Zoological Studies **36**(3): 186-193 (1997)

Zoological Studies

Growth and Development of Oophagous Tadpoles in Relation to Brood Care of an Arboreal Breeder, *Chirixalus eiffingeri* (Rhacophoridae)

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(Accepted March 28, 1997)

Yeong-Choy Kam, Yi-Huey Chen, Zhen-Shuo Chuang and Tsung-Shun Huang (1997) Growth and development of oophagous tadpoles in relation to brood care of an arboreal breeder, *Chirixalus eiffingeri* (Rhacophoridae). *Zoological Studies* **36**(3): 186-193. We studied the growth, development, and survivorship of *Chirixalus eiffingeri* tadpoles in 2 bamboo tree habitats at the Experimental Forest of National Taiwan University at Chitou from July to October 1994. We found 13 egg clutches in bamboo stumps of which 3 were deposited in stumps already containing tadpoles. We monitored the number and total length (TL) of all tadpoles in the water pool of every nest until no tadpoles were left. The number of post-hatching tadpoles found in pools was not correlated with clutch size. The survival rate of tadpoles before Gosner stage 30 varied widely and was not correlated with initial tadpole number. The decrease in the number of tadpoles may have been due to starvation, cannibalism, and/or predation. Tadpoles that did not receive trophic eggs failed to grow and develop, suggesting the importance of brood care. The growth and development of tadpoles were not correlated with initial tadpole density. The presence of tadpoles from an earlier clutch strongly affected the growth and development of tadpoles from a later clutch, but the mechanism(s) of interaction between the 2 cohorts of tadpoles has yet to be resolved.

Key words: Anuran, Ecology, Population, Brood care.

Deposition of eggs and tadpoles in arboreal pools such as tree holes, bamboo stumps, and bromeliad leaf axils occurs more commonly than originally thought (Noble 1929, Wassersug et al. 1981, Ueda 1986, Lannoo et al. 1987, Weygoldt 1987, Thompson 1992, Brust 1993, Jungfer 1996, Kam et al. 1996). However, the life history traits of arboreal tadpoles are almost unknown even though they are ecologically interesting. Arboreal pools are usually characterized by small volumes of water and they are food-limited microhabitats; thus, resource competition is expected to be severe (Laessle 1961, Wassersug et al. 1981, Kam et al. 1996). Also, nests are often re-used due to the scarcity of nest sites, resulting in 2 age classes of tadpoles in a single pool, but interactions among tadpole cohorts remain largely uninvestigated (Thompson 1992, Kam et al. 1996). Unlike the field enclosures employed in many studies, arboreal pools represent 'truly' natural systems, and in most cases, different cohorts of tadpoles in them can be identified and tracked throughout the larval period.

Many anurans have evolved oophagy during the larval period in response to food scarcity in arboreal pools (Duellman and Trueb 1986, Ueda 1986, Lannoo et al. 1987, Jungfer 1996), but the importance of trophic eggs for the development and growth of tadpoles remains unevaluated for most species. Available information indicates that tadpoles of *Dentrobates pumilio*, *Osteopilus brunneus*, *Anotheca spinosa*, and *Chirixalus eiffingeri* are probably obligately oophagous (Ueda 1986, Weygoldt 1987, Thompson 1992, Brust 1993, Jungfer 1996, Kam et al. 1996). Typically, a female frog re-visits her oviposition site to lay fertilized or unfertilized

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eggs into the pool to feed her young until metamorphosis (Ueda 1986, Thompson 1992, Brust 1993, Jungfer 1996). In theory, female frogs can deposit additional eggs in response to increased demands by either increased tadpole density or egg consumption as tadpoles grow.

The rhacophorid tree frog, *C. eiffingeri*, is endemic to Taiwan and 2 adjacent Japanses islands, Iriomote and Ishigaki (Kuramoto 1973, Ueda 1986, Lue 1990). During the breeding season, females lay fertilized eggs on the inner walls of tree holes, bamboo stumps, or water-filled buckets above the water surface (Kuramoto 1973, Chuang 1988). Upon hatching, tadpoles drop into the water pool where they grow and develop until metamorphosis. Due to the scarcity of nest sites, 40% of nests are re-used, which in some cases results in 2 age classes of tadpoles in a pool (Kam et al. 1996). Tadpoles are oophagous and are fed by females which lay unfertilized trophic eggs, in the absence of male frogs, directly into the water (Ueda 1986, Kam et al. 1996). However, the importance of eggs as a food source has never been assessed in the field even though available data from tadpole morphology, and a laboratory experiment suggest that they are obligately oophagous (Ueda 1986, Kam et al. 1996, Lin 1996).

