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INTER- AND INTRACLUTCH COMPETITION AMONG OOPHAGOUS TADPOLES OF THE TAIWANESE TREE FROG, *CHIRIXALUS EIFFINGERI* (ANURA: RHACOPHORIDAE)

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ABSTRACT: We studied the dynamic interactions within and between different hatching cohorts of tadpoles of *Chirixalus eiffingeri* reared in pools in bamboo stumps at the Experimental Forest of the National Taiwan University at Chitou, Taiwan, during 1997 and 1998. In a 2×3 factorial experiment (Experiment I), we assessed the effects of older tadpoles (none, 10 medium, or 10 large tadpoles) on the growth, survivorship, and metamorphosis of younger, small tadpoles in two densities (10 or 20 tadpoles). In most cases, tadpoles of both older size classes significantly affected the growth, survivorship, survival to metamorphosis, the length of larval period, and mass at metamorphosis of younger tadpoles. The effects of medium and large tadpoles on small tadpoles were similar. An increase in the clutch size of younger tadpoles prolonged the length of larval period but did not affect the mass at metamorphosis or survival to metamorphosis. In Experiment II, we studied the effects of the number of older tadpoles on the growth, survivorship, and metamorphosis of younger tadpoles. There were four treatments: 20 younger tadpoles (20S), 30 younger tadpoles (30S), 10 younger and 10 older tadpoles (10S 10L), and 10 younger and 20 older tadpoles (10S 20L). Older tadpoles decreased the growth and survival of younger tadpoles. An increase of the abundance of older tadpoles, from 20 to 30, affected the survival to metamorphosis of younger tadpoles. All younger tadpoles in the 10S 20L treatment died. Experiments I and II demonstrated that the number, but not the developmental stage, of older tadpoles had detrimental effects on the growth and development of the younger tadpoles, which has important implications for the reproductive strategies of female frogs. The maternal provisioning of eggs for nutrition of *C. eiffingeri* is energetically expensive; thus, the time when the second clutch of eggs is laid is critical to the overall reproductive success of female frogs. Female frogs should lay a second clutch of eggs only after the older tadpoles are low in number, which may reduce intraspecific competition between the two cohorts of tadpoles.

Key words: Anura; Clutch overlap; Maternal care; Phytotelmata; Priority effects; Tadpole oophagy

DEPOSITION of eggs and tadpoles in arboreal pools (phytotelmata) by anurans occurs more commonly than originally thought (Brust, 1993; Duellman and Trueb, 1986; Kam et al., 1996; Lannoo et al., 1987; Wassersug et al., 1981). Tree holes and cavities, bamboo stumps, and bromeliad leaf axils are used commonly by anurans that nest arboreally (Kam et al., 1996; Laessle, 1961; Wassersug et al., 1981). Most arboreal pools are small-volume, food-limited microhabitats (Laessle, 1961; Wassersug et al., 1981). As a result, tadpole oophagy has evolved in many species as a response to food scarcity (Brust, 1993; Caldwell, 1997; Caldwell and Olivera, 1999; Jungfer, 1996; Lannoo et al., 1987; Summers and Amos, 1997; Ueda,

1986; Wassersug et al., 1981). Tadpoles of *Dendrobates pumilio* and *Chirixalus eiffingeri* are obligatorily oophagous and are fed by female frogs (Brust, 1993; Kam et al., 1996; Ueda, 1986; Weygoldt, 1980). This type of maternal care is energetically expensive. Females of *C. eiffingeri* expend large amounts of energy to produce eggs that later become offspring, and they also must acquire extra energy needed to produce trophic eggs (i.e., unfertilized eggs) to feed their offspring. For example, each tadpole of *C. eiffingeri* consumes about 87 eggs during the larval period, and the average tadpole number in a pool is 22 ± 9 tadpoles (Kam et al., 1996, 1997).

In nature, arboreal nesting sites are uncommon microhabitats. Stewart and Pough (1983) reported that a population of *Eleutherodactylus coqui* increased after

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the number of bamboo frog houses used for nesting sites was increased experimentally. Donnelly (1989a,b) demonstrated that tadpole-rearing sites in bromeliads were limited, and that artificial supplementation of rearing sites increased the density of adults of *D. pumilio*. Kam et al. (1996) reported that only 40% of the available bamboo stumps were used by female *C. eiffingeri* as nest sites because of differences in their sizes and locations in the bamboo forests. During each breeding season, suitable stumps are reused. The number of reused bamboo stumps increases as the breeding season progresses (Kam et al., 1996). It is not unusual for new egg clutches to be deposited in stumps already containing tadpoles, resulting in two age classes of tadpoles with in a single pool. These two cohorts of tadpoles live together in the pools for about four weeks before older tadpoles metamorphose and leave the stumps (Kam et al., 1997). However, the intraspecific competition between two hatching cohorts of oophagous tadpoles has never been assessed, and the outcome of competition may relate to the nature of the food source. Tadpoles in arboreal pools eat trophic eggs that are highly nutritious and readily digestible (Ueda, 1986). However, trophic eggs are available only when the female frog visits the nest, and the number of trophic eggs laid is limited due to the small body size of female frogs. Furthermore, the food supply (trophic eggs) of larval *C. eiffingeri* in stumps is controlled and does not necessarily decrease over time, depending on the feeding effort of female frogs (Kam et al., 1998b). In contrast, herbivorous tadpoles that live in pond or stream habitats consume evenly dispersed food resources, such as suspended algae, plankton, organic detritus and plant materials, and the food supply in ponds is limited and often decreases over time.

