Zoological Studies **47**(6): 685-696 (2008)

Zoological Studies

Diet and Foraging of *Rana sauteri* and *Bufo bankorensis* Tadpoles in Subtropical Taiwanese Streams

Hong-Chuan Chen[1], Bo-Chi Lai[2], Gary M. Fellers[3], Wei-Lung Wang[1], and Yeong-Choy Kam[2,*]

[1]*Department of Biology, National Changhua University of Education, Changhua 500, Taiwan*
[2]*Department of Life Science, Tunghai University, Taichung 407, Taiwan*
[3]*United States Geological Survey, Western Ecological Research Center, Point Reyes National Seashore, Point Reyes, CA 94956, USA*

(Accepted April 18, 2008)

Hong-Chuan Chen, Bo-Chi Lai, Gary M. Fellers, Wei-Lung Wang, and Yeong-Choy Kam (2008) Diet and foraging of *Rana sauteri* and *Bufo bankorensis* tadpoles in subtropical Taiwanese streams. *Zoological Studies* **47**(6): 685-696. We collected 39 *Rana sauteri* and 18 *Bufo bankorensis* tadpoles from 6 sites at the Lienhuachih Research Center in central Taiwan from Oct. 2001 to Dec. 2002. We compared algae found in the alimentary canal of each species with algae found on tiles placed in the same streams. Algae collected from tiles primarily consisted of diatoms, green algae, and blue-green algae, with diatoms being the dominant taxa at all six of our study sites. Tadpoles of both species consumed mostly diatoms, and the food contents were similar between them. We found high similarities between the algal composition on the tiles and food in the alimentary canals of the tadpoles, suggesting that *R. sauteri* and *B. bankorensis* tadpoles are non-selective with respect to the type of algae they ingest. http://zoolstud.sinica.edu.tw/Journals/47.6/685.pdf

Key words: Algae, Anura, Diet, Tadpoles.

In lotic systems (streams and rivers), benthic algae are the predominant primary producers. Many species graze on freshwater benthic algae, including fish, larval amphibians, mayflies, stoneflies, caddisflies, snails, and midges. Previous studies showed that grazers reduce the biomass, taxonomic composition, physiognomy, and productivity of the freshwater benthic flora (Feminella and Hawkins 1995, Lamberti et al.1995, Steinman 1996). Tadpoles play important roles in these communities. Lamberti et al. (1992) reported that *Ascaphus truei* tadpoles at a density of 5 individuals/m^2 reduced the ash-free dry mass of benthic algae by 98%, and reduced chlorophyll by 82%. Rosenfeld (1997) and Flecker et al. (1999) also demonstrated that *Ascaphus* tadpoles reduced the biomass of benthic algae. Other studies showed that tadpoles feeding on vascular plants indirectly affected plant densities by reducing the number of small invertebrate herbivores (e.g., larval mayflies and caddisflies), and altered phytoplankton communities as a result of interference competition with other species of tadpoles (Ashkenas et al. 1992 1995, Lamberti et al. 1992, Kupferberg 1997a, Rosenfeld 1997, Kiffney and Richardson 2001).

In spite of the importance of tadpoles in lotic systems, there are few studies of the diet and foraging behaviors of tadpoles (Alford 1999). Larval anurans consume vascular plant and animal tissues, algae, cyanobacteria, dissolved organic matter, protozoa, and pollen (Kupferberg 1997b). Earlier studies showed that the type of food consumed has a significant effect on development, growth, and metamorphosis of anuran larvae (Steinwachser and Travis 1983, Ahlgren and Bowen 1991, Kupferberg et al. 1994, Britson and Kissell 1996). It might be advantageous for tadpoles to

---

*To whom correspondence and reprint requests should be addressed. Tel: 886-4-23550609. Fax: 886-4-23550609. E-mail:biyckam@thu.edu.tw select specific types of food; however, past studies showed varied results. Five species of tadpoles exhibited no selectivity in foraging behavior (*Pseudacris* (= *Hyla*) *crucifer*, *Bufo americanus*, *B. woodhousii fowleri*, *Rana catesbeiana*, and *R. sylvatica*; Seale and Beckvar, 1980), whereas *Acris crepitans* did show preferences (Johnson 1991). *Pseudacris regilla* tadpoles changed their usual non-selective foraging behavior and consumed disproportionately more pollen when it appeared in their ponds (Wagner 1986). Kupferberg (1997b) suggested that the foraging behavior of *P. regilla* tadpoles in a river system was probably selective. Tadpoles that live in lotic habitats may need to spend time searching for benthic algae because the distribution of algae is usually patchy, and algal species compositions vary among patches.

