

Intraspecific interactions among oophagous tadpoles (*Chirixalus eiffingeri*: Rhacophoridae) living in bamboo stumps in Taiwan

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Abstract

We studied the intraspecific interactions among oophagous *Chirixalus eiffingeri* tadpoles that occupied the same water-filled bamboo stumps at Chitou, Taiwan. We monitored the growth of newly-hatched tadpoles in unoccupied and occupied bamboo stumps in the field where the latter contained large tadpoles that hatched from earlier clutches. The growth of the small, late-hatching tadpoles in occupied nests was suppressed by the presence of large, early-hatching tadpoles. However, small tadpoles that were physically separated from large tadpoles in a perforated container grew at about the same rate as small tadpoles living in pools without large tadpoles. Thus, the slower growth of the late-hatching tadpoles was probably caused by behavioural interference competition with the early-hatching tadpoles. In the laboratory, we kept large and small tadpoles together in containers and did not feed them for 6 days. The large tadpoles did not cannibalize the small tadpoles. Although large tadpoles may scavenge dead tadpoles, the effects of scavenging on growth were negligible. Interactions among cohabiting *C. eiffingeri* tadpoles are similar to those among the oophagous tadpoles of several hylid species that use phytotelmata. Results suggest that behavioural interference competition is the principal type of intraspecific interactions among the oophagous, non-predatory tadpoles of hylid and rhacophorid frogs.

Key words: *Chirixalus eiffingeri*, intraspecific interactions, oophagy, Taiwan

INTRODUCTION

Arboreal water pools, which may occur in tree holes and cavities, bamboo stumps, bromeliad leaf axils, nut capsules and others sites, are unique and isolated microhabitats (Laessle, 1961; Wassersug, Frogner & Inger, 1981; Lannoo, Townsend & Wassersug, 1987; Caldwell, 1993; Kam, Chuang & Yen, 1996). For many organisms, arboreal pools serve as seasonal or permanent aquatic habitats in an otherwise terrestrial setting. Dipterans, helodid beetles and dragonflies are common in arboreal pools (Fish, 1983), as are other, non-insect invertebrates, including protozoans, flatworms, crustaceans, oligochaetes, ostracods, copepods and rotifers (Laessle, 1961; Fish, 1983). Anurans are the only vertebrates that use arboreal pools for breeding (Laessle, 1961; Duellman & Trueb, 1986; Caldwell, 1993; Kam *et al.*, 1996). However, their use of arboreal pools is not uniform and different species have evolved different reproductive modes (for details, see Duellman & Trueb,

1986). For example, *Dendrobates pumilio* females lay eggs in terrestrial leaf litter, and then transport newly hatched tadpoles to water-filled leaf axils on their back (Brust, 1993). Other species lay their eggs above, or in, arboreal water pools, and the tadpoles drop into the pools as soon as they hatch (Lannoo *et al.*, 1987; Caldwell, 1993; Jungfer, 1996, Kam *et al.*, 1996)

Arboreal pools typically contain small volumes of stagnant, hypoxic water, with limited food resources. Trophic eggs (fertilized or unfertilized) are the most common food for tadpoles and are provided intermittently by genetically related female frogs (Weygoldt, 1980; Lannoo *et al.*, 1987; Brust, 1993; Jungfer, 1996; Kam *et al.*, 1996; Caldwell & de Oliveira, 1999). The behaviour and life-history traits of frogs that breed in arboreal pools are diverse. Poisonous frogs in the genus *Dendrobates* have very small clutches (two to six eggs) and typically transport their tadpoles singly to small phytotelmata, such as bromeliad tanks or leaf axils. In contrast, hylid frogs in the genera *Anothea*, *Osteopilus* and *Osteocephalus* have large clutches (in hundreds) and an entire clutch of tadpoles will live in a small, arboreal pool (Jungfer, 1996; Thompson, 1996; Jungfer & Wey-

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goldt, 1999). Many species of tadpoles are predacious, consuming conspecifics (cannibalism) or heterospecifics (Caldwell, 1993; Caldwell & de Araújo, 1999; Summers, 1999). In some, but not all, species there is communication between the mother and her tadpoles (Brust, 1993; Caldwell & de Oliveira, 1999; Jungfer & Weygoldt, 1999).