The unique breeding sites (i.e., arboreal nests) together with reproductive mode (i.e., egg provisioning) make *C. eiffingeri* a model organism for studying many aspects of life-history traits of arboreal-nesting amphibians. *Chirixalus eiffingeri* is a small frog (SVL about 30–40 mm), endemic to

Taiwan and two adjacent small islands, Iriomote and Ishigaki (Kuramoto, 1973; Ueda, 1986). During the breeding season (February–August), male frogs call from bamboo stumps. Often times, more than one male frog is seen in a bamboo stump, and they scramble for a female frog (Yang, 1994). Female frogs deposit fertilized eggs above the waterline on the inner walls of tree holes or bamboo stumps (Kam et al., 1998a; Kuramoto, 1973). Upon hatching, tadpoles drop into the pool of water where they grow and develop until metamorphosis. Male frogs exhibit paternal care (i.e., moisten the eggs) during the embryonic stage, but they leave the stumps after embryos have hatched. Tadpoles are obligatorily oophagous and are fed by females that lay unfertilized, trophic eggs directly in the water, in the absence of male frogs (Ueda, 1986). Based on a one-month trapping experiment, Kam et al. (2000) reported that about 98% of the female frogs (54/55 females) attended (i.e., lay trophic eggs) a single bamboo stump. In addition, a total of 96% of the bamboo stumps (50/52 stumps) was each attended by one female frog. Female frogs visit and feed tadpoles at intervals of about eight days, and feeding occurs only at night (Kam et al., 2000). The length of larval period, from hatching to metamorphosis, is 50–60 days (Kam et al., 1998b). Tadpoles are not cannibalistic, but they sometimes scavenge the remains of dead siblings. The effects of scavenging on the growth and development of tadpoles are negligible (Kam et al., 1996, 1998b, 2000).

The purposes of this study were to evaluate the dynamic interactions within and between different hatching cohorts of *C. eiffingeri* tadpoles in pools of water in bamboo stumps. Specifically, we assessed the effects of (1) the clutch size of younger tadpoles, (2) the presence of older tadpoles, and (3) the number of older tadpoles on the survivorship, growth, and metamorphosis of younger tadpoles.

MATERIALS AND METHODS

Study Site

We conducted experiments from May–September, 1997 and 1998, in bamboo for-

ests 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, Taiwan. Chitou receives approximately 3 m of rainfall annually, but it is not distributed evenly throughout the year. Although rain falls in all months, the wet season begins in February and ends in late September. The mean annual air temperature is about 17 ± 3 C, and the monthly temperature difference was 1.7 C during the study period. Two species of bamboo, *Phyllostachys edulis* and *Sinocalamus latiflorus*, are the most abundant plants in the study sites. The bamboo is cut periodically for commercial purposes, and the stumps remain for several years before disintegrating. After they are cut, the hollow bamboo stumps collect rain water and become ideal nesting sites for *C. eiffingeri*. The pools of water in bamboo stumps also contain microorganisms (euglenoids, diatoms, paramecia, *Chlorella*, and rotifers) and the larvae of invertebrates (Culicidae, Chironomidae, and Tipulidae: Order Diptera; Lin, 1996). The other organisms in the pools do not appear to have a direct association with the tadpoles as they are neither food for nor the predators of the tadpoles, and they do not compete with tadpoles for trophic eggs (Kam et al., 1996; Ueda, 1986).

Experimental Design

Experiment I.—In 1997, we studied the effect the presence of older tadpoles of two size classes (medium and large tadpoles) on the survival, growth, and development of younger tadpoles of two clutch sizes. A 2×3 factorial design with 12 replicates of each treatment combination was used (Table 1). The factors were the number of younger tadpoles in a bamboo stump (10 or 20 small tadpoles) and the addition of older tadpoles (none, 10 medium, or 10 large). Each bamboo stump was a replicate. Ten older and 20 younger tadpoles represented the average ranges in the field (Kam et al., 1997; Kam, unpublished data). At the beginning of the experiment, we located bamboo stumps with fertilized eggs attached to the inner wall

above the pool. We monitored the egg clutches twice a week and collected the tadpoles after they hatched. At the same time, we located other bamboo stumps containing developing tadpoles and collected tadpoles that had reached designated sizes. Small tadpoles were about 1 wk old, 10–13 mm in total length (TL, snout to tail tip) and at Gosner stages 25–26 (Gosner, 1960). Medium tadpoles were about 3 wk old, 19–21 mm in TL and at Gosner stages 27–28. Large tadpoles were about 5 wk old, 26–28 mm and at Gosner stages 30–31. All tadpoles were collected and randomly assigned according to design. We used a total of 1080 small (35 clutches), 240 medium (10 clutches), and 240 large tadpoles (eight clutches) in this experiment.

