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Importance of Maternal Brood Care

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## DENSITY EFFECTS OF OOPHAGOUS TADPOLES OF *CHIRIXALUS EIFFINGERI* (ANURA: RHACOPHORIDAE): IMPORTANCE OF MATERNAL BROOD CARE

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**ABSTRACT:** We studied the density-dependent aspects of growth, development, and survivorship of arboreal tadpoles of *Chirixalus eiffingeri* in bamboo forests at the Experimental Forest of the National Taiwan University at Chitou, Taiwan, from May–September 1995. Newly hatched tadpoles were randomly assigned to one of the three treatments: low (LD), medium (MD), and high density (HD) (six, 18, and 54 tadpoles/bamboo stump, respectively), and each treatment consisted of 15 replicates. Tadpoles of *Chirixalus eiffingeri* are obligatorily oophagous; thus, growth, development, and survivorship of tadpoles are totally dependent upon trophic egg availability. Tadpoles in all treatments increased in mass during development, but LD and MD tadpoles grew faster and weighed significantly heavier than HD tadpoles by week 5. During the first five weeks of development, the biomass increase of tadpoles (BMI) in successful nests was substantially greater than zero and was significantly different between treatments, indicating that female frogs are capable of increasing the supply of trophic eggs as the tadpole number increased in MD and HD treatments. Body size at metamorphosis was density-dependent but the time required to reach metamorphosis was not, which was different from earlier studies on pond breeders. This discrepancy is probably due to the different feeding habits (i.e., herbivory versus oophagy) and size-selective feeding behavior. Results suggest that the energetic reserves of female frogs for brooding strongly affect the growth, development, and survivorship of tadpoles.

*Key words:* Anura; Ecology; Density effects; Tadpole oophagy; Maternal brood care; Phytotelmata

ANURANS are the only vertebrates that use phytotelmata, unique aquatic microhabitats that occur in leaf axils, flowers, tree holes, bamboo stumps, and nut capsules, for breeding purposes (Caldwell, 1993; Duellman and Trueb, 1986; Kam et al., 1996; Laessle, 1961), and many species exhibit fascinating adaptations. These aquatic microhabitats are isolated, small pools that are highly amenable to experimental manipulation. Unlike the field enclosures employed in many studies, phytotelmata represent “truly” natural systems, and in most cases, different cohorts

of tadpoles can be identified and tracked throughout the larval period. The unique features of their breeding sites, together with diverse reproductive modes, make arboreal nesting frogs (adults and tadpoles) superb model organisms for studying the ecological (Caldwell, 1993; Donnelly, 1989a,b; Kam et al., 1997; Steward and Pough, 1983), behavioral (Brust, 1993; Caldwell, 1997; Jungfer, 1996; Taigen et al., 1984; Townsend et al., 1984; Ueda, 1986; Weygoldt, 1980), and morphological and physiological adaptations (Brust, 1993; Lannoo et al., 1987; Ueda, 1986; Wassersug et al., 1981) to arboreal aquatic microhabitats.

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One of the most fascinating adaptations of arboreal breeders is the evolution of tadpole oophagy in response to food scarcity (Brust, 1993; Caldwell, 1997; Jungfer, 1996; Lannoo et al., 1987; Ueda, 1986; Wassersug et al., 1981). Evidence has shown that tadpoles of *Dendrobates pumilio* and *Chirixalus eiffingeri* are obligatorily oophagous and are fed by female frogs (Brust, 1993; Kam et al., 1996; Ueda, 1986). Typically, a female frog re-visits her oviposition site periodically and lays fertilized or unfertilized eggs in the pools, thus feeding her young until metamorphosis (Brust, 1993; Jungfer, 1996; Thompson, 1992; Ueda, 1986). Thus, the food supply is controlled, and the growth and development of tadpoles potentially regulated by the brooding efforts of female frogs; consequently, tadpoles may escape density-dependent stress caused by food shortage. In contrast, the tadpoles of pond breeders, which are herbivorous filter feeders or macrophages, receive no maternal care and their food supply is limited to that available in their ponds. As expected, larvae of pond breeders exhibit density-dependent responses to crowding, including decreased growth and survivorship, and an increase in the length of the larval period (Brockelman, 1969; Dash and Hota, 1980; Semlitsch and Caldwell, 1982; Wilbur, 1976 1977).