The objectives of this study were to report the growth, development, and survivorship of arboreal tadpoles from unmanipulated nests. Specifically, we studied (1) the fate of tadpoles that did not receive trophic eggs during the tadpole period and (2) the relationship between tadpole density and their growth and development. We also compared the growth, development, and body size distribution of tadpoles between singly used and re-used nests.

MATERIALS AND METHODS

Field studies were conducted in 2 bamboo tree habitats (approximately 20 m × 35 m each) from July to October 1994 at the Experimental Forest of National Taiwan University at Chitou (elevation 1016 m, approximately 23°39'20" N, 120°48'10" E) in Nantou County. Two species of bamboo trees, *Phyllostachys edulis* and *Sinocalamus latiflorus*, are the most abundant plants in the area and comprise more than 98% of the woody plants in the study sites. Bamboo trees are cut periodically for commercial purposes, and the bamboo stumps remain for several years before disintegrating. Bamboo stumps are frequently used by *C. eiffingeri* as oviposition sites. Bamboo trunks are hollow; when cut, the hollow stems collect water after rains, forming ideal nesting sites.

We marked every bamboo stump before the experiment in our study sites and checked them once every 3 days. We found 13 fertilized egg clutches which had been deposited on the bamboo wall above the water pool between 1 July and 5 August 1994. Fertilized eggs are characterized by having an animal and a vegetal hemisphere, and the eggs were usually under early development when we found them in the field. In contrast, unfertilized eggs do not have animal and vegetal hemispheres, and the egg yolk appears cloudy. We monitored the egg clutches weekly until the eggs hatched. We photographed tadpoles and monitored the number and total lengths (TL, snout to tail tip) of tadpoles until all tadpoles had left the stumps or died. In addition, before tadpoles reached a TL of about 20 mm, we recorded the presence of jelly capsules in the pools, which we took as evidence of tadpoles having being fed by the female frog. We did this because small tadpoles can only bite through the jelly capsule and suck the yolk, leaving the jelly capsule in the pool (Ueda 1986). As tadpoles grow larger, they usually ingest the whole egg including capsule. We also measured water pH, temperature, and depth during each visit. All macroorganisms in water, mainly tipulid (Diptera) larvae, were removed.

Tadpoles were inspected only once a week, therefore the size at metamorphosis was difficult to determine because a well-developed tadpole (e.g., Gosner stage 39) could reach metamorphosis and leave the pool between visits. To circumvent this problem, we used Gosner stage 30 as the end point of comparisons. Tadpoles in Gosner stage 30 are characterized by full development of the hindlimb buds with no interdigital indentations and paddle-shaped feet (Gosner 1960). It takes about 2 wk for a tadpole at Gosner stage 30 to reach metamorphosis, therefore, a tadpole at Gosner stage 29 or younger that we had seen previously would not have enough time to develop, reach metamorphosis, and leave the hole before our next visit. As a result, we concluded that any disappearance of tadpoles before Gosner stage 30 could only be due to tadpole mortalilty.

When a bamboo stump was reused by female frogs before all tadpoles had left the pool, we monitored the number and TL of tadpoles of both age classes until no tadpoles were left. Tadpoles that hatched from earlier clutches (called EARLY tadpoles hereafter) were significantly larger than tadpoles from later clutches (called LATE tadpoles hereafter) at the start of experiment (see Results), and the EARLY tadpoles were easily distinguished by either body size or developmental stage throughout the study period.

Statistical analyses: Data were analyzed by a SAS program (SAS Institute Inc. 1988). EARLY tadpoles were excluded from analyses unless noted. Means ± SD of all variables are reported unless noted, and a significant difference is declared when $p \leq 0.05$.

RESULTS

Breeding biology

We found 13 fertilized egg clutches in bamboo stumps with mean stump heights of 65 ± 34 cm and hole diameters of 72.4 ± 16.1 mm (n = 13). Water temperature, pH, and depth of pools were 19.48 ± 0.63 °C, 5.11 ± 0.68, and 91.5 ± 27 mm, respectively (n = 13). Of these, 3 egg clutches were deposited in stumps containing tadpoles at Gosner stage 30 or older (Table 1). At least 1 tadpole in each nest, except for nests 512 and 613, reached metamorphosis. The larval period was about 6 to 8 wk.