Experiment II.—In 1998, we studied the effects of presence and abundance of older tadpole on younger tadpoles using four treatments: 20 younger tadpoles (20S), 30 younger tadpoles (30S), 10 younger and 10 older tadpoles (10S 10L) and 10 younger and 20 older tadpoles (10S 20L; Table 1). Younger tadpoles were about 1 wk old, 10–13 mm in TL, and at Gosner stages 25–26. Older tadpoles were about 3–5 wk old, 19–28 mm in TL, and at Gosner stages 27–31. We used a total of 770 younger and 330 older tadpoles (from 21 and 10 clutches, respectively) in this experiment. Tadpoles were collected and randomly assigned to each treatment. Each treatment was replicated 11 times, and each bamboo stump was a replicate.

Experimental Protocol

Initially, we monitored tadpoles once a week, but when they reached Gosner stage 37 (Gosner, 1960), near metamorphosis, we checked the tadpoles 2–3 times per week until none remained. The disappearance of tadpoles was due to a combination of tadpole mortality (starvation and predation) and the departure of metamorphs. To facilitate the examination and measurement of tadpoles, on our first visit we sawed a V-shaped cut in each bamboo stump and detached the portion of the stump containing the water and tadpoles. This allowed us to pour out the water and

tadpoles. After data collection, the water and tadpoles were placed back in the detached portion of the stump, which was then placed in the V-shaped notch in the top of the remainder of the stump. The detached portion fit snugly in the notch and transparent tape was wrapped around the cut for additional support.

Older tadpoles were labeled by injecting fluorescent elastomer dye (Northwest Marine Technology, Inc.) into the base of the tail on the ventral side (Donnelly et al., 1994). The dye did not have detrimental effects on the tadpoles, judging from the tadpoles' activities, growth, and development. It lasted throughout the study period, and could be seen clearly with an ultraviolet flashlight. During each visit, we poured the tadpoles and water into a bucket and used a small net to transfer the fluorescent-labeled and unlabeled tadpoles to different Petri dishes. The tadpoles were counted and photographed with a ruler beneath the Petri dish to determine their TL. Handling time per replicate ranged from 15–35 min.

Because female frogs feed their tadpoles at night (Kam et al., 2000), we examined the bamboo stumps during the day to minimize disturbance. Prior to when the tadpoles reached a TL of about 20 mm, we recorded the presence or absence of gelatinous capsules in the pools. Gelatinous capsules in the pool indicated that female frogs had fed the tadpoles. We did this because small tadpoles can only bite through the gelatinous capsule and remove the yolk, leaving the capsule in the pool (Ueda, 1986). As tadpoles grow larger, they usually ingest the whole egg, including the capsule. Those tadpoles with a TL > 20 mm were examined for the presence of eggs in the distensible stomach, which serves as an egg storage organ (Chou and Lin, 1997).

In each bamboo stump, the water volume was maintained so that each tadpole, regardless of size, had about 10 ml of water (Kam et al., 1996). For example, bamboo stumps with 10 and 20 tadpoles contained 100 and 200 ml of water, respectively. We did this to minimize crowding (density-dependent) effects, if any, during

TABLE 1.—Design of Experiment I (1997) and II (1998) at Chitou, Taiwan.

Treatments	Experiment I					
	No. small tadpoles	No. medium tadpoles	No. large tadpoles	No. stumps	No. attended stumps ¹	No. successful broods ²
10S	10			12	10	10
20S	20			12	5	5
10S 10M	10	10		12	7	5
20S 10M	20	10		12	5	3
10S 10L	10		10	12	9	2
20S 10L	20		10	12	9	9
				Experiment II		
20S	20			11	7	7
10S 10 L	10		10	11	4	2
30S	30			11	10	9
10S 20L	10		20	11	9	0

¹ An attended stump (or fed brood) is defined as a stump that contains tadpoles (early- or late-hatching) that are fed by a female frog. See the materials and methods section for an explanation of how we determined whether or not tadpoles were fed.

² A successful brood is defined as a brood in which at least one small tadpole reached metamorphosis.

the study period (Gromko et al., 1973; Licht, 1967; Richards, 1958). We added distilled water to the bamboo stumps weekly to compensate for water loss due to evaporation and removed excess water due to rainfall.