We studied the response of oophagous tadpoles of *Chirixalus eiffingeri* to density stress and the extent to which growth, development, and survivorship are density-dependent. Specifically, we measured the effects of density on the time to metamorphosis, body size at metamorphosis, and survival to metamorphosis. During the breeding season, females of *C. eiffingeri* deposit fertilized eggs above the waterline on the inner walls of tree holes, bamboo stumps, or water-filled buckets (Chuang, 1988; Kuramoto, 1973). Upon hatching, tadpoles drop below the water pool where they grow and develop until metamorphosis. Tadpoles are obligatorily oophagous and are fed by females that lay unfertilized trophic eggs, in the absence of male frogs, directly in the water (Ueda, 1986).

## MATERIALS AND METHODS

### *Study Site and Egg Collection*

We conducted this experiment from May–September 1995 in bamboo forests at the Experimental Forest of the 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, which is not distributed evenly during the year. Although rain falls in all months, the wet season begins in February and ends in late September. Annual mean air temperature is about 17 C, and the temperatures are relatively constant during the study period with the maximum temperature difference <3 C. 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. Bamboo trunks are hollow; when cut, the hollow stems collect rain water and become ideal nesting sites for *C. eiffingeri*.

We located bamboo stumps with fertilized eggs attached to the inner wall above the pool. Fertilized eggs are characterized by having an animal and a vegetal hemisphere. Embryos were usually developing when we found the eggs. In contrast, infertile eggs do not have animal and vegetal hemispheres, and the egg yolk appears cloudy. We monitored the egg clutches twice a week and collected tadpoles after they hatched.

### *Experimental Design*

Newly hatched tadpoles from 40 clutches were randomly distributed among three different treatments: low (six tadpoles/stump), medium (18 tadpoles/stump), and high density (54 tadpoles/stump) (hereafter called LD, MD, and HD, respectively). These tadpole numbers represented the low, average, and high ranges, respectively, found in the field (Kam et al., 1997; Lin, 1996). We designated a bamboo stump as an experimental unit, and each treatment consisted of 15 randomly selected stumps. Only stumps in which tadpoles were found

were used for the experiment. In this experiment, the number of trophic eggs deposited by a female frog in a bamboo stump during the larval period was an unknown, thus the food level in each bamboo stump was uncontrolled.

We maintained the water volume of each bamboo stump at about 250 ml (Kam et al., 1996), and water was added as necessary to compensate for water loss due to evaporation. We also removed macroorganisms, mainly tipulid (Diptera) larvae which sometimes consume trophic eggs deposited by female frogs.

#### *Experimental Protocol*

Initially, tadpoles were examined each week, but when they reached Gosner stage 37 (Gosner, 1960) and neared metamorphosis, we increased our visits to 2–3 times per week until no tadpoles remained. To facilitate the examination and measurement of tadpoles, on our first visit we sawed a V-shaped cut in the bamboo stump, and the detached portion of the stump contains water and tadpoles. This allowed us to easily 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.

During each visit, we poured the tadpoles and water into a bucket and used a small net to transfer the tadpoles carefully to a Petri dish. The tadpoles were counted and photographed with a ruler beneath the Petri dish to determine their total lengths (TL). Depending on the number of tadpoles, it took two people 15–35 min to go through the entire procedure for each stump.

We minimized the disturbance of maternal feeding behavior by examining the bamboo stumps during the day, because female frogs fed their tadpoles at night (Chuang, 1988). Due to time constraints, we did not study the feeding behavior and schedule of female frogs in this experiment. 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 been 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 the capsule.

We determined (1) the number of tadpoles in each bamboo stump during development and the percentage of tadpoles that reached metamorphosis. Because it was impossible to collect all tadpoles at a certain developmental stage in the field, we defined metamorphosis as either Gosner stage 40 or 41; (2) the time required for each tadpole in each stump to reach metamorphosis and the time interval between when the first and last tadpole in a pool reached metamorphosis; and (3) the body mass of each tadpole at metamorphosis and changes in tadpole body mass during development. The body mass of each tadpole was estimated using its total length (TL, snout to tail tip) and a body mass–TL equation,  $\log(\text{body mass}) = 2.80 \log(\text{TL}) - 4.87$ , which was previously established ( $r = 0.98$ ,  $n = 71$ ). In addition, we calculated the coefficient of variation (CV) of body mass of all tadpoles in each stump when any tadpole in that stump reached metamorphosis; (4) the biomass increase (BMI) of tadpoles (g) in each bamboo stump during the first 5 wk of development as follows.

$$\text{BMI} = \sum_{i=1}^5 (\bar{x}_{i+1} - \bar{x}_i)n_{i+1}$$

where,  $\bar{x}_{i+1}$  is the mean body mass of tadpoles at  $(i + 1)$  th week,  $\bar{x}_i$  is the mean body mass of tadpoles at  $i$  th week and,  $n_{i+1}$  is the tadpole number at  $(i + 1)$  th week.

