swollen cloacas, with tubercles being present on the dorsal skin of adult males. Males never developed vocal sacs, nuptial pads or any other obvious structures used in amplexus. Males were smaller than females. Sex ratio of the breeding population was female-biased. Communal oviposition habitats, which were used repeatedly across years, were in sun-exposed, slow-flowing sections of the stream. Eggs were found on the underside of rocks, deposited in a single layer. Clutch size per female averaged 425 eggs and egg diameter 3.63 mm. Larvae spent up to 27 months in streams before completing metamorphosis. Mark-recapture data showed that 306–513 frogs were present during the breeding season along the 5.5 km long stream in 2006, but only 131 frogs were detected in 2010. Frogs tended to use the same oviposition sites across years. In light of these data we discuss conservation needs for this species, which has a restricted distribution, specialized habitat and extended larval period.

Key words: breeding, life history, oviposition habitat

INTRODUCTION

Two frog species in the genus *Feirana* are known from China (synonymized with *Nanorana* in Frost et al., 2006). Frogs in this genus are uniquely characterized by the swollen cloaca that occurs on both sexes during the breeding season. *Feirana quadrana* has a large range of about 290,000 km² and occurs on high-gradient streams (at elevations from 350 to 1850 m) in forest and shrublands in southern China (28–35°N, 103–112°E; Fei et al., 2009). *Feirana taihangnicus* has a smaller range of 30,000 km², breeding in mountainous streams at elevations from 400 to 1600 m in central China including northern Henan and southern Shanxi provinces (35–36°N, 112–113°E; Chen et al., 2002, 2004). So far, no data on the reproductive ecology of these two species are available.

Its occurrence at high elevations and relatively small range raise conservation concerns for *F. taihangnicus*, as both attributes are linked to elevated extinction risk (Beebe & Griffiths, 2005; Stuart et al., 2008; Sodhi et al., 2008). We here report on the natural history of this poorly known species, including breeding biology, habitat requirements, tadpole growth and population size.

MATERIALS AND METHODS

This study was conducted in Heilonggou in the Taihangshan National Nature Reserve (35°16'N, 112°04'E), north Henan province. Our study plot was a 5.5 km long stream (762–948 m elevation) located in a valley covered by temperate coniferous and broad-leaved mixed forests. Annual average air temperature at an elevation of 760 m was 11.1 °C with a total annual precipitation of 684 mm,

and both temperature and rainfall peaked in summer (June–August, Fig. 1).

In early March 2005, 2006 and 2010, we walked along the stream bank every day during daytime (0800–1800) and captured frogs encountered by hand. For each frog captured, we identified its breeding status (breeding or non-breeding) and sex based on secondary sexual traits: breeding frogs had white tubercles on the dorsal skin (males) or an inflated abdomen (females). We measured snout–vent length (SVL) using a vernier calliper to the nearest 0.1 mm. In 2006 and 2010, we marked frogs with a coloured cotton strip around the knee (Elmberg, 1989). Frogs were marked with different colours on different dates, to allow for identification of the number of days

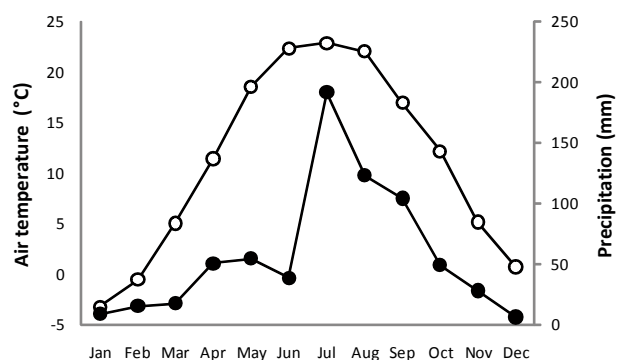


Fig. 1. Monthly changes in average air temperature (open circles) and total precipitation (closed circles) in the study area.