Because it was impossible, in the field, to collect all tadpoles at the same developmental stage, we defined metamorphosis as Gosner stages 40–41. The body mass of each tadpole was estimated using its TL and a previously established ($r^2 = 0.942$, $n = 122$) body mass–TL equation: $\log(\text{body mass}) = 2.932 \log(\text{TL}) - 4.998$.

Statistical Analyses

Each bamboo stump was an experimental unit. The treatment means of all measured variables were calculated from the means of the corresponding variables from each bamboo stump. Data were analyzed with SAS (SAS Institute Inc., 1988). In Experiment I, only data from the fed clutches (or attended stumps) were used to analyze the growth, survivorship, and survival to metamorphosis of tadpoles (Table 1). Data from stumps in which at least one younger tadpole reached metamorphosis were used to compare the length of larval period and mass at metamorphosis among treatments. We compared the growth and survivorship

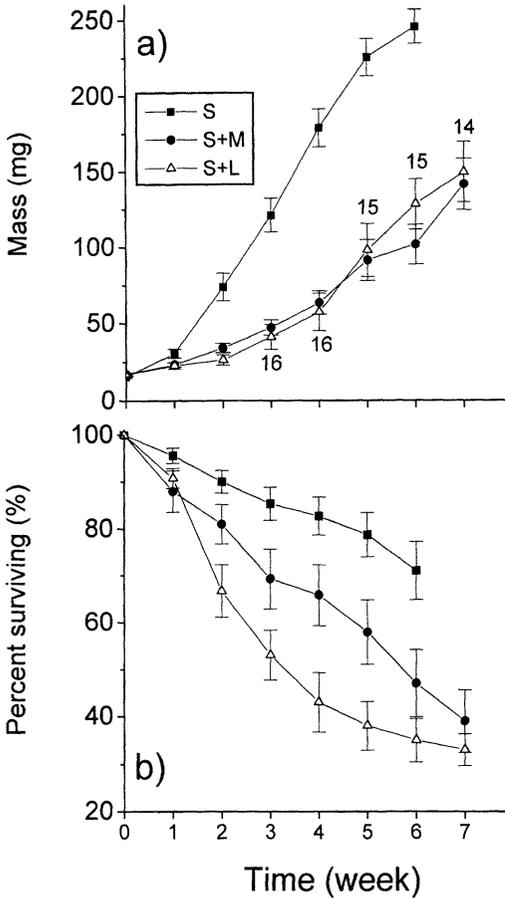


FIG. 1.—Changes in the (a) mass and (b) survival of small tadpoles in three treatments: S—small tadpoles only; S + M—medium tadpoles added; S + L—large tadpoles added. The sample sizes for the S and S + M treatments were 15 and 12 small tadpoles, respectively. In the S + L treatment, the sample size was 18 unless labeled. The last datum point of each line represents the time at which the first small tadpole in each treatment reached metamorphosis. Values are means \pm SE.

curves of younger tadpoles during the first 5 wk of development using repeated measures ANOVA. We pooled the data into S (small tadpoles with no older tadpoles), S + M (small tadpoles with medium tadpoles), and S + L (small tadpoles with large tadpoles) treatments (Fig. 1). We analyzed the survival to metamorphosis, the length of larval period, and mass at metamorphosis using a two-way ANOVA. Because these three response variables were measured from the same data, we used the

sequential Bonferroni method for multiple comparisons (Rice, 1989). Data were transformed to meet the parametric assumption of normality. Survivorship and survival to metamorphosis were arcsine transformed, while the length of larval period and mass at metamorphosis were log transformed.

In Experiment II, only data from the clutches of tadpoles that had been fed were used for statistical analyses of tadpole mass and survival to week 4 of development, and survival to metamorphosis. Furthermore, data from clutches in which at least one younger tadpole reached metamorphosis was used to compare length of larval period and mass at metamorphosis among treatments. We assessed the effects of older tadpole abundance on the growth and development of younger tadpoles by performing the following comparisons: 20S versus 30S and 10S 10L versus 10S 20L. We also assessed the effects of the presence of older tadpoles on the growth and development of the younger tadpoles by performing the following comparisons: 20S versus 10S 10L, and 30S versus 10S 20L. Due to small sample sizes, we used the Wilcoxon two-sample test to analyze the data. The means \pm 1 SD of all variables are reported unless specified otherwise.

RESULTS

Experiment I

This 2×3 factorial design experiment, conducted in 1997, used a total of 72 bamboo stumps. Female frogs fed the tadpoles in 45 stumps, while tadpoles in the remaining 27 stumps were not fed (Table 1). Tadpoles that did not receive any trophic eggs during development did not grow at all and disappeared after 3–4 wk. At least one small tadpole reached metamorphosis in each of the six treatments (Table 1).