Most researches have been conducted on

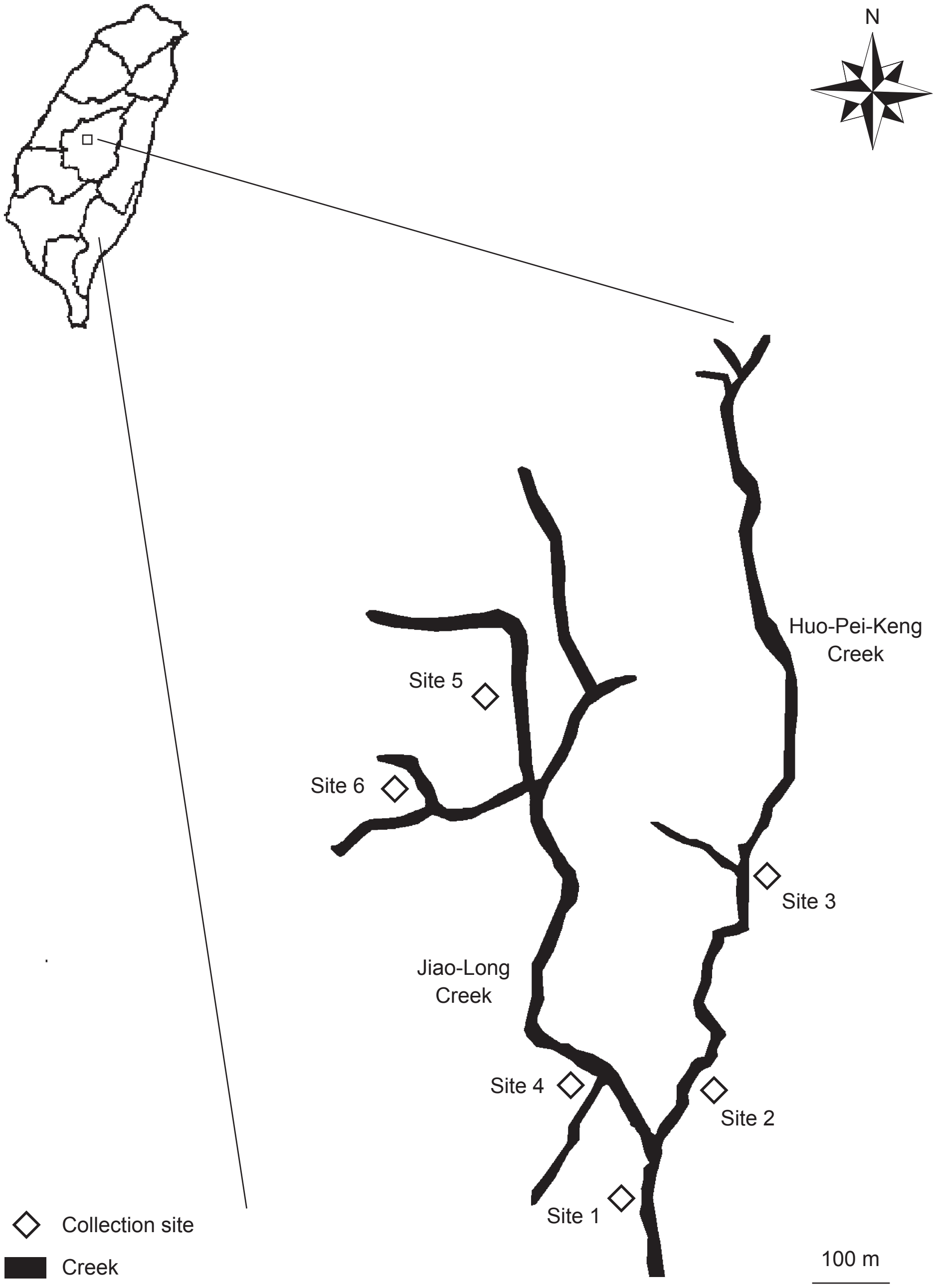

Fig. 1. Map of the stream system at Leinhuachih, Taiwan and the locations of the collection sites.

temperate zone tadpoles; there has been little research on subtropical and tropical species. We investigated algae consumed by *Rana sauteri* (Ranidae) and *Bufo bankorensis* (Bufonidae) tadpoles in a subtropical stream in Taiwan. Specifically, we hypothesized that tadpoles of both species are non-selective algal feeders and predicted that the compositions of algae found in the alimentary canals of these 2 species would be similar to those found on tiles placed in streams where the tadpoles were collected.

MATERIALS AND METHODS

Field methods

We conducted our studies from Oct. 2001 to Dec. 2002 at the Lienhuachih Biological Station (23°55'N, 120°52'E) of the Taiwan Forestry Research Institute Experimental Forest, Nantou County, central Taiwan. The station encompasses a 461-ha watershed. The area where we worked was covered by undisturbed lowland primary forest, characterized by low topography with elevations ranging 576-975 m. The mean annual air temperature was 21.1°C, and ranged from 9.9°C in Jan. to 30.0°C in July. The area receives approximately 2200 mm of rain annually. Although it rains in all months, the wet season is from May through Oct.

We collected 3 *R. sauteri* and *B. bankorensis* tadpoles each, if possible, from each of the 6 sites distributed in the upstream (sites 5 and 6), midstream (site 3), and downstream (sites 1, 2, and 4) portions of 2 main tributaries (Fig. 1). These sites were never dry, but sites 5 and 6 had little water during the dry season. The stream bank and bottom consisted of sand, gravel, boulders, and bedrock. Tadpole species identification was mainly based on the external morphology, body coloration, and mouth part morphology (Chou and Lin 1997). Dominant vegetation along the stream was *Ageratum houstonianum*, *Alocasia macrorrhiza*, *Bambusa stenostachya*, *Bidens pilosa*, *Crassocephalum rabens*, *Dendrocalamus latiflorus*, *Hedychium coronarium*, *Impatiens balsam*, *Mallotus japonicus*, *Miscanthus floridulus*, *Solanum nigrum*, and *Sphaeropteris lepifera*.

At each site, we put 8 unglazed clay tiles (23.4 × 14.3 × 1.8 cm thick) in the bottom of the stream each month. After 4 wk, the tiles were retrieved to collect algae that had attached to them. We collected algae from tiles instead of natural substrates because artificial substrates are a good substitute for natural substrates, and also because tiles reduce variability during sampling (Lamberti and Resh 1985). Site 6 had the least amount of water since local people build dams to block sand from drifting downstream. This meant that the tiles at this site were occasionally dry and sometimes covered with sand.

Laboratory methods

We scraped the upper surface of each tile to collect the algae. The scrapings were flushed with 100 ml water and subsampled (0.02 ml water), and a minimum of 250 units were counted at 400x magnification. One unit was equivalent to a cell for colonial and unicellular algae. For filamentous algae with very large cells or cells without obvious cell walls or coenocytic filaments, a 10 μm length of filament was defined as equivalent to 1 unit (Holomuzki 1998). Algae were identified to species or genus using standard references (Prescott 1962, Patrick and Reimer 1975, Yamagishi and Akiyana 1978-1998, Yamagishi 1992, Hartley et al. 1996).

Tadpoles were preserved in 70% alcohol after collection. For each tadpole, we measured body weight, length, and developmental stage; we then removed and opened the alimentary canal, and flushed the canal with 10 ml water. Identification of the developmental stage of tadpoles was based on the limb, mouth, and tail morphology (Gosner 1960). We then counted and identified the algae as described above for the tile samples. Other potential food sources such as macroinvertebrates and leaf detritus were recorded, if present.