Hatching rate per nest ranged from 14% to 94% (mean, 40 ± 25 %, n = 13). The number of newly-hatched tadpoles (called initial tadpole number hereafter) in pools was not correlated with egg clutch size (r = –0.11, n = 13, p = 0.72); the number of eggs that failed to hatch was positively correlated with clutch size (r = 0.95, n = 13, p = 0.0001) (Fig. 1).

Tadpoles reached Gosner stage 30 in 4 to 6 wk, and the percentage of tadpoles that survived to Gosner stage 30 varied widely among nests, ranging from 33% to 94% (68 ± 20%). The percentage of tadpoles surviving to Gosner stage 30 was not correlated with initial tadpole number (r = 0.02, n = 9, p = 0.968).

Table 1. Clutch size, total tadpole number (EARLY and LATE tadpoles), and the fate of 13 nests (S = successful and F = failed)

Nest	Number of eggs	Number of tadpoles	[b]Miminum number of tadpoles that reached Gosner stage 41	Fate
103	89	18	3	S
312	45	20	6	S
510	33	31	16	S
536	60	16	5	S
571	129	25	9	S
585	53	12	4	S
591	77	11	5	S
606	65	12	4	S
512	51	28	0	F
613	63	32	0	F
302[a]	34	20 (5)	6	S
309[a]	49	19 (2)	3	S
573[a]	42	39 (4)	13	S

[a]Represents reused nests, and the number of EARLY tadpoles is in parentheses.
[b]Because we surveyed bamboo stumps once a week, there were some tadpoles which reached Gosner stage 41 and left the stumps between visits.

Nests that did not receive eggs

No tadpoles from nests 512 and 613 reached Gosner stage 41 or older; we thus considered them to be failed nests. In contrast, 11 bamboo stumps with at least 1 tadpole which reached Gosner stage 41 were considered as successful nests (Table 1). Tadpoles in nest 512 did not receive any trophic eggs during development as evidenced by the absence of egg capsules throughout the study period, and they did not grow at all before they disappeared during the 5th week of the study period (initial TL, 10.95 ± 1.5 mm, n = 28, and TL at week 4 was 11.09 ± 1.29 mm, n = 5). Nest 613 contained the last egg clutch of the breeding season (i.e., deposited on 5 August 1994). Tadpoles in nest 613 did not receive any trophic eggs for the first 3 weeks, and they did not grow (TL at initial week and weeks 1, 2, and 3 were 12.09 ± 1.05 mm, n = 32; 11.48 ± 1.01 mm, n = 28;

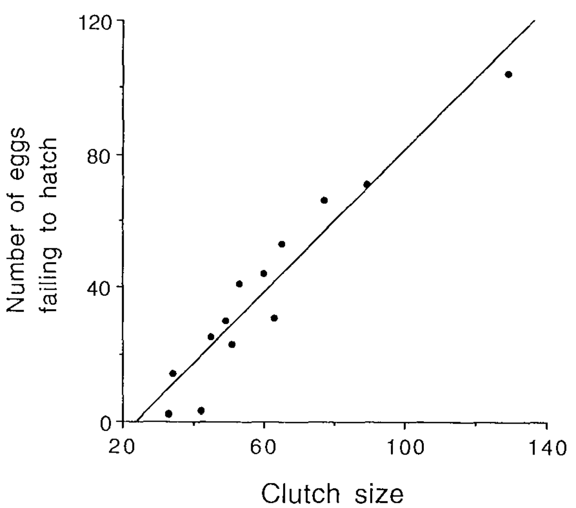

Fig. 1. Relationship between the number of eggs that failed to hatch and clutch size. r = 0.95, n = 13, p = 0.0001.

11.19 ± 0.98 mm, n = 28; and 11.82 ± 1.28 mm, n = 28, respectively). Then we found jelly capsules in the pool starting from week 3, and tadpoles began to grow at a constant rate and reached Gosner stage 30 seven wk later (TL = 24.96 ± 3.52, n = 14). However, the water level in the bamboo stump began to drop from mid-September, and the water dried up 2 wk later. All the tadpoles were stranded in the stump and died.

Growth and development

Because the water depth and hole diameter varied among stumps, we calculated the water volume and initial tadpole density (i.e., post-hatching density) of each nest. We used the mean TL of tadpoles at Gosner stage 30 and mean time to reach Gosner stage 30 of each nest to conduct correlation analyses. Neither the TL of tadpoles at Gosner stage 30 nor the time to reach Gosner stage 30 was correlated with initial tadpole density (r = −0.62, n = 8, p = 0.101; r = 0.34, n = 8, p = 0.402, respectively). The initial tadpole density was significantly correlated with initial tadpole number (r = 0.70, n = 8, p = 0.030).