Large tadpoles underwent metamorphosis significantly earlier than medium tadpoles (20.8 ± 3.8 days, range 16–25, $n = 12$, 35.6 ± 6.9 days, range 26–41, $n = 18$, respectively; $F_{1,28} = 42.88$, $P = 0.0001$). Thus, small tadpoles in pools coexisted with large tadpoles for 15 fewer days on average than small tadpoles living in pools with medium tadpoles.

TABLE 2.—Summary of the two-way ANOVA of survival to metamorphosis, larval period, and mass at metamorphosis of tadpoles in *Chirixalus eiffingeri*.

Variables	Source	df	SS	MS	F ratio	Pr > F
Survivorship at metamorphosis	Brood size	1	0.00494	0.00494	0.11	0.7427
	Older tadpoles	2	1.794052	0.89703	19.83	0.0001
	Interaction	2	0.04914	0.02457	0.54	0.5853
	Error	39	1.76446	0.04524		
Larval period	Brood size	1	0.02996	0.02996	7.41	0.011
	Older tadpoles	2	0.14375	0.07187	17.78	0.0001
	Interaction	2	0.00740	0.00370	0.92	0.4119
	Error	28	0.11318	0.00404		
Body mass at metamorphosis	Brood size	1	0.00042	0.00042	0.04	0.8388
	Older tadpoles	2	0.07338	0.03669	3.67	0.0385
	Interaction	2	0.02267	0.01133	1.13	0.3364
	Error	28	0.28914	0.01000		

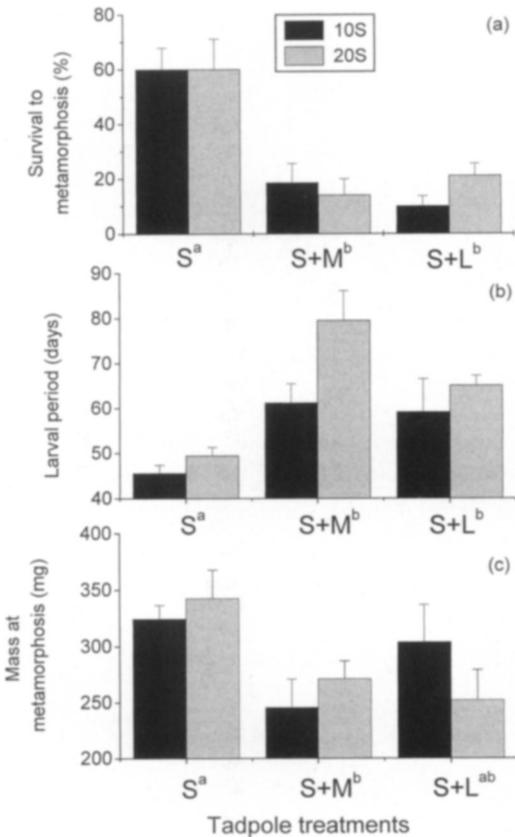


FIG. 2.—The (a) survival to metamorphosis, (b) larval period, and (c) mass at metamorphosis of younger tadpoles in six different treatments. Tadpole treatments (S, S + M, or S + L) with same superscripts were not significantly different. Values are means \pm SE. See Table 1 for the experimental design and sample size.

Medium and large tadpoles had detrimental effects on the growth (Repeated measures ANOVA, $F_{2,40} = 30.33$, $F = 0.0001$; Fig. 1a) and survivorship (Repeated measures ANOVA, $F_{2,42} = 16.08$, $F = 0.0001$; Fig. 1b) of small tadpoles during the first 5 wk of development. After week 5, small tadpoles of the S + L treatment grew somewhat faster than the small tadpoles of the S + M treatment (Fig. 1a). The survivorship of small tadpoles in the S + M treatments decreased linearly, while the survivorship of small tadpoles in the S + L treatments decreased exponentially (Fig. 1b).

The addition of older tadpoles (large or medium) significantly affected the survival to metamorphosis, larval period, and mass at metamorphosis of small tadpoles (Table 2). Small tadpoles reared alone had a significantly higher survival to metamorphosis and shorter larval period than tadpoles in the presence of larger tadpoles (Fig. 2a,b; $P < 0.05$). However, the mass at metamorphosis of the S treatment was only larger than that of S + M treatment (Fig. 2c). There was no difference between the effects of different size classes of older tadpoles (Fig. 2a–c).

An increase in the clutch size of younger tadpoles from 10–20 significantly increased the larval period (10S group: 51.82 ± 11.72 days, $n = 17$; 20S group: 63.03 ± 12.34 days, $n = 17$) but did not affect the mass at metamorphosis and survival to metamorphosis (Table 2).