Data analyses

For both the tadpole and tile samples, cells counts for each attached algal taxon (units or cells/cm^2) were converted to relative abundances (Holomuzki 1998). Relative abundance was used to calculate Stander's index of similarity (Johnson and Millie 1982) using NTSYS (vers. 1.70; Exeter Software, NY, USA). The index ranges from 0 to 1, with 0 indicating that 2 communities have no species in common, and 1 indicating that they are identical in both species composition and relative abundance. Statistical significance was evaluated using SAS (SAS Institute Inc. 1996) and $\alpha = 0.05$.

RESULTS

Rana sauteri and *B. bankorensis* tadpoles were found only from Oct. to Dec. (Table 1). We collected a total of 39 *R. sauteri* tadpoles (at Gosner stages 25-37; Table 1); tadpoles were present at sites 2, 3, and 5 during each of these months, and at site 4 during Oct. and Nov. On the other hand, we collected a total of 18 *B. bankorensis* tadpoles (at Gosner stages 27-36; Table 1); tadpoles were present every month at site 4, but only once at sites 1 and 5 (Oct.) and site 3 (Nov.).

Algal community on the tiles

We found 85 species of algae on the tiles at the 6 study sites. These included green algae (32 species in 18 genera), diatoms (49 species in 20 genera), and blue-green algae (4 species in 4 genera) (Appendix 1). We identified 75, 62, 67, 69, 65, and 49 algal species from sites 1-6, respectively. Diatoms comprised more than 85% of total species at all sites except site 5 (Figs. 2, 3). At site 5, green algae, diatoms, and blue-green algae each comprised about 1/3 of the total (Figs. 2, 3). The most dominant algae were *Achnanthidium minutissimun* (Chromophyta: Bacillariophyceae) at sites 1, 2, 3, and 4; *Aphanocapsa elachista* (Cyanophyta: Cyanophyceae) at site 5; and *Navicula cryptocephala* (Chromophyta: Bacillariophyceae) at site 6 (Table 2).

Tadpole diet

The alimentary canals of *R. sauteri* and *B. bankorensis* tadpoles contained algae but no macroinvertebrates or leaf detritus. There were 67 species of algae found in the alimentary canals of *R. sauteri* tadpoles. These included 26 species in 14 genera of green algae (Chlorophyta: Chlorophyceae), 37 species in 17 genera of diatoms (Chromophyta: Bacillariophyceae), and 4 species in 4 genera of blue-green algae (Cyanophyta: Cyanophyceae). Diatoms were the dominant group (Table 2; Fig. 2). By comparison, 54 species of algae were found in the alimentary canals of *B. bankorensis* tadpoles, including 18 species in 12 genera of green algae (Chlorophyta: Chlorophyceae), 32 species in 16 genera of diatoms (Chromophyta: Bacillariophyceae), and 4 species in 4 genera of blue-green algae (Cyanophyta: Cyanophyceae). Similar to *R. sauteri*, diatoms were the dominant algae (Table 3; Fig. 3).

In *R. sauteri*, the number of algal cells in the alimentary canals was significantly correlated with the body mass ($r = 0.70$, $p < 0.0001$, $n = 39$) and body length ($r = 0.67$, $p < 0.0001$, $n = 39$). For *B. bankorensis* tadpoles, significant correlations were also found between the number of algal cells and both body mass ($r = 0.54$, $p = 0.019$, $n = 18$) and body length ($r = 0.63$, $p = 0.005$, $n = 18$). The number of algal cells per unit of body weight (mg) was 4299 ± 1083 cells/mg ($n = 39$) in *R.*

Table 1. Number of *Rana sauteri* and *Bufo bankorensis* tadpoles collected at each study site during Oct., Nov., and Dec. 2001

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Oct.						
Rana sauteri	3	3	3	3	3	3
Bufo bankorensis	3	-	-	3	3	-
Nov.						
Rana sauteri	-	3	3	3	3	-
Bufo bankorensis	-	-	3	3	-	-
Dec.						
Rana sauteri	-	3	3	-	3	-
Bufo bankorensis	-	-	-	3	-	-
Totals	6	9	12	15	12	3

sauteri tadpoles, and 10,098 ± 3575 cells/mg in *B. bankorensis* tadpoles ($n = 18$).

Tadpole and tile comparisons

The dominant algae on the tiles were *Achnanthes*, *Achnanthidium*, *Navicula*, *Rossithidium*, and *Synedraa*, which were also the dominant genera in the diets of both *R. sauteri* and *B. bankorensis*. Average values of Stander's index of similarity for algal compositions between tadpoles and tiles were 0.85 ± 0.12 ($n = 13$) for *R. sauteri* and 0.86 ± 0.10 ($n = 6$) for *B. bankorensis* (Table 4).

Table 2. Dominant species of algae in the alimentary canals of *Rana sauteri* tadpoles and on tiles at 6 study sites from Oct. to Dec. 2001. Sites 1 and 6 have samples only from Oct., whereas site 4 has samples from Oct. to Nov.