Used vs. re-used nests

Nests 302, 309, and 573 contained 5, 2, and 4 EARLY tadpoles, respectively (Table 1). At the start of the experiment, the size differences between EARLY and LATE tadpoles within a water pool were significant in all 3 nests (Nest 302, EARLY tadpoles 27.78 ± 0.47 mm, n = 4, LATE tadpoles 14.16 ± 2.17 mm, n = 16, t = 12.24, p < 0.0001; Nest 309, EARLY tadpoles 22.99 ± 4.20 mm, n = 2, LATE tadpoles 12.24 ± 0.75 mm, n = 17, t = 11.49, p < 0.0001; Nest 302, EARLY tadpoles 25.16 ± 2.88 mm, n = 4, LATE tadpoles 12.63 ± 1.02 mm, n = 35, t = 18.6, p < 0.0001). EARLY tadpoles in re-used nests maintained a size advantage over LATE tadpoles throughout the larval period (Fig. 2). EARLY tadpoles reached metamorphosis 4 wk after the start of experiments

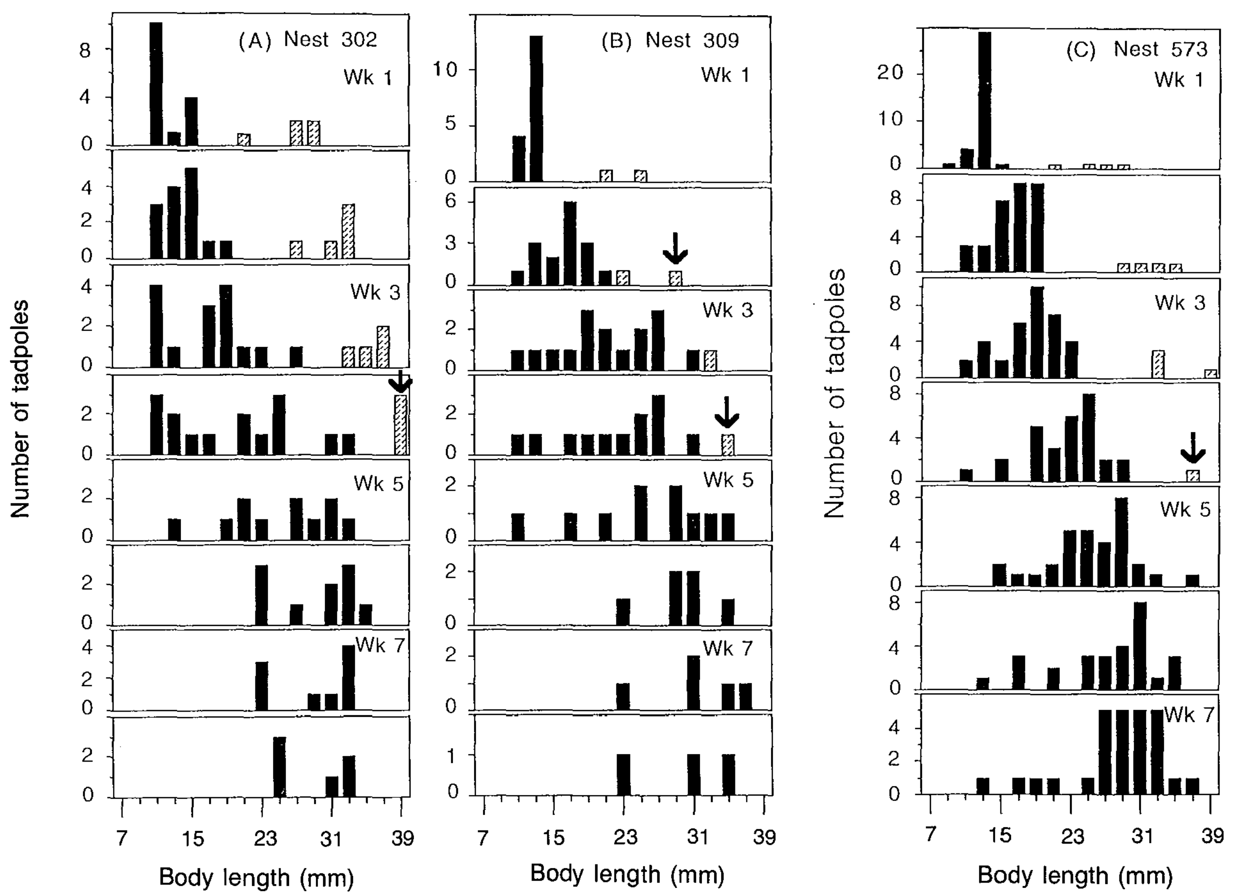

Fig. 2. Weekly changes in the TL distribution of tadpoles from reused nests (A) 302, (B) 309, and (C) 573. Solid and dashed bars represent tadpoles from late and early egg clutches, respectively. Arrows indicate when EARLY tadpoles reached metamorphosis. The bottom figure for each nest represents the week when LATE tadpoles reached metamorphosis.

whereas LATE tadpoles reached metamorphosis 7 to 8 wk after they hatched.