Experiment II

Conducted in 1998, this experiment had four treatments and used a total of 44 bamboo stumps. Female frogs fed the tadpoles in 30 stumps, while tadpoles in the remaining 14 stumps were not fed (Table 1). There were seven, two, nine, and zero stumps in which at least one smaller tadpole reached metamorphosis in the 20S, 10S 10L, 30S and 10S 20L treatments, respectively (Table 1).

The older tadpoles in the 10S 10L and 10S 20L treatments reached metamorphosis between weeks 4 and 6. The initial mass of the younger tadpoles in each of the four treatments was statistically similar ($F_{3,40} = 1.36$, $P = 0.912$). By week 4, the survivorship and mass of younger tadpoles that coexisted with 20 older tadpoles were significantly lower than those of 30 younger tadpoles that grew alone (Wilcoxon two-sample test, $Z = -2.172$, $P = 0.031$ and $Z = -3.199$, $P = 0.0014$, respectively). In contrast, respective measured variables of younger tadpoles that coexisted with 10 older tadpoles were statistically similar to those of 20 younger tadpoles that grew alone ($Z = -1.041$, $P = 0.291$ and $Z = -1.028$, $P = 0.3036$, respectively; Fig. 3a,b). Neither an increase in the number of older tadpoles (10S 10L versus 10S 20L), nor an increase in the number of younger tadpoles in the absence of older tadpoles (20S versus 30S) significantly reduced the survivorship and mass of younger tadpoles (10S 10L versus 10S 20L: $Z = 0.237$, $P = 0.813$ and $Z = 0.904$, $P = 0.366$, respectively; 20S versus 30S: $Z = 0.393$, $P = 0.696$ and $Z = 0.536$, $P = 0.591$; Fig. 3a,b).

The survival to metamorphosis of younger tadpoles that coexisted with 20 older tadpoles was significantly lower than those of 30 younger tadpoles that grew alone (Wilcoxon two-sample test, $Z = -3.84$, $P = 0.0001$; Fig. 4a). In addition, an increase in the number of older tadpoles (from 10L to 20L) significantly reduced the survival to metamorphosis of younger tadpoles (Wilcoxon two-sample test, $Z = 2.085$, $P = 0.037$; Fig. 4a). In fact, none of the younger tadpoles in the 10S 20L treatment

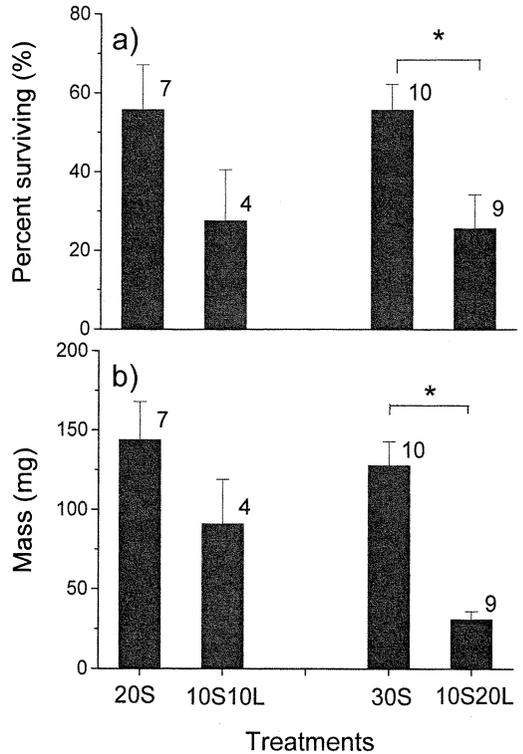


FIG. 3.—The (a) mass and (b) survival of younger tadpoles at week 4 of development. Comparisons (Wilcoxon two-samples test) were made for 20S vs. 30S, 10S 10L vs. 10S 20L, 20S vs. 10S 10L, and 30S vs. 10S 20L. Means that are significantly different ($P \leq 0.05$) are indicated by an asterisk (*). Sample sizes are indicated at the top of each bar. Values are means \pm SE. See the materials and methods section for descriptions of the treatments.

survived. Of the younger tadpoles that survived to metamorphosis, the mass at metamorphosis and larval period were statistically similar between treatments (20S versus 30S: $Z = 0.635$, $P = 0.524$ and $Z = 1.227$, $P = 0.219$, respectively; 20S versus 10S10L: $Z = -0.14$, $P = 0.880$ and $Z = 1.328$, $P = 0.184$, respectively; Fig. 4b,c).