	Tadpoles		Tiles	
Site(Month)	Dominant species	(%)	Dominant species	(%)
1(Oct.)	*Achnanthidium minutissimun*[d]	22.6	*Achnanthidium minutissimun*[d]	25.0
	Navicula cryptocephala[d]	14.1	*Navicula cryptocephala*[d]	15.3
	Rossithidium linearis[d]	22.0	*Rossithidium linearis*[d]	18.9
	Synedra ulna[d]	7.1	*Synedra ulna*[d]	5.2
2(Oct.-Dec.)	*Rossithidium linearis*[d]	33.2	*Achnanthidium minutissimun*[d]	33.0
	Achnanthidium minutissimun[d]	23.8	*Rossithidium linearis*[d]	32.6
	Navicula cryptocephala[d]	7.1	*Achnanthes deflexa*[d]	11.7
	Synedra ulna[d]	6.5	*Achnanthes nollii*[d]	4.7
	Encyonema lacustre[d]	5.1		
3(Oct.-Dec.)	*Navicula cryptocephala*[d]	18.9	*Achnanthidium minutissimun*[d]	45.9
	Achnanthidium minutissimun[d]	16.5	*Rossithidium linearis*[d]	17.9
	Rossithidium linearis[d]	11.7	*Achnanthes nollii*[d]	7.3
	Oscillatoria sp.[bg]	6.5	*Navicula cryptocephala*[d]	6.7
	Synedra ulna[d]	6.2		
	Cymbella turgidula[d]	5.8		
	Nitzschia sinuata var. *tabellaria*[d]	5.2		
4(Oct.-Nov.)	*Achnanthidium minutissimun*[d]	30.5	*Achnanthidium minutissimun*[d]	62.9
	Navicula cryptocephala[d]	10.6	*Rossithidium linearis*[d]	8.3
	Synedra ulna[d]	7.6	*Navicula cryptocephala*[d]	4.3
	Rossithidium linearis[d]	7.3	*Achnanthes nollii*[d]	3.4
	Encyonema wallaceana[d]	6.2		
	Zygnema sp.[g]	6.0		
5(Oct.-Dec.)	*Oocystis lacustis*[bg]	19.5	*Aphanocapsa elachista*[bg]	25.1
	Aphanocapsa elachista[bg]	17.1	*Achnanthidium minutissimun*[d]	18.5
	Navicula cryptocephala[d]	12.0	*Oocystis lacustis*[g]	17.0
	Achnanthidium minutissimun[d]	11.2	*Navicula cryptocephala*[d]	10.4
	Oscillatoria sp.[bg]	8.2	*Staurastrum manfeldtii*[g]	5.2
	Staurastrum manfeldtii[g]	6.3		
6(Oct.)	*Navicula cryptocephala*[d]	62.1	*Navicula cryptocephala*[d]	18.9
	Navicula radiosa[d]	8.7	*Achnanthidium minutissimun*[d]	18.6
	Achnanthidium minutissimun[d]	5.9	*Eunotia vanheurckii*[d]	13.9
	Encyonema wallaceana[d]	4.3	*Encyonema wallaceana*[d]	13.0
	Eunotia vanheurckii[d]	2.8	*Rossithidium linearis*[d]	7.3
	Surirella angusta[d]	2.8	*Surirella angusta*[d]	6.1

[d], diatom; [g], green-alga; [bg], blue-green alga.

During our study, we were able to collect both *R. sauteri* and *B. bankorensis* tadpoles from the same site at the same time on 5 occasions (Table 1). The algal compositions in the alimentary canals of these tadpoles were highly similar (values of Stander's index of similarity were 0.93, 0.98, 0.97, 0.98, and 0.90, with an average of 0.95 ± 0.03).

DISCUSSION

We were able to collect *R. sauteri* and *B. bankorensis* tadpoles only from Oct. to Dec. at Lienhuachih probably because these species are fall breeders, and tadpoles are present only during fall and early winter (Hsu et al. 2006). Our results showed that both *R. sauteri* and *B. bankorensis* tadpoles fed predominantly on diatoms (Chromophyta: Bacillariophyceae). This is similar to what has been reported for tadpoles in temperate areas. Holomuzki (1997) found that algae in the alimentary canals of stream-dwelling *Bufo americanus* (Bufonidae) tadpoles in the US were mostly diatoms, with only small amounts of green and blue-green algae. The dominant diatoms were *Achnanthes* (> 65%) with the most dominant species being *A. minutissima*. Peterson and Boulton (1999) examined the excrement of *Limnodynastes tasmaniensis* (Leptodactylidae) tadpoles in Australian streams and found that diatoms were the most commonly eaten type of

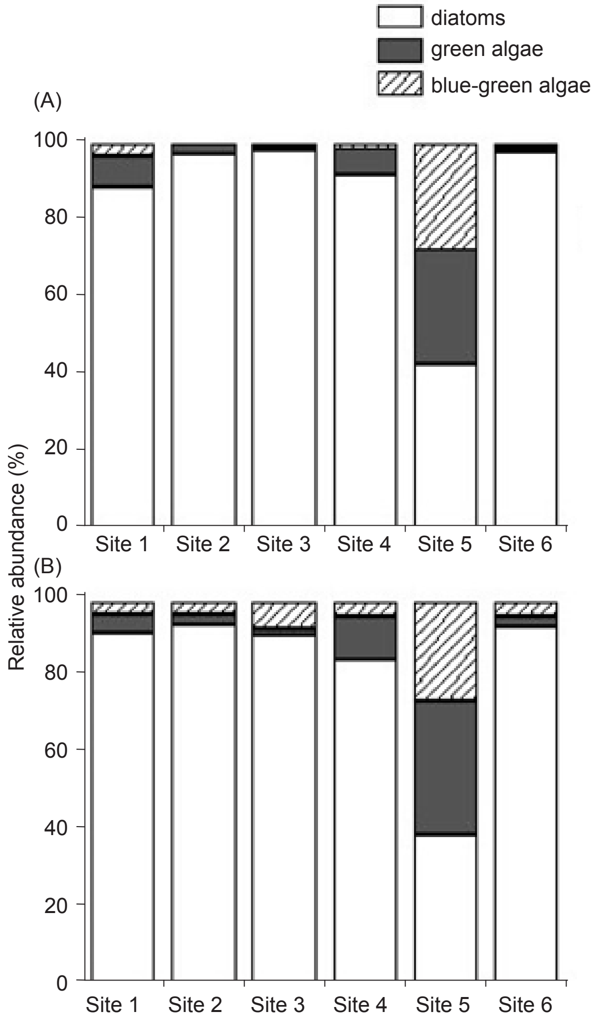

Fig. 2. Relative abundances of 3 types of algae collected from (A) tiles placed in the stream and (B) the alimentary canals of *Rana sauteri* tadpoles.