To date, most field research on the growth, and intraspecific and interspecific interactions between arboreal tadpoles has been conducted on various hylid and dendrobatid species in Central and South America. There has been much less research on arboreal tadpoles in the Old World. In the Oriental region, some species of *Chirixalus* and *Philautus*, family Rhacophoridae, are arboreal breeders whose tadpoles live in tree holes or bamboo stumps (Wassersug *et al.*, 1981; Kam *et al.*, 1996). *Chirixalus eiffingeri* breeds mainly in bamboo stumps in moist, montane areas in Taiwan (Kam *et al.*, 1996). Female *C. eiffingeri* use only 40% of the available bamboo stumps as nest sites, and suitable stumps are reused 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 in a single pool. Relatively little is known about the interactions between the tadpoles in the two cohorts. Cannibalism should be common among *C. eiffingeri* tadpoles (Crump, 1992) because they usually live in extremely crowded conditions (nine tadpoles/100 ml or equivalent to 65 506 tadpoles/m³) (Kam *et al.*, 1998a) and trophic eggs are available only sporadically and for brief periods of time.

In this study, we investigated the intraspecific interactions between *C. eiffingeri* tadpoles from different cohorts and assessed the prevalence of tadpole cannibalism among tadpoles.

MATERIALS AND METHODS

Natural history of *C. eiffingeri*

The rhacophorid tree frog, *C. eiffingeri*, is a small frog with a snout–vent length of 30–40 mm. It is endemic to Taiwan and 2 nearby, small islands, Iriomote and Ishigaki (Kuramoto, 1973; Ueda, 1986; Lue, 1990). During the breeding season (February–August), female frogs deposit fertilized eggs on the inner walls of bamboo stumps or tree holes, just above the waterline (Kuramoto, 1973; Kam, Yen & Hsu, 1998b). Male frogs exhibit paternal care during the embryonic stage, but they leave the stumps after the embryos have hatched. Upon hatching, tadpoles drop into the water pool where they grow and develop until metamorphosis. Tadpoles are obligatorily oophagous and are fed by females that, in the absence of male frogs, lay unfertilized trophic eggs directly in the water. Female frogs visit and feed tadpoles only at night, at intervals of about 8 days (Kam *et al.*, 2000). The length of the tadpole period, from hatching to metamorphosis, is from 50 to 60 days (Kam *et al.*, 1998a).

Study site

All experiments were conducted in bamboo forests at the Experimental Forest of National Taiwan University, Chitou (elevation 1016 m, approximately 23° 39'20" N, 120° 48'10" E), Nantou County, Taiwan. Chitou receives approximately 3 m of rainfall annually. 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° C.

Experiment 1: growth and survivorship of *C. eiffingeri* tadpoles in unmanipulated, unoccupied and occupied nests

We conducted this experiment from July to October 1994, in 2 bamboo (*Phyllostachys edulis*) groves of approximately 20 × 35 m each. Near the end of the breeding season, in early August, we found 13 fertilized egg clutches above the water line on the inner wall of bamboo stumps. Fertilized eggs have distinct animal and vegetal hemispheres and 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. In three bamboo stumps, eggs were laid above pools that already contained developing tadpoles. Tadpoles from earlier clutches are hereafter called EARLY tadpoles, and those from later clutches are hereafter called LATE tadpoles. EARLY tadpoles could be easily distinguished from LATE tadpoles by their larger body size and later developmental stage. The inner diameter of stumps and the water depth were measured to calculate tadpole density.

We monitored the growth and survivorship of all tadpoles for 4 weeks. To facilitate the examination and measurement of tadpoles, on our first visit we sawed a V-shaped cut in the base of the bamboo stump and detached the portion of the stump containing the 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 stump base. The detached portion fitted 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 carefully transfer tadpoles to petri dishes. The tadpoles were counted and photographed; a ruler was placed beneath the petri dish to determine their total length (TL).

Because female frogs feed their tadpoles at night, we minimized disturbance of maternal feeding behaviour by examining the bamboo stumps during the day (Kam *et al.*, 2000). Due to time constraints, we did not study the feeding behaviour of female frogs. 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 out the yolk, leaving the jelly capsule in the pool (Ueda, 1986). As tadpoles grow larger, they usually ingest the whole egg, including the capsule.