We compared the life history traits of tadpoles between singly used and re-used nests since the total tadpole numbers (includes EARLY and LATE tadpoles) between nests were statistically similar (Table 2). Some LATE tadpoles from reused nests reached Gosner stage 30 at the same time as tadpoles from singly-used nests, and their TL at Gosner stage 30 did not differ between groups (Table 2). However, if all LATE tadpoles were included in the analysis, the mean TL of LATE tadpoles from reused nests was significantly smaller, but the variance of TL was larger than that of tadpoles from singly used nests (Table 2; Figs. 2, 3). Also, LATE tadpoles from reused nests had a longer larval period than tadpoles from singly used nests (Table 2).

DISCUSSION

Egg and tadpole mortality

Ueda (1986) reported a high fertilization rate of *Chirixalus eiffingeri* eggs (96% to 100%) among different clutch sizes, which refutes the possibility that larger egg clutches may have lower fertilization rates. A possible explanation for the findings of no correlation between clutch size and number of tadpoles per nest is that larger clutches are more susceptible to fungal infection and predation. Fungal infection of eggs was common, and once some eggs were infected, the infection spread quickly (Kam et al. 1996). Large egg clutches are also more likely to attract predators such as slugs and ants than are small egg clutches, resulting in higher egg mortality.

Tadpoles reached Gosner stage 30 in 4 to 6 wk; thus, any decline in the number of tadpoles before Gosner stage 30 can only be due to tadpole mortality which can be due to starvation, cannibalism, and/or predation. Starvation occurred when small tadpoles were outcompeted by larger tadpoles for trophic eggs (i.e., unfertilized eggs) that were deposited by the female frog directly into the water. Without available eggs, small tadpoles stopped growing, and eventually died of starvation and/or were probably cannibalized by conspecifics. Even though we did not witness it, cannibalism is a common phenomenon among amphibian larvae (Crump 1992, Thompson 1992, Jungfer 1996). Kam et al. (1996) reported that in some nests, all tadpoles disappeared between weekly visits, suggesting that predation exists. Since macroorganisms were removed from the water pools, predation, if it occurred, was most likely caused by terrestrial intruders.

Nests that did not receive trophic eggs

The death of tadpoles in nests 512 and 613 suggests that the growth, development, and survivorship of *C. eiffingeri* tadpoles are totally dependent upon the trophic egg availability, which supports findings from earlier studies (Ueda 1986, Kam et al. 1996). If, for any reason, no female deposits additional eggs in a pool, as happened in nest 512, the tadpoles will not grow or develop and will later die. On the other hand, the retarded

Table 2. Comparisons between tadpoles from singly used and re-used nests of survivorship, total length (TL), and time required to reach Gosner stage 30. We used the Wilcoxon two-sample test to do comparisons, and Z statistics are reported. EARLY tadpoles from re-used nests were excluded from the analyses except for the total tadpole number

	Singly used	Re-used	Z statistics	Probability
Sample size	8	3		
Total tadpole number	18.1 ± 7.03	26.0 ± 11.2	1.23	0.247
Survival (%)[a]	70.0 ± 20.6	74.0 ± 16.5	0.10	0.919
TL of tadpoles at Gosner stage 30 (mm)[a]	32.41 ± 2.29	30.00 ± 0.90	−1.74	0.083
Time required to reach Gosner stage 30 (wk)[a]	4.88 ± 0.64	5.00 ± 0	0.26	0.794
TL of all tadpoles (mm)[a]	30.17 ± 2.43	25.45 ± 0.58	−2.35	0.019
Variance of TL of all tadpoles [a,b]	11.75 ± 8.15	38.15 ± 12.9	2.14	0.032
Last tadpole seen in water pool (wk)	8.75 ± 2.12	12.3 ± 0.58	2.01	0.045

[a]Measurements were taken when any tadpole in the water pool reached Gosner stage 30.
[b]We used the variance of tadpole TL of each nest to calculate mean variance.

growth of tadpoles in nest 613 due to delayed maternal care resulted in a prolonged larval period. As water levels in the bamboo stumps dropped rapidly starting from mid-September (Kam et al. 1996), tadpoles did not have enough time to grow before the pool dried up.