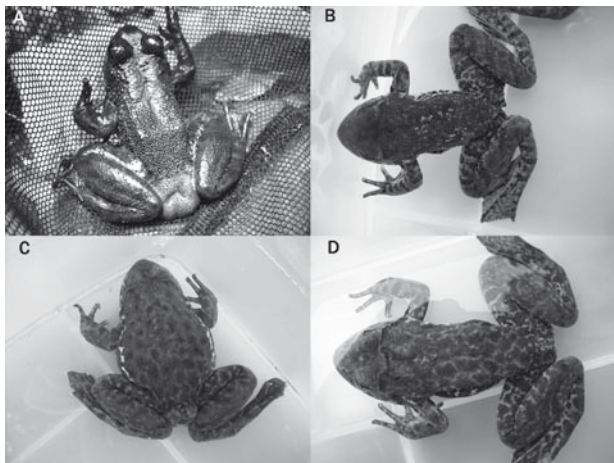


Fig. 2. Appearance of adult *Feirana taihangnicus*. A: male during the breeding period; B: male after the breeding period; C: female during the breeding period; D: female after the breeding period.

between recaptures. Field observations suggested that the marking did not harm the frogs or disrupt their activities. All animals examined were released at the point of capture. We estimated the numbers of frogs inhabiting the stream using the Jolly–Seber method based on multiple mark–recapture data (Borchers et al., 2002) according to the formula:

$$N_i = M_i n_i / m_i$$

where N_i is the expected number of animals at time i , n_i is the number of animals (both marked and unmarked) captured at sample time i , and m_i is the number of previously marked animals captured at time i . M_i , the number of previously marked animals before time i , was calculated as:

$$M_i = (S_i Z_i / R_i) + m_i$$

where S_i is the number of animals (both marked and unmarked) released at time i , R_i is the number of animals released alive at time $i + 1$ (i.e. just after time i), and Z_i is the number of animals marked before time i and recaptured after time i .

We determined oviposition habitats through observing their activities. To check for the presence of egg clutches, we carefully overturned smaller rocks and inspected big-

ger rocks or felt into cracks and spaces where eggs may have been deposited. Developmental stages of the eggs were determined according to Gosner (1960). Tadpoles were collected in the stream using a hand-held seine in May, July and October of 2006. After we had checked their developmental stage and measured their body size, tadpoles were released at the site of capture.

RESULTS

Sexual dimorphism

The earliest emerging frogs were found in mid March. There were no external differences between sexes for individuals collected shortly after emergence. From early April onwards, males were characterized by white tubercles with black tips on the dorsal skin (Fig. 2A); these characters disappeared about one week after the breeding season (mid May, Fig. 2B). The cloaca of male frogs became swollen only during the oviposition period. Males had no vocal sacs, nuptial excrescences on the fingers or any notable prehensile structures on the forelimbs or ventral surface throughout the breeding season. Females were characterized by an inflated abdomen due to fully developed eggs and by a swollen cloaca during the oviposition period (Fig. 2C), which disappeared immediately after oviposition (Fig. 2D).

Population composition

A total of 86 adult males and 190 adult females were detected during the three breeding seasons, with a sex ratio biased towards females (1:2.2, $\chi^2=39.19$, $P<0.001$). A female-biased sex ratio was also found for 41 museum specimens (preserved in the Zoological Museum, Henan Normal University, Xinxiang) collected during the non-breeding season (16 males and 25 females, 1:1.6), although the bias in this sample was not significant ($\chi^2=1.98$, $P=0.15$). The smallest individuals with reproductive characters had an SVL of 47.8 mm in males (the white tubercles were present on the dorsal skin) and 51.4 mm in females (eggs were visible through the skin of the abdomen). On average, breeding males were significantly smaller than breeding females (Table 1). For neither sex was there was a significant difference in average body size across years (males, $F_{2,83}=0.79$, $P=0.46$; females, $F_{2,187}=1.84$, $P=0.16$).

Some individuals had an SVL above the minimum size for reproductive adults reported above, but exhibited no

Table 1. Sex differences in SVL (mm) of *Feirana taihangnicus* sampled during the breeding season. Frogs were individually marked and only measured once in each year.