Experiment 2: indirect effects of large tadpoles on the growth and survivorship of small tadpoles

We conducted this experiment from March to July 1998. To begin, 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 bamboo stumps containing developing tadpoles and collected the tadpoles when they reached designated sizes. The small tadpoles were about 1 week old, 10–13 mm in TL, and at Gosner stage 25–26 at the start of the experiment (Gosner, 1960). The large tadpoles were about 5 weeks old, 26–28 mm long, and at Gosner stage 30–31.

We removed all the tadpoles from 32 bamboo stumps and then placed 10, randomly selected, newly hatched tadpoles into each of the 32 stumps. We designated a bamboo stump as an experimental unit, and each treatment group consisted of 16 randomly selected stumps. For the experimental group, we placed a perforated centrifuge tube (50 ml; height \times outer diameter: 105 \times 29 mm) containing 5 large tadpoles into the pool in each of 16 bamboo stumps. For the control group, we put a perforated centrifuge tube with no tadpoles into the pool in each of the remaining 16 bamboo stumps. The centrifuge tubes were capped so that the large tadpoles could not receive trophic eggs from female frogs. Water could flow freely between the centrifuge tube and the pool in which each was immersed, allowing tadpole excrement, which consists of very fine suspended particles, and soluble chemicals to circulate freely (Y-C. Kam, per. obs.). We replaced the large tadpoles in the centrifuge tubes weekly with tadpoles of similar size so the large tadpoles did not starve. Fasting for 1 week was unlikely to cause any ill effect on the large tadpoles because, under natural conditions, *C. eiffingeri* tadpoles are fed by female frogs at intervals of about 8 days (Kam *et al.*, 2000). Between feedings, trophic eggs stored in a tadpole's distensible stomach are the main source of energy (Chou & Lin, 1997)

We maintained the water volume of each pool such that there were 10 ml of water for each tadpole, regardless of tadpole size. For example, pools with 10 and 15 tadpoles contained 100 and 150 ml of water, respectively. This was the average tadpole density we observed under natural conditions, as in Experiment 1. We added distilled water to compensate for water loss from evaporation and removed excess water from rainfall.

We monitored the growth and survivorship of small tadpoles for 4 weeks using the same protocol as in Experiment 1.

Experiment 3: incidence of cannibalism among *C. eiffingeri* tadpoles

We assessed the incidence of tadpole cannibalism using 3 treatments: 10 small tadpoles (S treatment); 10 small and 10 large tadpoles (LS treatment); 10 large tadpoles (L treatment). The small and large tadpoles were the same as in Experiment 2. All large tadpoles were fasted for at least 7 days until their stomachs were empty of stored, trophic eggs, which can be determined easily with the naked eye.

Each treatment had 5 replicates. In each replicate the tadpoles were kept in a plastic cup at a density of 1 tadpole per 10 ml water, regardless of tadpole size. The number of surviving tadpoles in each replicate were counted each day for 6 days. The large tadpoles were weighed at the start and end of the 6 days of the experiment. Each tadpole was weighed separately. We tared a small petri dish containing water, added a tadpole, and recorded the body mass.

Statistical analyses

Data were analysed using a SAS program (SAS Institute, 1996). Each stump was an experimental unit. The treatment mean for all measured variables was calculated from the mean of the corresponding variable from each clutch. In Experiment 1, 2 clutches in the 10 unoccupied nests were not fed by female frogs. In Experiment 2, there was no evidence of maternal feeding of 5 of 16 clutches in both the control group and the experimental group. Clutches of unfed tadpoles were excluded from statistical analyses. We used analysis of covariance (ANCOVA) to analyse tadpole growth, with initial TL as a covariate. We used repeated measures ANOVA to analyse tadpole survivorship. We used *t*-tests or Mann–Whitney tests to compare the means or mediums of 2 samples, respectively. For all variables means \pm SE are reported, unless otherwise noted.