We used the BMI to estimate maternal feeding efforts (i.e., the number or mass of trophic eggs deposited) of female frogs in each bamboo stump. This is justified because the tadpoles are obligatorily oophagous (Kam et al., 1996; Ueda, 1986), so increases in biomass must have come from consumption of trophic eggs. In a previous

study, tadpoles that did not receive trophic eggs failed to grow (Kam et al., 1996, 1997), indicating that cannibalism and scavenging effects on BMI are negligible. Low levels of BMI in failed nests (Fig. 3) were due to the metabolic contribution from residual yolk of hatchlings. We assumed that the digestive efficiencies of tadpoles in all treatments were similar. Because some tadpoles in all three treatments reached metamorphosis after week 5, data after that time were excluded from calculations.

### Statistical Analyses

Each stump was an experimental unit. The treatment means of all measured variables were calculated from the means of the corresponding variables of each bamboo stump. Data were analyzed by a SAS program using a General Linear Model procedure (SAS Institute Inc., 1988). If measurements were significantly different between treatments, we used Duncan's Multiple Range Test for comparisons. Data from failed nests, defined as nests in which no tadpoles reached metamorphosis, were excluded from analyses. In contrast, a successful nest was defined as one in which at least one tadpole reached metamorphosis. Body mass was log transformed. Means  $\pm$  1 SD of all variables are reported unless otherwise noted.

### RESULTS

There were nine, 11, and nine successful, and six, four, and six failed nests in the LD, MD, and HD treatments, respectively. We excluded two bamboo stumps with successful nests in the HD treatment from subsequent statistical analyses because they were knocked over by farmers harvesting bamboo shoots during the course of the experiment. Most failed nests did not receive any trophic eggs during the development as evidenced by the absence of egg capsules throughout the study period, and the tadpoles did not grow at all before they disappeared 3–4 wk later. Two, two, and one failed nests in the LD, MD, and HD treatments, respectively, did receive trophic eggs in the first 2 wk, and tadpoles grew as large as 98 mg at week 4; however,

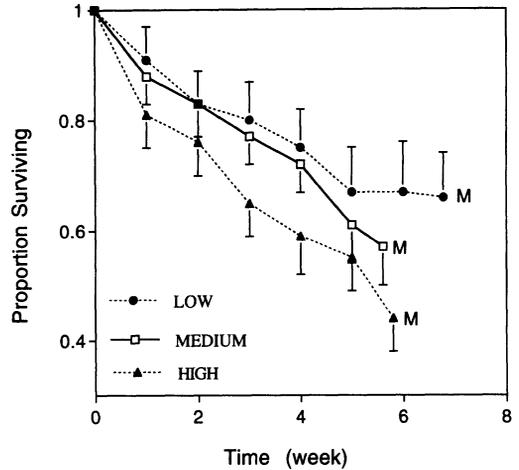


FIG. 1.—The mean proportion of surviving tadpoles to metamorphosis. Time for the first tadpole to reach metamorphosis is indicated by "M" symbols. Values are means  $\pm$  SE.

they stopped growing after that and died later.

### Tadpole Survivorship

The number of tadpoles in all treatments decreased during development, yet the relative density levels between LD, MD, and HD treatments were maintained (Fig. 1). Before reaching metamorphosis, decrease in the number of tadpoles was due to mortality, but after metamorphosis, a combination of mortality and the departure of newly metamorphosed froglets accounted for the decline. The metamorphic rate differed significantly among treatments ( $F_{2,24} = 4.93$ ,  $P = 0.016$ ), and multiple comparisons of the means showed that metamorphic rate of tadpoles in the HD treatment was significantly lower than in the LD and MD treatments (Table 1).

### Body Mass Change during Development

The tadpoles in all treatments increased in mass during development but the rates of mass increase were different (Fig. 2). Tadpoles in the LD and MD grew exponentially and attained  $\bar{x} = 180 \pm 83$  and  $\bar{x} = 168 \pm 32$  mg, respectively, by week 5. Tadpoles in the HD treatment increased mass at a constant rate and attained  $\bar{x} = 111 \pm 40$  mg by week 5. Body mass was significantly different between treatments

TABLE 1.—Life history characteristics of tadpoles of *Chirixalus eiffingeri* in low, medium, and high density treatments. Means with different letters are significantly different ( $P < 0.05$ ); values are mean  $\pm$  SD.