Year	Male			Female			Significance
	<i>n</i>	Mean ± SD	Range	<i>n</i>	Mean ± SD	Range	
2005	4	66.2±7.8	59.8–77.4	9	80.8±4.8	70.3–86.7	$t_{11}=4.23$, $P=0.001$
2006	54	66.1±5.6	47.8–79.3	86	75.6±9.4	51.5–94.2	$t_{138}=6.70$, $P<0.001$
2010	28	67.9±6.5	53.5–80.1	95	74.7±9.3	51.4–93.1	$t_{121}=3.65$, $P=0.001$
Total	86	66.7±6.0	47.8–80.1	190	75.4±9.2	51.4–94.2	$t_{274}=8.02$, $P<0.001$

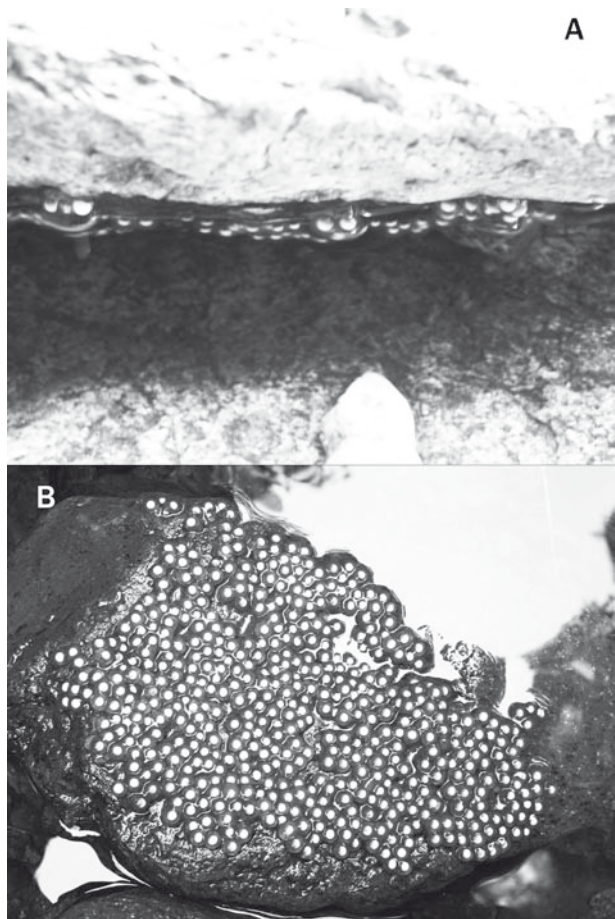


Fig. 3. Eggs of *Feirana taihangnicus*. A: lateral view, B: frontal view of a different egg mass.

obvious characters associated with reproduction. These included five males with thin tubercles recorded between early April and mid May (mean SVL \pm SD = 55.3 \pm 4.0 mm, range 48.9–58.8 mm) and 13 females without inflated abdomens recorded shortly before the oviposition period (64.9 \pm 2.9 mm, 59.2–68.1 mm). During the three breeding seasons, a total of 14 individuals that had SVLs shorter than 50 mm (39.5 \pm 6.4 mm, 25.3–49.4 mm) and exhibited no reproductive characters were encountered. Examination of five museum specimens of females collected shortly after the oviposition period showed that the ovaries contained developing oocytes (diameters 1.2–1.8 mm) and the oviducts were thin, indicating that they did not breed in the year of capture.

Oviposition habitat

Oviposition sites were located in sun-exposed stream sections (2.6–6.2 m in length, 2.5–3.0 m in width; $n=4$), where water flowed slowly and was relatively shallow (maximum depth 22–72 cm). The frogs seemed to be faithful to particular oviposition sites because two of the three sites found in 2005 were also used in 2006. Only one new oviposition site was detected in 2010, when four sites recorded in previous years were destroyed by road construction.