RESULTS

Experiment 1 was aimed to monitor the growth and survivorship of tadpoles in unoccupied and occupied nests. At the beginning of the experiment, EARLY tadpoles (24.5 ± 2.79 mm, $n = 3$) in occupied nests were significantly larger than LATE tadpoles (12.57 ± 0.35 mm, $n = 3$; Mann–Whitney test, $Z = 1.94$, $P = 0.048$). EARLY tadpoles maintained a size advantage over LATE tadpoles throughout the tadpole stage. EARLY and LATE tadpoles lived together for about 4 weeks until EARLY tadpoles reached metamorphosis.

Because stump hole diameter and water depth varied, we calculated the water volume and tadpole density. The tadpole density in unoccupied nests (7.99 ± 5.4 tadpole/100 ml water, $n = 8$) was not significantly different from that in occupied nests (8.30 ± 5.4 tadpole/100 ml water, $n = 3$; Mann–Whitney test, $Z = 0.102$,

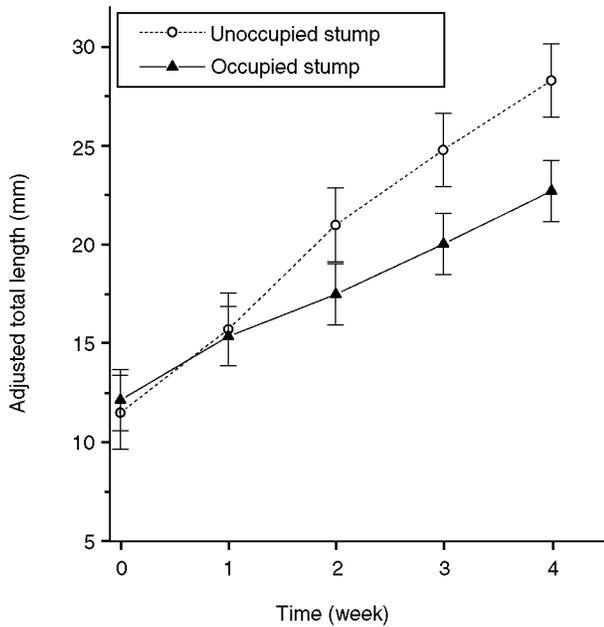


Fig. 1. Total length of small (late-hatching) tadpoles in occupied stumps and tadpoles in unoccupied stumps in Experiment 1. Total length of tadpole was adjusted by ANCOVA, and initial length was used as a covariate. Values are means \pm SE. Sample sizes are three and eight bamboo stumps for respective groups.

$P=0.918$). The growth of LATE tadpoles in occupied nests was significantly slower than that of small tadpoles in unoccupied nests (ANCOVA, $F_{1,8}=5.85$, $P=0.042$; Fig. 1). In contrast, the survivorship of the tadpoles in these two treatments was not significantly different (repeated measure ANOVA, $F_{1,9}=0.68$, $P=0.432$)

Experiment 2 was aimed to assess the indirect effects of large tadpoles on the growth and survivorship of small tadpoles. Results showed that the growth (ANCOVA: $F_{1,19}=0.03$, $P=0.8688$; Fig. 2a) and survival (repeated measures ANOVA: $F_{1,20}=0.10$, $P=0.753$; Fig. 2b) of small tadpoles in the control and experimental groups were not significantly different.

Experiment 3 was aimed to assess the prevalence of cannibalism among tadpoles. Throughout the study period, we have never observed large tadpoles attacking small tadpoles in the LS treatment. By the end of the experiment, the number of small tadpoles in the S and LS treatments had decreased from 10 to 8.4 ± 0.9 ($n=5$) and 9.0 ± 0.7 ($n=5$), respectively. These numbers were not significantly different ($t=1.177$, $P=0.273$).

All large tadpoles in the LS and L treatments survived to the end of the experiment, but they all lost weight. The mean initial body mass of large tadpoles in the LS treatment was 139.5 ± 16.8 mg ($n=5$), and they lost an average of 8.74 ± 2.37 mg during the experiment. The mean initial body mass of large tadpoles in the L treatment was 138.1 ± 12.6 mg ($n=5$), and they lost an average of 11.80 ± 3.36 mg. There was no significant difference in the weight loss of large tadpoles in the LS and L treatments ($t=1.67$, $P=0.135$).