Growth and development

Our findings disagree with earlier studies on the population ecology of amphibian larvae in which larvae reared at high densities took longer to reach metamorphosis and were smaller in size than those reared at low densities (Brockelman 1969, Wilbur 1977, Dash and Hota 1980, Semlitsch and Caldwell 1982, Petranka and Sih 1986). The density-independent growth of *C. eiffingeri* tadpoles suggests that the accumulation of harmful products (Richards 1958, Licht 1967, Warner 1991, Schmuck et al. 1994) and behavioral interactions such as increased "social stress" as a result of frequent contacts (Adolph 1931, Gromko et al. 1973, Alford and Crump 1982) probably do not affect the growth of the tadpoles that we studied. Earlier studies have shown that tadpoles that live in harsh environments (such as arboreal pools and ephemeral ponds) and foam nests exhibit a relatively strong tolerance of high ammonia levels, hypoxia, or increased activity of the ornithine cycle (Candelas and Gomez 1963, Shoemaker and McClanahan 1973, Lannoo et al. 1987, Schmuck et al. 1994).

Competition for food is another factor considered in density-dependent growth in many earlier studies (Brockelman 1969, DeBenedictis 1974, Wilbur 1977, Dash and Hota 1980, Semlitsch and Caldwell 1982). However, *C. eiffingeri* tadpoles receive food (i.e., trophic eggs) from female frogs; thus, within reproductive limitations, the number of eggs that a female frog deposits could potentially vary depending on the tadpoles' demand, this would result in density-independent growth. Ueda (1986) reported an 'egg begging' behavior

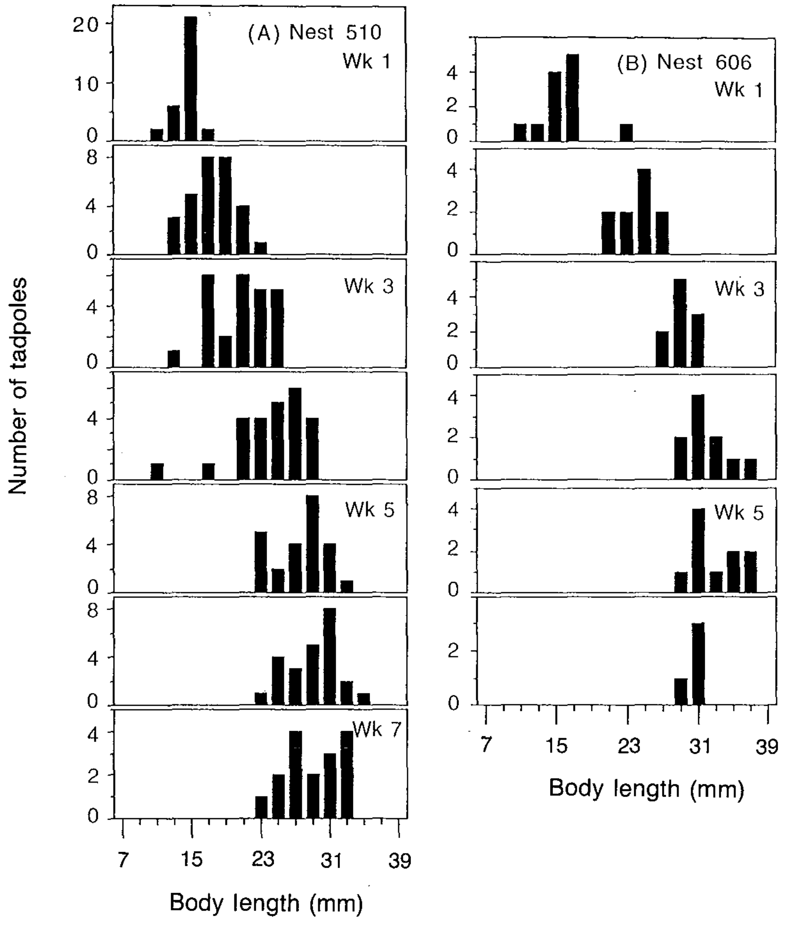

Fig. 3. Weekly changes in the TL distribution of tadpoles from singly-used nests (A) 510 and (B) 606. Nests 510 and 606 represent bamboo stumps with a high and low density of tadpoles, respectively. The bottom figure of each nest represents the week when tadpoles reached metamorphosis.

by tadpoles, which is similar to that of *D. pumilio* and *A. spinosa* tadpoles (Brust 1993, Jungfer 1996). It is possible that a female can sense tadpoles' demands by the degree and frequency of "poking" on her skin around the cloaca and thigh areas.