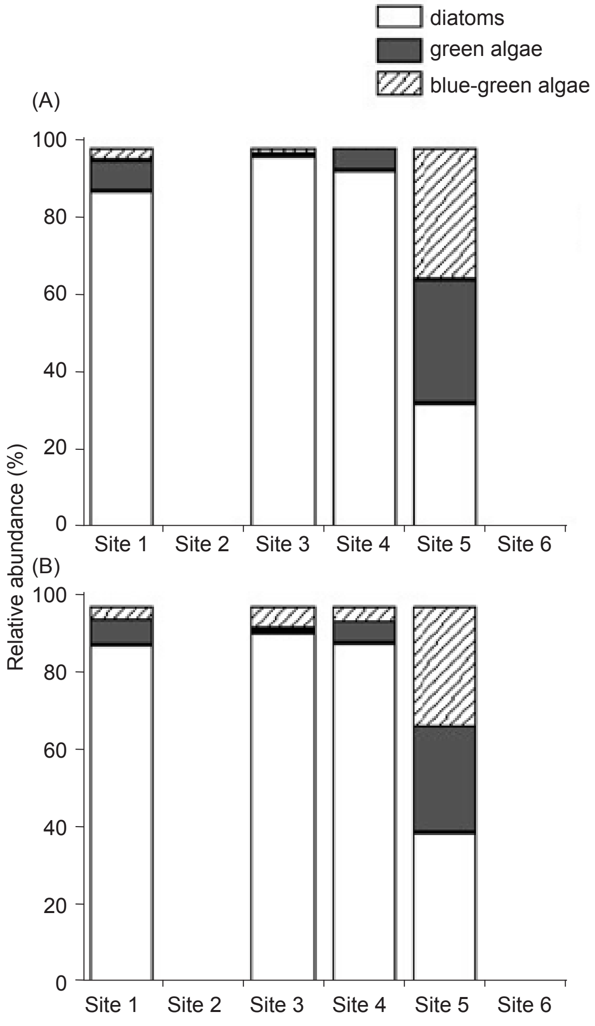

Fig. 3. Relative abundances of 3 types of algae collected from (A) tiles placed in the stream and (B) the alimentary canals of *Bufo bankorensis* tadpoles.

food. The similarity in tadpole diets in subtropical and temperature streams may be because 1) algae are the predominant primary producers in streams, regardless of region, 2) diatoms are typically the dominant algal group (Shortreed and Stockner 1983, Stevenson 1996, Lam and Lei 1999), or 3) diatoms contain more calories (in the form of fat and protein) than other algae and hence they are a preferred food (Kupferberg 1997b).

In contrast, the food sources for tadpoles in lentic habitats are more diverse, typically including Euglenophyta, Pyrrophyta, Cryptophyta, and Chromophyta (Diaz-Paniagua 1989, Johnson 1991, Bradsley and Beebee 1998, Eterovick 2000). The proportion of algae consumed varies among tadpole species; some feed primarily on diatoms (*B. americanus* in the US; Holomuzki 1997, *Acris crepitans* in the US; Johnson 1991, *B. crucifer* in Brazil; Eterovick 2000), while others fed on green algae (*Pelodytes punctatus* in Spain; Diaz-Paniagua 1989) or a mixture of diatoms and green algae (*B. bufo* and *B. calamita* in the UK; Bradsley and Beebee 1998). These differences might reflect the fact that lentic tadpoles not only graze on the substrate, but also filter algae suspended in the water column (Hoff et al. 1999). McCann and Test (1976) observed that *B. americanus* tadpoles shifted feeding mode from grazing to filtering as suspended algae increased. Other lentic tadpoles may also shift their mode of feeding depending on food availability and the distribution of food within a habitat, resulting in variations in tadpole diets.

Bufo bankorensis tadpoles contained twice the amount of algae than did *R. sauteri* per unit body mass, suggesting that the alimentary canals of *B. bankorensis* are longer, larger, or both. Amphibian larvae devote most of their energy to growth and development so they can metamorphose as quickly as possible (Wilbur 1980). Studies of herbivorous tadpoles have shown that the time food takes to pass through the alimentary canal (i.e., the clearance time) is relatively short, at only 1-6 h (Savage 1962, Costa and Balasubramanian 1965, Altig and McDearman

Table 3. Dominant species of algae in the alimentary canals of *Bufo bankorensis* tadpoles and on tiles at 6 study sites from Oct. to Dec. 2001. Sites 1 and 5 had samples only from Oct., whereas site 3 had samples only from Nov.

	Tadpoles		Tiles	
Site(Mo)	Dominant species	(%)	Dominant species	(%)
1(Oct.)	*Navicula cryptocephala*[d]	20.5	*Achnanthidium minutissimun*[d]	25.0
	Achnanthidium minutissimun[d]	17.5	*Rossithidium linearis*[d]	18.9
	Synedra ulna[d]	9.8	*Navicula cryptocephala*[d]	15.3
	Rossithidium linearis[d]	8.9	*Synedra ulna*[d]	5.2
	Encyonema wallaceana[d]	4.5		
3(Nov.)	*Navicula cryptocephala*[d]	16.8	*Achnanthidium minutissimun*[d]	44.9
	Rossithidium linearis[d]	20.0	*Rossithidium linearis*[d]	17.6
	Achnanthidium minutissimun[d]	13.2	*Achnanthes nollii*[d]	9.8
	Encyonema lacustre[d]	8.6	*Navicula cryptocephala*[d]	7.1
	Nitzschia sinuata var. *tabellaria*[d]	7.3		
4(Oct.-Dec.)	*Achnanthidium minutissimun*[d]	31.3	*Achnanthidium minutissimun*[d]	66.3
	Navicula cryptocephala[d]	14.6	*Rossithidium linearis*[d]	8.1
	Rossithidium linearis[d]	11.2	*Navicula cryptocephala*[d]	3.9
	Synedra ulna[d]	6.5	*Achnanthes nollii*[d]	3.2
5(Oct.)	*Oocystis lacustis*[g]	23.5	*Aphanocapsa elachista*[bg]	31.1
	Aphanocapsa elachista[bg]	20.9	*Oocystis lacustis*[g]	28.3
	Navicula cryptocephala[d]	16.5	*Achnanthidium minutissimun*[d]	13.0
	Oscillatoria sp.[bg]	9.8	*Navicula cryptocephala*[d]	8.4
	Achnanthidium minutissimun[d]	8.7	*Navicula radiosa*[d]	3.0

[d], diatom; [g], green-alga; [bg], blue-green alga.