Treatments	Low	Medium	High
Sample size	9	11	7
Body mass at metamorphosis (mg)	271 $\pm$ 55 <sup>a</sup>	237 $\pm$ 34 <sup>ab</sup>	212 $\pm$ 33 <sup>b</sup>
Time to metamorphosis (days)	49.6 $\pm$ 9.3	47.4 $\pm$ 4.6	54.2 $\pm$ 5.9
Metamorphic rate (%)	63.0 $\pm$ 29.6 <sup>a</sup>	49.0 $\pm$ 21.7 <sup>ab</sup>	27.3 $\pm$ 9.53 <sup>b</sup>
Time for the first tadpole to reach metamorphosis (days)	47.5 $\pm$ 10.4 <sup>a</sup>	39.5 $\pm$ 4.7 <sup>b</sup>	41.0 $\pm$ 2.7 <sup>ab</sup>
Time for the last tadpole to reach metamorphosis (days)	53.7 $\pm$ 8.54 <sup>a</sup>	61.7 $\pm$ 13.6 <sup>a</sup>	77.9 $\pm$ 15.8 <sup>b</sup>
Time interval between when the first and last tadpoles reach metamorphosis (days)	6.2 $\pm$ 6.5 <sup>a</sup>	22.3 $\pm$ 10.4 <sup>b</sup>	36.9 $\pm$ 18.4 <sup>c</sup>
Coefficient of variation of body masses of all tadpoles when any tadpole reaches metamorphosis (%)	27.1 $\pm$ 23.6 <sup>a</sup>	38.0 $\pm$ 12.6 <sup>a</sup>	60.4 $\pm$ 11.9 <sup>b</sup>

at week 5 ( $F_{2,23} = 3.46$ ,  $P = 0.048$ ). Multiple comparisons of the means found no differences between LD and MD tadpoles but both treatments were significantly heavier than HD tadpoles ( $P < 0.05$ ) (Fig. 2).

#### Developmental Time

The time required for tadpoles to reach metamorphosis was not significantly different between treatments ( $F_{2,24} = 2.47$ ,  $P =$

0.104). The time for the first and last tadpole to reach metamorphosis and the time interval from when the first and last tadpole(s) reached metamorphosis were significantly different between treatments ( $F_{2,24} = 3.60$ ,  $P = 0.043$ ;  $F_{2,24} = 7.23$ ,  $P = 0.0035$ ;  $F_{2,24} = 10.75$ ,  $P = 0.0005$ , respectively) (Table 1). In other words, the fastest growing tadpole in the MD treatment reached metamorphosis earlier than those in the LD treatment, and, as a whole, it took significantly longer for all MD and HD tadpoles to reach metamorphosis than did it for all LD tadpoles (Table 1).

#### Body Mass at Metamorphosis

The body masses of tadpoles at metamorphosis were significantly different between treatments ( $F_{2,24} = 4.51$ ,  $P = 0.021$ ): i.e., the LD tadpoles were significantly heavier than HD tadpoles (Table 1). We calculated the coefficient of variation (CV) of body mass of all tadpoles in each stump when any tadpole in that stump reached metamorphosis, and found that the CV of HD tadpoles was 1.5 and 2.5 times larger than that of MD and LD tadpoles, respectively (Table 1).

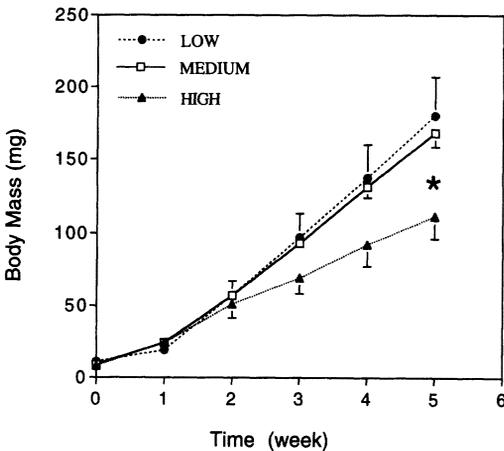


FIG. 2.—Changes in tadpole body mass as a function of time in successful nests. Sample sizes are 9, 11, and 7 bamboo stumps in the low, medium, and high density treatments. Absence of error bars indicated that bars were too small to be seen; \* represents an overall significant difference at  $\alpha = 0.05$ . Multiple comparisons of the means found no differences between tadpoles of low and medium densities, but both treatments were significantly heavier than tadpoles of high density. Values are means  $\pm$  SE.