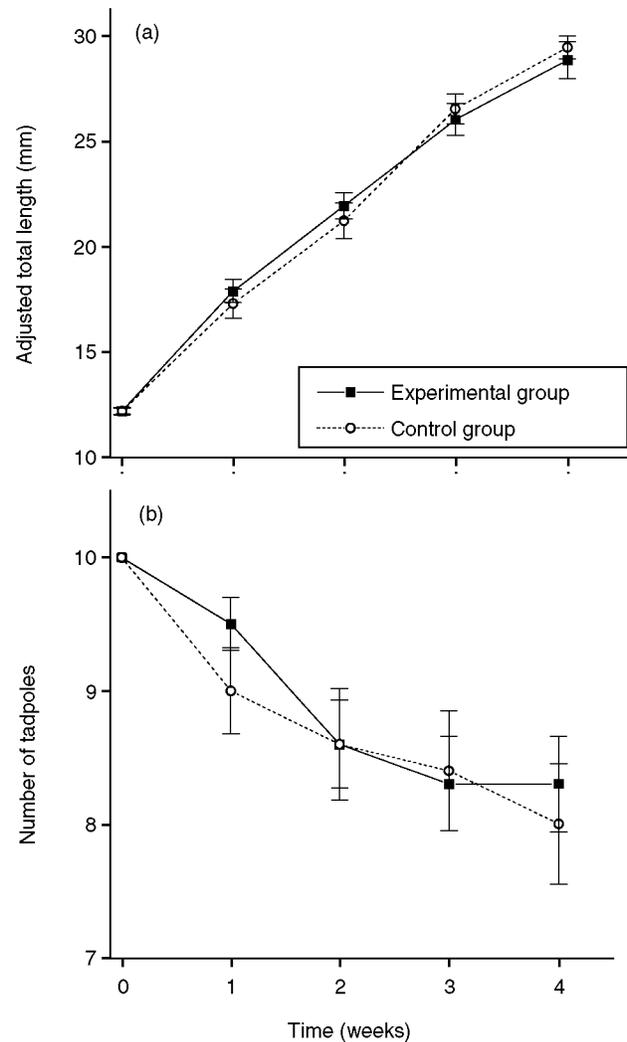


Fig. 2. The (a) total length and (b) number of surviving tadpoles during development in Experiment 2. The total length of tadpoles was adjusted by ANCOVA, and initial length was used as a covariate. Values are means \pm SE. Sample sizes are 11 bamboo stumps for each group.

DISCUSSION

In Experiment 1, in pools in which two clutches of tadpoles of different ages coexisted, tadpoles in the late hatching cohort (LATE tadpoles) grew slower than small tadpoles in pools lacking large tadpoles (Fig. 1). This indicates that tadpoles in early hatching cohorts (EARLY tadpoles) exert negative effects on the growth of LATE tadpoles. In Experiment 2, in which large tadpoles were physically separated from the small tadpoles in the same pool, the small tadpoles grew at the same rate as tadpoles in the control group (Fig. 2a,b). Elimination of the behavioural interactions between large and small tadpoles allowed for normal growth of the small tadpoles, suggesting that behavioural interference competition has probably caused the decreased growth of LATE *C. eiffingeri* tadpoles. Size- and age-specific competition has been used to explain disparities

in the growth of other amphibian larvae (Savage, 1952; Wilbur, 1977; Semlitsch & Caldwell, 1982). *Chirixalus eiffingeri* tadpoles are obligatorily oophagous and are fed intermittently by females that lay unfertilized, trophic eggs. When a female frog returns to the pool, tadpoles immediately aggregate around her. Tadpoles begin stiffing their tails, vibrating vigorously and nipping at the skin around her cloaca and thigh areas (Ueda, 1986). Without the presence of male frogs, the female then begins to lay trophic eggs, a few at a time. As soon as the eggs are laid, the tadpoles bite them and suck out the yolks in seconds (Ueda, 1986; Lin, 1996). EARLY tadpoles are bigger and stronger, and better able to fight for a position in the vicinity of the cloaca. In addition, their vigorous swimming movements may prevent LATE tadpoles from getting near the cloaca. We suggest that EARLY tadpoles outcompete LATE tadpoles by monopolizing most of the eggs laid by the female frog. As a result, LATE tadpoles were unable to obtain sufficient food and grow more slowly than conspecifics of the same age that do not have to compete with older tadpoles (Fig. 1).