DISCUSSION

Clutch desertion by females of *C. eiffingeri* is common (Kam et al., 1997, 1998b). Tadpoles in deserted clutches were not fed, did not grow and develop, and died after several weeks due to starvation. We obtained similar results in an earlier study in which we monitored the growth, development, and survivorship of tadpoles in

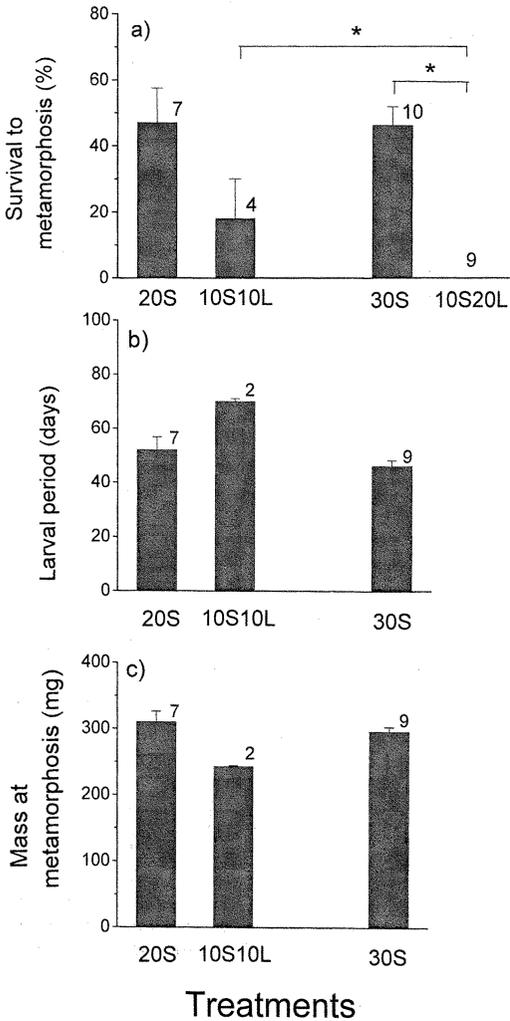


FIG. 4.—The (a) survival to metamorphosis, (b) larval period, and (c) mass at metamorphosis of younger tadpoles in different treatments. Comparisons are the same as in Fig. 3. Because no small tadpoles from the 10S 20L treatment reached metamorphosis, we could not compare their larval period and mass at metamorphosis with those of tadpoles in the 10S 10L treatment. Means that are significantly different ($P \leq 0.05$) are indicated by an asterisk (*). Values are means \pm SE. Sample sizes are indicated at the top of each bar. See the materials and methods section for descriptions of the treatments.

unmanipulated clutches (Kam et al., 1997). The proportion of bamboo stumps that were deserted by female frogs during this study (37.5%) was similar to that observed during an earlier study conducted in the same region (Kam et al., 1998b). Based on a field-manipulated experiment,

Kam et al. (2000) demonstrated that females of *C. eiffingeri* were unable to differentiate kin from non-kin, but they were able to orient themselves to their nesting bamboo stumps. Thus, mixing of tadpoles from different clutches should not result in clutch desertion. Based on our field observations (Kam et al., 1997, 1998b, this study), most clutch desertion was caused by predation on female frogs and clutch abandonment following disturbance by researchers and local farmers.

Effects of Older Tadpoles on the Growth, Development, and Metamorphosis of Younger Tadpoles

The presence of older tadpoles adversely affected the growth and development of younger tadpoles. In Experiment II, older tadpoles in the 10S 20L treatment denied younger tadpoles access to trophic eggs, and all younger tadpoles died. Older tadpoles are probably able to outcompete younger tadpoles for trophic eggs due to their larger size (Kam et al., 1997), and this is likely due to exploitative and/or behavioral interference competition (Kam, unpublished data). Similar size-selective feeding behaviors have been documented for other anuran tadpoles (Savage, 1952; Semlitsch and Caldwell, 1982; Wilbur, 1977). For tadpoles that rely on trophic eggs, the competitive advantage of larger size is further magnified by the nature of the food source. Tadpoles of *C. eiffingeri* are obligatorily oophagous (Kam et al., 1996; Ueda, 1986), and although the trophic eggs are a highly nutritious and concentrated source of nutrition, they are limited in number and available only when the female frog is present. Older tadpoles, whose larger size gives them an advantage over younger tadpoles, are able to monopolize most of the eggs laid by the female frog. During our weekly censuses, we rarely observed yolk in the stomachs of younger tadpoles. Younger tadpoles that obtained trophic eggs only occasionally grew slowly and took longer to reach metamorphosis. Prolonged starvation resulted in a failure to reach metamorphosis and death. The effect of older tadpoles on younger tadpoles is analogous to the priority effects

where researchers studied the effects of the order or temporal separation of species' arrivals on inter-specific competition (Alford and Wilbur, 1985; Caldwell, 1993; Lawler and Morin, 1993; Wilbur, 1997; Wilbur and Alford, 1985). These studies found that size-specific competition is the crucial mechanism underlying tadpole interactions.