1975). Diaz-Paniagua (1989) suggested that long alimentary canals not only contain more food, but also retain food longer which facilitates digestion and absorption. At our study site, both *B. bankorensis* and *R. sauteri* bred around mid-Sept. and tadpoles were abundant beginning in Oct. However, we began to encounter *B. bankorensis* froglets along the stream banks around Nov., prior to the metamorphosis of *R. sauteri*, suggesting that *B. bankorensis* tadpoles develop faster. Determining whether the difference in development rates is related to the length and/or size of the alimentary canals requires further study.

Algal compositions on the tiles were similar to algal compositions in the alimentary canals of both *R. sauteri* and *B. bankorensis*, suggesting that tadpoles were not selecting specific algal species. Seale and Beckvar (1980) compared the ability of *H. crucifer*, *B. americanus*, *B. woodhousei fowleri*, *R. catesbeiana*, and *R. sylvatica* tadpoles to ingest suspended blue-green algae. They found that these 5 anurans were not selectively feeding, and suggested that it was not possible to do so on small suspended algae. Wagner (1986) described how *P. regilla* tadpoles behaviorally select pollen by ingesting pollen grains at the water surface. Kupferberg (1997b) found that tadpoles in a coastal California river were selectively feeding. This contrasts with our findings, but the benthic algae in her study area were patchily distributed, unlike the more-even distribution of species found at our study sites in Taiwan.

We found that algae growing on tiles closely reflected those in tadpole diets. This was especially notable at site 5 where the proportion of diatoms on the tiles was much less than those at the other 5 sites, and that difference was mirrored in the diets of both *R. sauteri* and *B. bankorensis*. This emphasizes that both of these tadpole species are non-selective algal feeders. We believe that algae in lotic habitats are too small for *R. sauteri* and *B. bankorensis* tadpoles to discriminate while foraging. In addition, the majority of the algae consumed by *R. sauteri* and *B. bankorensis* tadpoles are attached algae, either benthic, epilithic, epipelic, or epiphytic. When tadpoles forage on the substrate in streams, they need to keep from being swept away by currents; this would add to the difficulty of trying to discriminate species and perhaps would make it more likely that they eat whatever they encounter.

Table 4. Stander's index of similarity between algae found in the alimentary canals of *Rana sauteri* and *Bufo bankorensis* tadpoles and on tiles placed in the stream from 6 collection sites visited in Oct. to Dec. 2001

		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Oct.	*R. sauteri*	0.99	0.93	0.86	0.90	0.94	0.66
	B. bankorensis	0.94	-	-	0.89	0.92	-
Nov.	*R. sauteri*	-	0.93	0.73	0.88	0.92	-
	B. bankorensis	-	-	0.69	0.80		-
Dec.	*R. sauteri*		0.90	0.59	-	0.89	-
	B. bankorensis	-	-	-	0.90	-	-

Even though tadpole diets closely matched the composition on the tiles, there were 4 cases where the similarity of the algal compositions was < 0.8. It is possible that grazing tadpoles changed the composition of the algal community, perhaps by altering the competitive advantage of different algal species (Feminella and Hawkins 1995, Steinman 1996). Kiffney and Richardson (2001) also suggested that higher densities of *Ascaphus truei* tadpoles would reduce the biomass of benthic algae; this might lead to differences between algal compositions on the substrate and in tadpole diets.

Acknowledgments: This study was supported by National Science Council grants (NSC90-2621-B-018-002-A10 and NSC91-2311-B-029-008) to Y.C. Kam. We thank the staff of the Taiwan Forestry Research Institute at the Lienhuachih field station for providing accommodations and permitting us to work at the station. Joan Fellers provided useful comments on the manuscript.

REFERENCES

Ahlgren MO, SH Bowen. 1991. Growth and survival of tadpoles (*Bufo americanus*) fed amorphous detritus derived from natural waters. Hydrobiologia **218:** 49-51.

Alford RA. 1999. Ecology: resource use, competition, and predation. *In* RW McDiarmid, R Altig, eds. Tadpoles: the biology of anuran larvae. Chicago, IL: Univ. of Chicago Press, pp. 240-279.

Altig R, W McDearman. 1975. Percent assimilation and clearance times of five anuran tadpoles. Herpetologica **31:** 67-69.

Ashkenas LR, DM Denicola, SV Gregory, CP Hawkins, GA Lamberti, RC Wildman. 1992. Plant-herbivore interactions in streams near Mount St. Helens. Freshwater Biol. **27:** 237-247.

Ashkenas LR, SV Gregory, GA Lamberti, JL Li, AD Steinman, CD McIntire. 1995. Influence of grazer type and abundance on plant-herbivore interactions in streams. Hydrobiologia **306:** 179-188.

Bradsley L, TJC Beebee. 1998. Interspecific competition between *Bufo* larvae under condition of community transition. Ecology **79:** 1751-1759.

Britson CA, RE Kissell Jr. 1996. Effects of food type on developmental characteristics of an ephemeral pond-breeding anuran, *Pseudacris Triseriata feriarum*. Herpetologica **52:** 374-382.

Chou WH, JY Lin. 1997. Tadpoles of Taiwan. Taichung, Taiwan: National Museum of Natural Science, Special Publication **no. 7**.

Costa HH, S Balasubramanian. 1965. The food of the tadpoles of *Rhacophorus cruciger* (Blyth). Ceylon J. Sci. **5:** 105-109.

Diaz-Paniagua C. 1989. Larval diets of two anuran species, *Pelodytes punctatus* and *Bufo bufo*, in SW Spain. Amphibia-Reptilia **10:** 71-75.

Eterovick PC. 2000. Effect of aggregation on feeding of *Bufo crucifer* tadpoles (Anura, Bufonidae). Copeia **2000:** 210-215.

Feminella JW, CP Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. J. North Am. Benthol. Soc. **14:** 465-509.

Flecker AS, BP Ferfared, BW Taylor. 1999. Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. Copeia **1999:** 495-500.