Eggs were found beneath rocks in the stream and arranged in a single layer (Fig. 3A, B). Egg clutches were located 5–28 cm (13.6 \pm 8.3 cm, $n=7$) above the streambed and 3–8 cm (5.5 \pm 2.1) beneath the water surface. At one oviposition site, eggs were deposited under 3–7 rocks, and the distances between rocks used for egg deposition were 0.1–1.5 m (0.7 \pm 0.4 m, $n=9$). Some females may have oviposited beneath bigger rocks or cliffs that we could not adequately survey for the presence of eggs. Under a single rock, the number of eggs at the same developmental stage ranged between 20 and 550 (Table 2). The number of eggs derived from museum specimens ranged between 302 and 611 (425 \pm 105 eggs, $n=8$) and was positively correlated with female body size ($r=0.73$, $P=0.04$). Therefore, eggs of a female may be deposited on either a single rock or under several neighbouring rocks. Also, eggs at two distinct stages were found attached to the same rock, presumably laid by more than one female at different times. Diameters of the embryos before stage 7 (blastula formation) averaged 3.63 \pm 0.39 mm (3.31–4.07 mm, $n=3$ clutches, 14 to 58 individual embryos measured per clutch).

Breeding season

No amplexant pairs were observed during this study. The dates on which the first and last fresh egg clutches were found in 2005 and 2006 coincided with the occurrence of female reproductive traits (Table 3). In 2010, only two clutches were detected and they were deposited on 5 and 6 May, falling within the expected breeding season. All of the 13 adult female museum specimens (SVL >50 mm) collected after mid May in 2010 exhibited regressed ovaries and oviducts without developed eggs. Therefore, we conclude that oviposition takes place between late April and early May, lasting about one week. The observed annual variation in breeding time may be linked with local climatic conditions. At a neighbouring lower-elevation stream (611–623 m), the first egg clutches in 2006 were observed on 5 April, 18 days earlier than those at higher elevation.

Table 2. Characters of egg-deposition rocks and patterns of egg clutch distribution.

Observation date	Area of rock substrate (mm)	Gosner stage – egg numbers
24 April 2005	60 × 54	1 – 373
24 April 2005	62 × 59	5 – 100; 1 – 550
27 April 2005	38 × 28	5 – 200
27 April 2005	76 × 52	5 – 350
27 April 2005	178 × 55	? – over 400
29 April 2005	33 × 19	? – 494
23 April 2006	32 × 22	1 – 20; 7 – 500
24 April 2006	100 × 80	1 – over 300
8 May 2010	237 × 186	11 – 490; 13 – 210

Table 3. Dates of the first and last clutches and percentage of females with SVL >50 mm (sample size in parentheses) across three breeding seasons. *Date on which the earliest spent females were firstly observed; **date after which all the females found had already oviposited.

	2005	2006	2010
Egg-laying date			
First clutch date	24 April	23 April	2 May*
Last clutch date	29 April	30 April	8 May**
% spent females			
Within one week before the first clutch date	–	0 (12)	0 (9)
Between the first and last clutch date	75 (4)	50 (72)	63 (19)
Within one week after the last clutch date	100 (5)	100 (48)	100 (33)

Larvae

Larvae at different stages of development were present in the stream from May through October (Fig. 4). It is likely that the late April–early May larvae at stage 25–27 are one year old, and develop to stages 37–38 in late June or early July, and to stages 39–40 prior to winter. Tadpoles around stage 40 therefore should be in their third year, and probably metamorphose in July. In accordance with this assertion, freshly metamorphosed frogs were found on 2 July. Late June–early July larvae at stage 25–26 should be those that hatched in that year and they may reach a stage around 26–27 in October. We expect that low temperatures in winter will delay larval development. Larvae entering winter in their first or second year (at about stages 26 or 39) will be forced to develop over an extended period in very low water temperatures. Larvae at stage 30–35 were rarely found, probably because these stages occurred in early April, outside our sampling months. Taken together, our data suggest that larvae spend 27 months and experience two winters in streams before metamorphosing into juveniles.

Population size estimate

The mark–recapture data during 23 April to 10 May 2006 showed that there were 306–513 frogs living in the 5.5-km long stream (Table 4). The population size apparently declined over time in 2006, presumably because some frogs became inactive after reproduction. On 2 May 2010, the breeding population was estimated to have only 131 individuals.