Used vs. reused nests

The finding of a greater disparity in TL distribution of tadpoles in re-used nests than in singly used nests (Table 2; Figs. 2, 3) suggests that the presence of EARLY tadpoles strongly affects the growth and development of LATE tadpoles, but the mechanism(s) of interaction between the EARLY and LATE tadpoles is yet to be resolved. EARLY tadpoles outcompete LATE tadpoles for trophic eggs due to size differences (Kam, unpubl. data) and monopolize most of the eggs deposited by the female frog; thus, LATE tadpoles had to scramble for the remaining eggs left by EARLY tadpoles (exploitative competition). Similar behavioral interactions between large and small tadpoles were observed in *Bufo americanus* (Wilbur 1977), *Rana temporaria*, *R. esculenta*, *Bufo bufo*, and *B. calamita* (Savage 1952). LATE tadpoles that succeeded in feeding on eggs grew normally and reached Gosner stage 30 at the same time as tadpoles from singly used nests, but those that fed on eggs only occasionally, or not at all, grew slowly, which resulted in the wider TL range (Table 2; Fig. 2A-C). Tadpoles that only obtained eggs occasionally grew more slowly, and consequently took longer to reach metamorphosis (Table 2). The 2nd explanation for the disparity in growth and development between LATE tadpoles of re-used nests and tadpoles of singly used nests is due to interference competition; i.e., EARLY tadpoles may release inhibitory substances which retard the growth of LATE tadpoles in re-used nests. Earlier studies have demonstrated that the growth of tadpoles inhibited when they are raised in water previously crowded by other larger tadpoles (Richards 1958, Licht 1967, Gromko et al. 1973).

Acknowledgements: This study was supported by an NSC Grant (NSC 84-2311-B-018-001) and an intramural grant from National Changhua University of Education to YCK. We thank C.-F. Yen, C.-M. Yu, I.-S. Tzeng, M.-I. Shi, and many others for field and laboratory assistance. Thanks are also due to the Experimental Forest of National Taiwan University at Chitou for providing accomodations and permitting us to work inside the park. We also thank A. F. Warneke for helpful comments on an earlier draft of the manuscript.

REFERENCES

Adolph EF. 1931. The size of the body and the size of the environment in the growth of tadpoles. Biol. Bull. **61:** 350-375.

Alford RA, ML Crump. 1982. Habitat partitioning size classes of larval southern leopard frogs, *Rana utricularia*. Copeia **1982:** 367-373.

Brockleman WY. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology **50:** 632-644.

Brust DG. 1993. Maternal brood care by *Dendrobates pumilio*: a frog that feeds its young. J. Herpetol. **27:** 96-98.

Candelas C, M Gomez. 1963. Nitrogen excretion in tadpoles of *Leptodactylus albilabris* and *Rana catesbeiana*. Am. Zool. **3:** 521-522.

Chuang KS. 1988. The reproductive biology of *Chirixalus eiffingeri*. Master's thesis, National Taiwan Normal University, Taiwan, 74 pp. (in Chinese).

Crump ML. 1992. Cannibalism in amphibians. *In* MA Elgar, BJ Crespi, eds. Cannibalism. Ecology and evolution among diverse taxa. New York: Oxford University Press, pp. 256-276.

Dash MC, AK Hota. 1980. Density effects on the survival, growth rate, and metamorphosis of *Rana tigrina* tadpoles. Ecology **61:** 1025-1028.

DeBenedictis PA. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: an experimental field study. Ecol. Monogr. **44:** 129-151.

Duellman WE, L Trueb. 1986. Biology of Amphibians. New York: McGraw-Hill, 670 pp.

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

Gromko MH, FS Mason, SJ Smith-Gill. 1973. Analysis of the crowding effect in *Rana pipiens* tadpoles. J. Exp. Zool. **186:** 63-72.

Jungfer KH. 1996. Reproduction and parental care of the coronated treefrog, *Anotheca spinosa* (Steindachner, 1864) (Anura: Hylidae). Herpetologica **52:** 25-32.

Kam YC, ZS Chuang, CF Yen. 1996. Reproduction, oviposition-site selection, and tadpole oophagy of an arboreal nester, *Chirixalus eiffingeri* (Rhacophoridae), from Taiwan. J. Herpetol. **30:** 52-59.