#### Biomass Increase (BMI) during Five Weeks of Development

The BMI of successful nests was significantly different between treatments ( $F_{2,24} = 11.20$ ,  $P = 0.0004$ ). Multiple comparisons of the means showed that the BMI of tadpoles in the HD treatment was 2.87

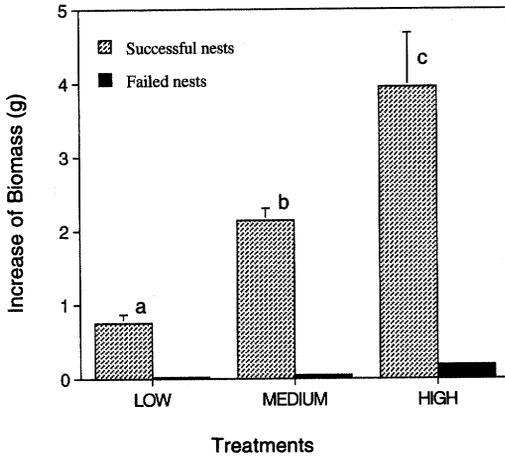


FIG. 3.—Biomass increase of tadpoles during the first 5 wk of development. Sample sizes are 9, 11, and 7 bamboo stumps for successful nests and 6, 4, and 6 bamboo stumps for failed nests in the low, medium, and high density treatments, respectively. For successful nests, means with different letters are significantly different between treatments ( $P < 0.05$ ). Absence of error bars indicated that bars were too small to be seen. Values are means  $\pm$  SE. See materials and methods for definitions of biomass increase of tadpoles, and of successful and failed nests.

and 5.29 times higher than that of tadpoles in the MD and LD treatments, respectively (Fig. 3). In contrast, the BMI of tadpoles in failed nests in all treatments were negligible (Fig. 3)

#### DISCUSSION

Nest desertion by female frogs is common in this species. Tadpoles in the deserted nests were not fed and did not grow and develop, and they died several weeks later due to starvation, which agrees with the findings by Kam et al. (1997) where they monitored the growth, development, and survivorship of tadpoles in unmanipulated nests. Our field observations concluded that predation on female frogs and nest abandonment by female frogs due to human disturbances by researchers and local farmers accounted for the nest desertion. We recorded nine species of snakes on 19 occasions in our study site during the study period and observed a colubrid snake (*Dinodon rufozonatum*) swallowing an adult frog. Local farmers harvested bamboo shoots by scraping the leaf litter

and topsoil, which might disturb female frogs or interfere with the homing ability of female frogs, particularly if chemical cues were used. Handling the bamboo stumps, even carefully, would be a disturbance to female frogs.

#### Growth, Survivorship, Body Size, and Time to Reach Metamorphosis

Tadpoles of *Chirixalus eiffingeri* are obligatorily oophagous (Kam et al., 1996; Ueda, 1986); thus, growth, development, and survivorship of tadpoles are totally dependent upon trophic egg availability. If, for any reason, a female does not return to deposit trophic eggs into the pool, as happened with the failed nests, the tadpoles cannot grow and develop, and eventually die of starvation (Kam et al., 1997).

Tadpoles in successful nests reached metamorphosis (Fig. 2) and had a BMI substantially greater than zero (Fig. 3), indicating that they were fed. Significant differences in the BMI between treatments (Fig. 3) suggest that female frogs are capable of increasing the supply of trophic eggs in response to greater number of tadpoles. Ueda (1986) reported an "egg begging" behavior by tadpoles, which is similar to that of larval *D. pumilio* and *A. spinosa* (Brust, 1993; Jungfer, 1996). When a female of *C. eiffingeri* enters the pool of water, tadpoles aggregated around her immediately with vigorous "nipping" at her skin around the cloaca and thigh areas (Ueda, 1986). The female then begins to lay trophic eggs little by little without the presence of a male. Eggs were bitten by tadpoles immediately after being laid, and the yolk was sucked out in seconds (Ueda, 1986). Female frogs could potentially sense tadpoles' demands by the degree and frequency of "nipping" by tadpoles on her skin around the cloaca and thigh areas (Kam et al., 1997).