From Experiment 2 we inferred that chemical interference is unimportant among *C. eiffingeri* tadpoles (Fig. 2a,b). If chemical interference competition among *C. eiffingeri* tadpoles were important, small tadpoles in the LS treatment, which lived in water conditioned by the large tadpoles, would have grown more slowly than tadpoles in the S treatment. However, the growth and survival of small tadpoles in the control and experimental groups were not significantly different (Fig. 2a,b). To date, few experiments have assessed the incidence and importance of chemical interference competition in tadpole populations in natural habitats, under natural conditions. Petranka (1989) experimentally demonstrated that chemical interference competition among tadpoles of the southern leopard frog *Rana utricularia* is uncommon in natural habitats, even though it has been demonstrated in laboratory populations of this species (Steinwascher, 1978) and several, closely related congeners (Richards, 1958, 1962; Licht, 1967; Steinwascher, 1979a,b). Steinwascher (1978) found that water taken from local aggregates inhibited growth only when tadpoles densities were extremely high (14 557 tadpoles/m³ or two tadpoles/100 ml). In this study, there was no evidence for chemical interference competition among *C. eiffingeri* tadpoles, even at a density of nine tadpoles/100 ml. It is possible that ambient pH, exposure to UV radiation, consumption of, or competition with, micro-organisms by tadpoles prevent inhibitory substances, yeast cells in particular, from reaching concentrations sufficient to cause chemical interference (Petranka, 1989).

In Experiment 3, large tadpoles did not cannibalize conspecific tadpoles, although there was some tadpole mortality. Large tadpoles in the SL treatment lost as much weight as those in the L treatment. Large tadpoles did consume tadpoles that had died, but these were apparently insufficient to support the basic, energy requirements of the large tadpoles. We reached a similar

conclusion based on the results of earlier field studies (Kam *et al.*, 1998a; Kam *et al.*, 2000). Under natural conditions, female *C. eiffingeri* abandon about 30% of the nests and the tadpoles do not receive trophic eggs. If scavenging were important, we would expect some tadpoles in abandoned nests to scavenge dead tadpoles, grow and maybe even reach metamorphosis. However, these studies showed that no orphaned tadpole increased in weight (Kam *et al.*, 1998a, 2000). In addition, the other life forms (euglenoids, diatoms, parameciums, *Chlorella*, rotifers and dipteran larvae) in the pools do not appear to have a direct association with the tadpoles as they are neither food for nor predators of the tadpoles (Y.-C. Kam, pers. obs.).

Arboreal pools are restricted microhabitats, thus competition for space and food among the inhabitants may be severe. Many species of *Dendrobates* have evolved predatory behaviour to eliminate competitors or predators (Weygoldt, 1987; Caldwell & de Araújo, 1999; Summers, 1999). Cannibalism is thought to be a secondary outcome of this predatory behaviour (Crump, 1992). In contrast to tadpoles of the *Dendrobates histrionicus* species group (Myers, Daly & Martínez, 1984; Weygoldt, 1987; Brust, 1993), the hylid species *Osteopilus brunneus*, *Osteocephalus oophagous* and *Anotheca spinosa* (Jungfer, 1996; Thompson, 1996; Jungfer & Weygoldt, 1999) and the rhacophorid *C. eiffingeri* are not predaceous. It is common to find many tadpoles of these species coexisting peacefully in arboreal pools. Jungfer (1996) reported that when many (> 10) *A. spinosa* tadpoles were present in a container, two distinct groups the members of which differed in size and developmental stage could soon be recognized. Those that regularly received nutritive eggs grew rapidly, while those that obtained few or no eggs had stunted growth. Observations were made in *O. brunneus* (Thompson, 1996) and *C. eiffingeri* (Kam *et al.*, 1998b). Thus, large tadpoles apparently prevent small tadpoles from getting food through behavioural interference competition. As more of the starved tadpoles die, tadpole density in the pool is reduced.

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