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

Hartley B, HG Barber, Carter JR., PA Sims. 1996. An atlas of British diatoms. Bristol, UK: Biopress.

Hoff KvS, AR Blaustein, RW McDiarmid, R Altig. 1999. Behavior: Interactions and their consequences. *In* RW McDiarmid, R Altig, eds. Tadpoles: the biology of anuran larvae. Chicago, IL: Univ. of Chicago Press, pp. 215-240.

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

Holomuzki JR. 1998. Grazing effects by green frog tadpoles (*Rana clamitans*) in a woodland pond. J. Freshwater Ecol. **13:** 1-8.

Hsu MY, YC Kam, GM Fellers. 2005. Temporal organization of an anuran acoustic community in a Taiwanese subtropical forest. J. Zool. **269:** 331-339.

Johnson BE, DF Millie. 1982. The estimation and applicability of confidence intervals of Stander's similarity index (SIMI) in algae assemblage comparisons. Hydrobiologia **89:** 3-8.

Johnson LM. 1991. Growth and development of larval northern cricket frogs (*Acris crepitans*) in relation to phytoplankton abundance. Freshwater Biol. **25:** 51-59.

Kiffney PM, JS Richardson. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. Copeia **2001:** 422-429.

Kupferberg SJ. 1997a. Facilitation of periphyton production by tadpole grazing: functional differences between species. Freshwater Biol. **37:** 427-439.

Kupferberg SJ. 1997b. The role of larval diet in anuran metamorphosis. Am. Zool. **37:** 146-159.

Kupferberg SJ, JC Marks, ME Power. 1994. Effect of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life-history traits. Copeia **1994:** 446-457.

Lam PK, A Lei. 1999. Colonization of periphytic algae on artificial substrates in a tropical stream. Diatom Res. **14:** 307-322.

Lamberti GA, SV Gregory, LR Ashkenas, JL Li, AD Steinman, CD McIntire. 1995. Influence of grazer type and abundance on plant-herbivore interactions in streams. Hydrobiologia **306:** 179-188.

Lamberti GA, SV Gregory, CP Hawkins, RC Wildman, LR Ashkenas, DM Denicola. 1992. Plant-herbivore interactions in streams near Mount St Helens. Freshwater Biol. **27:** 237-247.

Lamberti GA, V Resh. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae, and macro invertebrates. Freshwater Biol. **15:** 21-30.

McCann RG, FH Test. 1976. Foraging behavior of *Bufo americanus* tadpoles in response to high densities of micro-organisms. Copeia **1976:** 576-578.

Patrick R, CW Reimer. 1975. The diatoms of the United States, exclusive of Alaska and Hawaii. Vol. 2. Lititz, PA: Sutter House Lititz.

Peterson DG, AJ Boulton. 1999. Stream permanence influences microalgal food availability to grazing tadpoles in arid-zone springs. Oecologia **118:** 340-352.

Prescott GW. 1962. Algae of the western Great Lakes area. Dubuque, IA: Brown Company Publisher.

Rosenfeld JS. 1997. The effect of large macroinvertebrate herbivores on sessile epibenthos in a mountain stream. Hydrobiologia **344:** 75-79.

SAS. 1996. SAS/STAT User's Guide. Gary, NC: SAS Inst. Inc.

Savage RM. 1962. The ecology and life history of the common frog (*Rana temporaria temporaria*). New York: Hafner Publ. Co.

Seale B, ND Beckvar. 1980. The comparative ability of anuran larvae (genera: *Hyla*, *Bufo*, and *Rana*) to ingest suspended blue-green algae. Copeia **1980:** 495-503.

Shortreed KRS, JG Storckner. 1983. Periphyton biomass and spices composition in British Columbia: effects of environment changes caused by logging. Can. J. Fish. Aquat. Sci. **40:** 1887-1895.

Steinman AD. 1996. Effects of grazers on freshwater benthic algae. *In* RJ Stevenson, ML Bothwell, RL Lowe, eds. Algal ecology: freshwater benthic ecosystems. New York: Academic Press, pp. 341-373.

Steinwascher K, J Travis. 1983. Influence of food quality and quantity on early larval growth of two anurans. Copeia **1983:** 238-242.

Stevenson RJ, ML Bothwell, RL Lowe. 1996. Algal ecology: freshwater benthic ecosystems. New York: Academic Press.

Wagner WE Jr. 1986. Tadpoles and pollen: observations on the feeding behavior of *Hyla regilla* larvae. Copeia **1986:** 802-804.

Wilbur HM. 1980. Complex life cycles. Ann. Rev. Ecol. Syst. **11:** 67-93.

Yamagishi T. 1992. Plankton algae in Taiwan (Formosa). Tokyo: Uchida Rokakuho.

Yamagishi T, M Akiyana. 1978-1998. Photomicrographs of the freshwater algae. Vol. 1-20. Tokyo: Uchida Rokakuho.

APPENDIX 1. Benthic algae collected from tiles placed in a stream and from the alimentary canals of *Rana sauteri* and *Bufo bankorensis* at Lienhuachih, Taiwan. Superscripts on the scientific names represent the ecological habits of algae (1, planktonic; 2, attached algae)