The growth rate of the tadpoles of *C. eiffingeri* raised in the low density (LD) treatment was high, and the tadpoles were able to exceed the minimum body size for initiation of metamorphosis and maximize their size at metamorphosis (Table 1, Fig. 2); in contrast, tadpoles raised in the crowded HD treatment grew more slowly

and metamorphosed as soon as they reached the threshold size for metamorphosis (Wilbur and Collins, 1973). However, density did not affect the time required to reach metamorphosis. This is in contrast to studies on the herbivorous tadpoles of pond breeders, which receive no maternal care. Those pond tadpoles reared at high densities reach metamorphosis later than those reared at low densities (Brockelman, 1969; Dash and Hota, 1980; Semlitsch and Caldwell, 1982; Wilbur, 1977). This discrepancy is probably due to different feeding habits (oophagy versus herbivory) and size-selective feeding behavior (Semlitsch and Caldwell, 1982; Wilbur, 1977). Trophic eggs are highly concentrated, nutritious, and digestible food sources that were limited in number and available only when the female frog was present. Trophic eggs were laid by female frogs at an interval of  $\bar{x} = 8.7 \pm 1.9$  days ( $n = 14$  bamboo stumps; Kam, unpublished data). The larger tadpoles were able to outcompete smaller tadpoles for eggs (Kam et al., 1997), thus monopolization of trophic eggs is much easier than monopolization of the more evenly dispersed food resources, such as suspended algae, planktons, organic detritus, and plant materials, consumed by the tadpoles of pond breeders (Seale, 1987; Wassersug, 1980; Wassersug and Heyer, 1988). As a result, large individuals in the HD treatment were able to obtain disproportionately more eggs and grew as fast or faster than tadpoles raised in the LD treatment (Table 1). In other words, a few individuals grew at the expense of the smaller members of the cohort, evidenced by a large variation in body size (Table 1). Similar size-selective feeding behaviors are reported for *Rana temporaria*, *Rana esculenta*, *Bufo bufo*, and *Bufo calamita* (Savage, 1952), *Bufo americanus* (Wilbur, 1977), and *Scaphiopus holbrooki* (Semlitsch and Caldwell, 1982). Those tadpoles in MD and HD treatments that obtained eggs only occasionally, or not at all, grew slowly. As their body size fell behind, small tadpoles took longer to reach metamorphosis (Table 1). Prolonged starvation even resulted in

higher mortality (Fig. 1) and a lower metamorphic rate (Table 1).

Our findings on the growth, development, and survivorship of tadpoles at three different densities (Table 1) are best explained by a food shortage (i.e., insufficiently fed trophic eggs) rather than crowding effects (i.e., accumulation of harmful materials, lack of oxygen, frequent contacts between tadpoles, and, or, growth inhibition) (Adolph, 1931; Gromko et al., 1973; Licht, 1967; Richards, 1958). Earlier studies on oophagous tadpoles of *D. pumilio* and *O. brunneus* also indicate that the availability of trophic eggs determines the growth and development of tadpoles (Brust, 1993; Thompson, 1992). Although female frogs do increase the food supply (i.e., trophic eggs) in response to the increased tadpole numbers (Fig. 3), it is likely that food is still not enough for the metabolic requirements of tadpoles, particularly in high density situations. Tadpoles of *C. eiffingeri* increased egg consumption as they grew (Kam et al., 1996). However, we do not know if female frogs provided more trophic eggs by increasing meal size or visit frequency. Brust (1993) studied seven tadpoles of *D. pumilio*, each in a water pool in a bromeliad axil, and reported that genetic mothers were the only frogs to feed their offspring, and females did not increase meal size as the tadpoles grew.

#### CONCLUSION

The reproductive strategies of *C. eiffingeri* differ from those of species that provide no maternal care for larvae. It is clear that maternal brood care is critical to the growth, development, and survivorship of tadpoles, and the number of froglets produced is constrained by the energetic reserves for brooding in female frogs. Also, the high energetic cost of maternal care (i.e., production of trophic eggs) (Kam et al., 1996) affects the frequency of reproduction. A female of *C. eiffingeri* has multiple clutches during an extended breeding season (February–August) (Kam et al., 1996), but each clutch is well separated temporally (Chuang, 1987; Ueda, 1986). Female frogs will mate and lay a second clutch of eggs only after the tadpoles from

the first clutch are few in number or have left the bamboo stumps (Kam et al., 1997); this delay presumably reduces the cost of brooding.

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