Comparison of the Effects of Medium and Large Tadpoles on the Growth, Development, and Metamorphosis of Younger (Small) Tadpoles

In Experiment I, during the first 5 wk of development, small tadpoles in the S + L treatments experienced much higher mortality than small tadpoles in the S + M treatments despite demonstrating similar growth pattern. Large tadpoles probably exert a greater competitive impact on small tadpoles than medium tadpoles. As a result, small tadpoles in the S + L treatments suffered higher mortality, leaving a lower number of small tadpoles in the bamboo stumps. A lower number of small tadpoles reduced intra-cohort food competition, perhaps enabling the survivors to grow at a rate similar to that of small tadpoles in the S + M treatments. Earlier studies have documented similar "ecological release" phenomena where stunted tadpoles that are released from intra- and interspecific competition experience favorable conditions for growth and metamorphose at a body size comparable to or larger than tadpoles raised in the low density (Morin, 1983; Parris and Semlitsch, 1998; Semlitsch and Caldwell, 1982).

Small tadpoles in the S + L treatments had an average of 15 more days without larger tadpoles in their pool than small tadpoles in the S + M treatments. The duration of temporal overlap may significantly affect the growth and development of younger tadpoles (Lawler and Morin, 1993). As large tadpoles in the S + L treatments underwent metamorphosis and left the bamboo stumps, small tadpoles experienced a release in competitive suppression. However, the effects of the large and medium tadpoles on small tadpole mass at metamorphosis and time of metamorpho-

sis were not significantly different. Apparently, 15 days of competitive release were insufficient to influence significantly the growth and development of small tadpoles in the S + L treatments. This is in part because small tadpoles in the S + M treatments were gradually released from competitive suppression of the medium tadpoles as the latter underwent metamorphosis during weeks 4–6. It is also possible that the tadpoles' growth history determined the timing of metamorphosis, as has been shown in other studies of anuran larvae (Hensley, 1993; Leips and Travis, 1994; Tejedo and Reques, 1994; Travis, 1984). In other words, due to low food availability experienced by all small tadpoles in the S + M and S + L treatments early in the larval period, a low developmental rate was maintained throughout the larval period.

Effects of Clutch Size of Younger Tadpoles on the Survivorship and Mass at Metamorphosis of Younger Tadpoles

In Experiment I, an increase in the clutch size of younger tadpoles from 10 to 20 significantly increased the larval period but did not affect the mass at metamorphosis or survival to metamorphosis. Other studies have found that tadpoles of various species reared at high densities undergo metamorphosis later than those reared at low densities (Brockelman, 1969; Dash and Hota, 1980; Semlitsch and Caldwell, 1982; Wilbur, 1977). Kam et al. (1998b) presented indirect evidence that females of *C. eiffingeri* are capable of increasing the food supply (i.e., the number of trophic eggs) in response to an increase in the tadpole number within limits. As a result, an increase of clutch size did not affect the growth and development of younger tadpoles, as shown in Experiment I (10S to 20S) and II (20S to 30S). However, those younger tadpoles that coexisted with older tadpoles were probably still unable to obtain sufficient food due to severe competition with older tadpoles.

Ecological Implications

Chirixalus eiffingeri breeds from February–August. Females produce multiple

clutches during the breeding season (Kam et al., 1996). Bamboo stumps are selectively used and reused within a breeding season. Based on field observations (Kam et al., 1996, 2000; this study), most of the female frogs probably reuse the same or nearby stumps. Kam et al. (1997) reported that females of *C. eiffingeri* deposited new clutches of eggs in bamboo stumps containing developing tadpoles, and these two cohorts of tadpoles lived together in the pools for about four weeks. However, experimental results have demonstrated that tadpoles of an early-hatching cohort suppressed the growth, increased larval period, and reduced survivorship of tadpoles of a late-hatching cohort. One potential advantage that offsets the risk of tadpole mortality is that successive nesting attempts could reduce the chance of another female finding the nesting site and laying fertile eggs in it. Furthermore, females of *C. eiffingeri* could simultaneously care for two sets of offspring in different stages of development, which may reduce the time interval between successive nesting attempts and enable rapid production of multiple clutches, much like some birds. For example, the Mourning Dove (*Zenaida macroura*) may eliminate nesting intervals altogether by overlapping nesting cycles and simultaneously caring for two sets of offspring at different stages of development (Burley, 1980; Westmoreland et al., 1986). Our experiments demonstrated that the number, but not the developmental stages, of older tadpoles had significant effects on the growth and development of the younger tadpoles. This suggests that when a female frog reuses a bamboo stump, the time when the second clutch of eggs is produced is critical to the success of that clutch. If older tadpoles are abundant, then the female frog should continue feeding them trophic eggs, rather than laying a new clutch of fertile eggs. The female frog should lay a second clutch of eggs only after the older tadpoles are low in number. Such a strategy reduces intraspecific competition between the two cohorts of tadpoles and enables the female frog to maximize her overall reproductive

output by caring for two sets of offspring simultaneously.

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