DISCUSSION

Sexual dimorphism

Unlike most anurans, male *F. taihangnicus* have no nuptial pads or other structures used to maintain amplexus (Duellman & Trueb, 1986). In species for which such traits are lacking, oviposition occurs without amplexus

(Kunte, 2004), and we indeed failed to find amplexing pairs of *F. taihangnicus*, although a large number of adult frogs were encountered. Female *F. taihangnicus* were larger than males, as in most anuran species (Shine, 1979). Sexual dimorphism in skin texture is common in anurans but these traits vary greatly in structure and function according to species. The tubercles on the dorsum of male *F. taihangnicus* and the swollen cloaca of both sexes are typical of *Feirana* species. Their functions remain unknown. A possible role of these traits in reproductive activities is to facilitate chemical communication in water for orientation or sex recognition, as suggested for other stream-dwelling anurans in which males have no vocal sacs (Belanger & Corkum, 2009).

Habitat selection

Feirana taihangnicus were highly selective with respect to oviposition habitats. Their preference for sun-exposed, shallow stream sections may be because these sites provide warmer conditions that favour rapid egg development. Sites used for egg-depositing were also close to the water surface, which may also optimize thermal conditions. The oviposition method with eggs in a monolayer in sites with slowly flowing water may reduce the likelihood of the eggs being washed away by the current, as each individual egg is attached to the substrate. Eggs close to the surface in mono-layers may also maximize oxygen exchange (Seymour & Bradford, 1995; Wells, 2007). Some pond-breeding northern anurans such as *Rana septentrionalis* in North America attach their egg masses to stems of submerged vegetation, often more than 1 m below the water surface to avoid freezing (Vogt, 1981). This strategy is not adopted by our study species because the stream does not freeze during the breeding season, whereas heat acquisition could be a critical factor limiting development of their embryos.

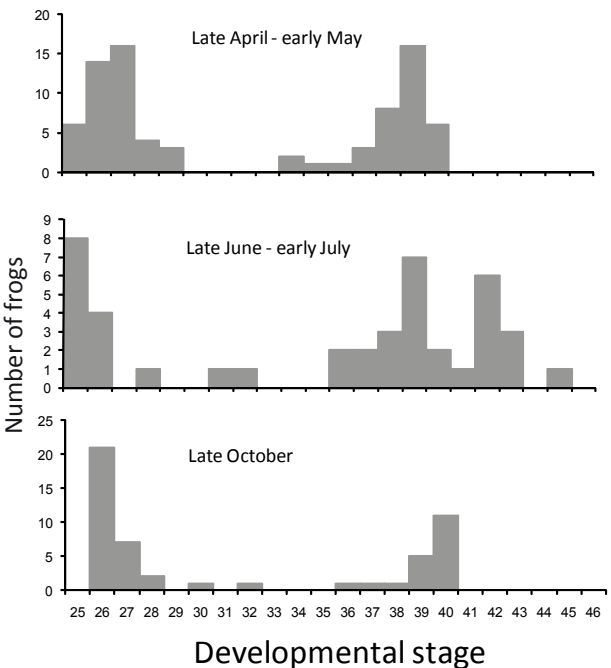


Fig. 4. Distribution of *Feirana taihangnicus* larvae at different developmental stages.

Table 4. Mark–recapture parameters based on Jolly–Seber method during two breeding seasons (23 April to 10 May 2006; 19 April to 15 May 2010). No values are provided for the cases where m_i and/or R_i were zero. For explanations of symbols, see text.