Classification	Site						*R. sauteri*	*B. bankorensis*
	1	2	3	4	5	6		
Chlorophyta								
Chlorophyceae								
Chlorococcales								
Chlorellaceae								
Tetraedon caudatum^1			x					
Tetraedon minimum^1	x	x	x	x	x		x	x
Kirchneriella contorta var. *gracillima*^{1}	x				x		x	
Oocystaceae								
Ankistrodesmus falcatus var. *mirabilis*^{1}	x	x	x	x	x	x	x	x
Oocystis lacustris^1	x	x	x	x	x		x	x
Oocystis sp.^{1}	x	x	x	x	x	x	x	x
Hydrodictyaceae								
Pediastrum duplex^1	x						x	
Pediastrum obtusum^1							x	
Pediastrum tetras^1	x		x	x	x		x	x
Scenedesmaceae								
Scenedesmus actiformis^1	x		x	x	x		x	x
Scenedesmus acuminatus^1	x	x	x	x				x
Scenedesmus quadricuda^1	x	x	x	x	x	x	x	x
Scenedesmus spinoso-aculeolatus^1	x	x	x	x	x		x	
Scenedesmus spinosus^1	x	x	x	x	x		x	x
Coelastraceae								
Coelastrum cambricum^1	x	x	x	x	x	x	x	x
Coelastrum reticulatum^1	x	x		x	x			
Ulotrichales								
Ulotrichinae								
Ulotrichaceae								
Geminella sp.^{1}	x	x	x	x		x	x	x
Microsporaceae								
Microspora sp.^{2}	x	x	x	x				
Chaetophoraceae								
Stigeoclonium sp.^{2}	x	x	x	x	x	x	x	x
Zygnematales								
Zygnemataceae								
Mougeotia sp.^{2}	x	x	x	x	x	x		
Spirogyra sp.^{2}	x	x	x	x		x	x	x
Zygnema sp.^{2}	x	x	x	x	x	x	x	x
Desmidiales								
Desmidiaceae								
Closterium ehrenbergii^1			x		x	x	x	x
Closterium sp.^{1}	x			x			x	x
Tetmemorus sp.^{1}					x			
Staurastrum manfeldtii^1	x			x	x		x	
Staurastrum tetracerum^1	x	x	x				x	
Euastrum ansatum var. *pyxidatum*^{1}					x			
Euastrum sp.^{1}					x			
Cosmarium laeve^1	x	x		x	x		x	
Cosmarium meneghinii^1	x	x	x	x	x	x	x	x
Cosmarium pachydermun^1	x			x	x		x	

APPENDIX 1. (Cont.)

Classification	Site						*R. sauteri*	*B. bankorensis*
	1	2	3	4	5	6		
Cosmarium sportella[1]	x	x	x	x	x	x	x	x
Cosmarium sp.[1]							x	
Chromophyta								
Bacillariophyceae								
Centrales								
Cocinodiscineae								
Melosiraceae								
Aulacoseria varians[1]	x	x	x	x		x	x	x
Pennales								
Araphidineae								
Fragilariaceae								
Fragilaria construens[2]	x			x	x		x	x
Synedra rumpens[2]	x	x	x	x		x		
Synedra rumpens var. *familiaris*[2]					x			
Synedra ulna[2]	x	x	x	x	x	x	x	x
Eunotiaceae								
Eunotia curvata[2]	x		x	x	x	x	x	x
Eunotia perminuta[2]					x			
Eunotia vanheurckii[2]	x	x	x	x	x	x	x	x
Biraphidineae								
Naviculaceae								
Caloneis alpestris[2]	x	x	x	x	x	x	x	
Gyrosigma sp.[2]			x		x		x	
Navicula capitatoradiata[2]	x	x	x	x	x	x	x	x
Navicula cryptocephala[2]	x	x	x	x	x	x	x	x
Navicula menisculus[2]	x	x	x	x	x		x	x
Navicula radiosa[2]	x	x	x	x	x	x	x	x
Pinnularia mesolepta[2]	x	x	x	x	x	x	x	x
Stauroneis smithii[2]	x		x			x		x
Cymbellaceae								
Cymbella cymbiformis[2]	x	x	x	x	x	x	x	x
Cymbella pusilla[2]	x	x						
Cymbella tumida[2]	x	x	x	x	x		x	x
Cymbella turgidula[2]	x	x	x	x	x	x	x	x
Encyonema lacustre[2]	x	x	x	x	x	x	x	x
Encyonema minutum[2]	x	x	x	x	x		x	x
Encyonema silesiacum[2]	x	x	x	x	x	x	x	x
Encyonema wallaceana[2]	x	x	x	x	x	x	x	x
Gomphonema affine[2]	x	x	x	x	x	x	x	x
Gomphonema angustatum[2]	x	x	x	x	x	x	x	x
Gomphonema globiferum[2]					x		x	
Gomphonema gracile[2]	x	x	x	x	x	x		
Gomphonema parvalum var. *subelliptica*[2]	x	x	x	x	x			
Gomphonema parvulum[2]	x	x	x	x	x	x	x	x
Gomphonema tenellum[2]	x	x	x	x	x	x	x	x
Gomphonema truncatum var. *capitatum*[2]	x	x	x				x	
Reimeria sinuate[2]	x	x	x	x				
Bacillariaceae								
Nitzschia clausii[2]	x	x		x	x		x	
Nitzschia linearis[2]	x	x	x	x		x		
Nitzschia palea[2]	x		x	x		x		
Nitzschia sinuata var. *tabellaria*[2]	x	x	x	x			x	x

APPENDIX 1. (Cont.)

Classification	Site						*R. sauteri*	*B. bankorensis*
	1	2	3	4	5	6		
Surirellaceae								
Cymatopleura sp.[2]				x				
Surirella angusta[2]	x	x	x	x	x	x	x	x
Surirella robusta[2]	x		x	x	x	x	x	x
Monoraphidineae								
Achnanthaceae								
Achnanthes crenulata[2]	x			x	x		x	
Achnanthes deflexa[2]	x	x	x	x	x	x	x	x
Achnanthes exigua[2]	x	x	x	x				
Achnanthes nollii[2]	x	x	x	x	x	x	x	x
Achnanthes thermalis[2]	x	x	x	x	x	x	x	x
Achnanthidium minutissimun[2]	x	x	x	x	x	x	x	x
Cocconeis placentula var. euglypta[2]	x	x	x	x	x	x	x	x
Rossithidium linearis[2]	x	x	x	x	x	x	x	x
Cyanophyta								
Cyanophyceae								
Chroococcales								
Chroococcaceae								
Aphanocapsa elachista[1]	x	x	x	x	x	x	x	x
Merismopedia sp.[1]	x		x			x	x	x
Hormogonales								
Oscillatoriaceae								
Lyngbya sp.[2]	x	x	x	x	x	x	x	x
Oscillatoria sp.[1]	x	x	x	x	x	x	x	x
Total: 42 genera, 87 species	38 75	33 62	34 67	36 69	34 65	32 49	35 67	32 54