Kuramoto M. 1973. The amphibians of Iriomote of the Ryukyu Islands: ecological and zoogeographical notes. Bull. Fukuoka Univ. Educ. **22** (III): 139-151.

Laessle AM. 1961. A micro-limnological study of Jamaican bromeliads. Ecology **42:** 499-517.

Lannoo MJ, DS Townsend, RJ Wassersug. 1987. Larval life in the leaves: arboreal tadpole types, with special attention to the morphology, ecology, and behavior of the oophagous *Osteopilus brunneus* (Hylidae) larvae. Fieldiana Zool. Serial **38:** 1-31.

Licht LE. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. Ecology **48:** 736-745.

Lin CF. 1996. Maternal reproductive investment and population ecology of tadpoles in *Chirixalus eiffingeri*. Master's thesis, National Taiwan University, Taipei. (in Chinese, English abstract).

Lue KY. 1990. The amphibians and reptiles of Taiwan. The manuals of wildlife resources inventory in Taiwan (2). Taipei:

Council of Agriculture, Executive Yuan, 123 pp.
Noble GK. 1929. The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Staurois*. Bull. Amer. Mus. Nat. Hist. **58:** 291-334.
Petranka JW, A Sih. 1986. Environmental instability, competition, and density-dependent growth and survivorship of a stream-dwelling salamander. Ecology **67:** 729-736.
Richards CM. 1958. The inhibition of growth in crowded *Rana pipiens* tadpoles. Physiol. Zool. **31:** 138-151.
SAS Institute, Inc. 1988. SAS/STAT User's guide. Gary: SAS Inst. Inc., 1028 pp.
Savage RM. 1952. Ecological, physiological and anatomical observation on some species of anuran tadpoles. Proc. Zool. Soc. London **122:** 467-514.
Schmuck R, W Geise, KE Linsenmair. 1994. Life cycle strategies and physiological adjustments of reedfrog tadpoles (Amphibia, Anura, Hyperoliidae) in relation to environmental conditions. Copeia **94:** 996-1007.
Semlitsch RD, JP Caldwell. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. Ecology **63:** 905-911.
Shoemaker VH, LL McClanahan. 1973. Nitrogen excretion in the larvae of a land-nesting frog (*Leptodactylus bufonius*). Comp. Biochem. Physiol. **44A:** 1149-1156.
Thompson RL. 1992. Reproductive behaviors and larval natural history of the Jamaican brown frog, *Osteopilus brunneus* (Hylidae). Master's thesis, University of Florida, Gainesville, 65 pp.
Ueda H. 1986. Reproduction of *Chirixalus eiffingeri* (Boettger). Sci. Rep. Lab. Amphibian Biol., Hiroshima Univ. **8:** 109-116.
Warner SC, WA Dunson, J Travis. 1991. Interaction of pH, density, and priority effects on the survivorship and growth of two species of hylid tadpoles. Oecologia **88:** 331-339.
Wassersug RJ, KJ Frogner, RF Inger. 1981. Adaptations for life in tree holes by rhacophorid tadpoles from Thailand. J. Herpetol. **15:** 41-52.
Weygoldt P. 1987. Evolution of parental care in dart poison frogs (Amphibia: Anura: Dendrobatidae). Zeitschr. Zool. Syst. Evolut.-forsch. **25:** 51-67.
Wilbur HM. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. Ecology **58:** 196-200.

艾氏樹蛙 (樹蛙科) 食卵蝌蚪之成長發育與母蛙撫育之研究

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本研究探討艾氏樹蛙蝌蚪的成長、發育及存活。實驗在溪頭臺灣大學實驗林進行。實驗期間一共追蹤 13 個竹筒，其中三個竹筒內有前次產卵所孵化的蝌蚪。蝌蚪孵出後，我們每個星期追蹤蝌蚪數量及體長直到最後一隻蝌蚪不見爲止。蝌蚪數及到達 Gosner 30 期的存活率與卵數不相關。蝌蚪數在發育過程中減少的主要原因可能是饑餓、互相殘殺及被掠食。沒有被餵卵的蝌蚪不會成長與發育，這說明母蛙撫育的重要性。蝌蚪成長及發育與密度相關性不顯著。在有兩批不同年齡蝌蚪的竹筒，先前孵化的大蝌蚪很明顯會影響後來孵化的小蝌蚪的成長發育，但其中的機制則有待進一步去了解。

關鍵詞：無尾類, 生態, 族群, 母蛙撫育。

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