Year	i	n_i	S_i	m_i	R_i	Z_i	M_i	N_i
2006	1	9	9	0	0	–	–	–
	2	18	18	0	4	0	–	–
	3	27	18	1	3	3	19.0	513
	4	33	33	3	4	3	27.8	306
	5	28	26	6	3	1	14.7	69
	6	13	13	4	–	–	–	–
2010	1	7	7	0	0	–	–	–
	2	5	5	0	3	0	–	–
	3	10	9	0	0	3	–	–
	4	17	16	0	1	3	–	–
	5	2	2	0	0	4	–	–
	6	8	6	0	1	4	–	–
	7	17	14	1	0	4	–	–
	8	3	3	0	0	4	–	–
	9	9	9	1	2	3	14.5	131
	10	12	12	1	0	4	–	–
	11	15	15	1	0	3	–	–
	12	2	2	1	0	2	–	–
	13	12	12	2	0	0	–	–
	14	23	0	0	–	–	–	–

Life history

Female *F. taihangnicus* of an average SVL of 75 mm produced around 450 eggs with diameters averaging 3.6 mm. According to Duellman & Trueb’s (1986) list of clutch size and egg size of 41 anuran species with aquatic eggs and larvae, 71% ($n=29$) have a clutch size of more than 450 eggs (1513±2524 eggs, 27–15000 eggs) and only 5% ($n=2$) have eggs with diameters of more than 3.5 mm (1.8±0.8 mm, 0.8–4.0 mm). This suggests that *F. taihangnicus* trade offspring size against offspring number. A similar pattern was observed in *Ascaphus truei*, a stream-breeding frog from North America (Brown, 1990). Large egg size of frogs has an association with montane breeding habitats and stream-breeding habits (Summers et al., 2007). Because larger eggs and larvae have advantages for survival in harsh environments where total investment in annual reproduction is limited (Kaplan & King, 1997), this life history strategy should be adaptive in cold stream conditions. We examined ten museum specimens collected before the oviposition period and found the stomachs of all these frogs were filled with aquatic (Neuroptera) and terrestrial insects (Diptera), suggesting intensive feeding before breeding. However, many temperate anurans start breeding immediately after emergence without

foraging because the energy required for egg production and mating activities has been accumulated before winter (Lu, 2004; Lu et al., 2008; Jackson & Ultsch, 2010; reviewed in Wells, 2007). Therefore, nutritional constraints on reproduction are expected to be large in this stream-dwelling species.

Length of the larval period in anurans varies greatly (145±256 days, 18–1080 days, 5 or 13% of the 38 species more than 270 days; based on data summarized by Duellman & Trueb, 1986). In several stream-dwelling species such as *Ascaphus truei* (Brown, 1990; Wallace & Diller, 1998; Bury & Adams, 1999), *Heleophryne purcelli* and *Amietia fuscigula* (Wagner, 1965), age at metamorphosis ranges from one to four years depending on latitude or elevation. Song & Li (2010) collected *F. quadrana* larvae in the season of hatching and reared them in the laboratory. Only 5% of these larvae achieved metamorphosis by 163–192 days, while the remaining 95% failed to do so by 200 days. Our data for *F. taihangnicus* suggest that it takes 27 months for larvae to finish metamorphosis. Many northern anurans spawning in lentic ponds have tadpoles that overwinter. These tadpoles are usually those that hatch late in the season and their development is delayed by low temperatures (Tattersall & Ultsch, 2008). Unlike these species, the long duration of development experienced by larvae of *Feirana* frogs is an obligate feature of development rather than an outcome of egg deposition late in the breeding season.

Species conservation

Feirana taihangnicus is specialized for life in mountainous streams. Their communal breeding behaviour, strong fidelity to oviposition site and prolonged larval period render the frogs very vulnerable to habitat alteration. In 2007, a tourism development project was conducted in our study area, which affected one regular oviposition site as most of the egg-deposition rocks were moved. Tourists frequently overturn rocks in the stream to search for crabs, which may also lead to adverse effects on the frogs. Our field surveys showed that *F. taihangnicus* were rare outside the nature reserve, most likely as a result of illegal fish-catch using chemicals and extensive fluctuations in water level due to establishment of dams. The current data show some evidence of local, short-term declines in breeding population size, although we do not know whether missing frogs died or have simply missed breeding due to lack of appropriate egg deposition sites in 2010 or some other climate or environmental perturbation. Monitoring of streams across the range of this species is needed to understand long-term threats to its persistence.

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