

ECOLOGICAL FUNCTIONS OF THE FOAM NESTS OF THE JAPANESE TREEFROG, *RHACOPHORUS ARBOREUS* (AMPHIBIA, RHACOPHORIDAE)

TAMOTSU KUSANO, AKI SAKAI AND SUMIO HATANAKA

Department of Biology, Faculty of Science, Tokyo Metropolitan University, Hachioji, Japan

Using both field observations and laboratory experiments, thermal and nutritional functions of the arboreal foam nests of the Japanese treefrog *Rhacophorus arboreus* were examined in early summer in the years 2000–2002. The temperature at the centre of the nests and ambient air temperature were monitored using a data logger in the field for several days. The results showed thermal regulation by the foam mass; the inside of the nests was maintained up to 6°C cooler by the foam masses when the ambient temperature was high (>25°C). Laboratory experiments also showed that hatching success of the embryos was very low at high temperatures (near 30°C). The insulation effect of the foam nests is, therefore, considered to be adaptive for *R. arboreus*. Hatchling growth was examined for a week under different food conditions: water only (no food), foam mass and boiled lettuce. Larvae showed no significant growth without food, but they grew to be 2–5 times heavier in dry body mass than hatchlings when supplied with foam mass or boiled lettuce. Foam mass proved to be at least as effective as boiled lettuce as a food for hatchlings. The present study demonstrates the thermal and nutritional effects of the foam nests of *R. arboreus*.

Key words: Amphibia, hatching success, nutritional effect, thermal advantage,

INTRODUCTION

Anuran amphibians exhibit diverse patterns of breeding, and one adaptation to both aquatic and terrestrial breeding is the construction of foam nests in which eggs are deposited in a mass of dense fluid that is whipped into foam by the frogs. Foam-nesting has evolved several times and occurs in at least six families: Rhacophoridae, Leptodactylidae, Myobatrachidae, Hylidae, Microhylidae, and Hyperoliidae (Duellman & Trueb, 1994; Seymour & Loveridge, 1994). A number of possible functions of foam nests have been suggested from the point of view of ecological and adaptive significance: (1) prevention of desiccation of eggs and larvae (Dobkin & Gettinger, 1985; Downie, 1988, 1993); (2) protection against egg predation (Heyer, 1969; Downie, 1988, 1990); (3) thermal advantage (Gorzula, 1977; Dobkin & Gettinger, 1985); (4) potential food resources for hatchlings (Tanaka & Nishihira, 1987); and (5) gas exchange (Seymour & Loveridge, 1994).

The Japanese treefrog, *Rhacophorus arboreus*, is a medium-sized rhacophorid species, usually 50–80 mm in snout-vent length, and distributed across the Honshu and Sado Islands, Japan. It lives in a variety of habitats at elevations from sea level to over 2000 m, but is more abundant in mountain regions. It breeds in early summer, chiefly in ponds surrounded by forested areas (Maeda & Matsui, 1999). Since this species exhibits interesting breeding habits and mating system, e.g. arboreal spawning and multi-male breeding, many researchers have studied its breeding ecology and mating behaviour (e.g., Kato, 1955, 1956; Toda, 1989; Kasuya *et al.*, 1996;

Kusano, 1998). Female *R. arboreus* make foam nests attached to branches or leaves of trees along the shore of still waters. We monitored temperatures within and outside the nests for several days using a data logger, and conducted rearing experiments to examine the effect of foam masses on hatchling growth. In the present paper, we report on the thermal and nutritional effects of the foam nests on the embryos and hatchlings of *R. arboreus*, and discuss the ecological functions of the foam nests.

MATERIALS AND METHODS

STUDY SITE

This study was carried out at a secondary forest, consisting chiefly of *Quercus serrata*, *Q. myrsinaefolia* and *Q. glauca*, within the campus of the Tokyo Metropolitan University (35°37'N, 139°23'E) in Hachioji, Tokyo from May through July of 2000–2002. The forest is approximately 10 ha in area, and contains a small natural pond (“Imori” pond; 10 m diameter, 0.5 m maximal depth) on its western side, at an altitude of 120 m. Since the pond was covered by the canopy of surrounding trees, the shore of the pond was shady during most of the daytime. The breeding population of *R. arboreus* constructed a total of 14–21 foam nests at the shore of the pond every year (2000–2002). This pond is used not only by *R. arboreus* but also by several other amphibian species for breeding: *Bufo japonicus formosus*, *Rana ornativentris*, *R. rugosa*, *Rhacophorus schlegelii*, *Cynops pyrrhogaster* and *Hynobius tokyoensis*.

The climate of the study site is relatively mild, and yearly mean air temperature and yearly rainfall were, on average, 14.3°C and 1563 mm during 1983–2000 at the nearest weather station of the Automated Meteorolo-

logical Data Acquisition System (AMEDAS), which is located 8 km north-west of the study site, 123 m in altitude (Japan Meteorological Agency, 2005).

THERMAL EFFECTS OF FOAM NESTS

We monitored long-term fluctuations of temperature within foam nests in the field using a data logger (SK Sato SK-L200T) during the breeding seasons of 2001–2002. We collected a newly constructed foam nest, and attached it to a small branch (about 1–1.5 m above the ground) near the shore of the pond. An electronic thermistor probe (20 mm in length, 5 mm in diameter) connected to the data logger was inserted into the centre of the foam nest, and another probe was placed 1 cm away from the surface of the nest to monitor the ambient air temperature. The temperature was measured to the nearest 0.1°C at intervals of 15 min for 1–7 days. We monitored nest and air temperatures for eight foam nests. Air temperature was also monitored 1.5 m above the ground at the shore of the pond throughout the breeding seasons.

In order to ascertain the effects of temperature on developing embryos of *R. arboreus*, we monitored embryonic development under different temperature regimes, and examined the relationship between temperature and hatching success. We collected a foam nest just after it had been constructed in the pond. Sixty eggs were collected from the nest and divided randomly into three groups (20 per group). The eggs of each group were placed in a Petri dish (15 cm in diameter), which was filled with 400 ml of distilled water, together with a small amount of foam mass. The eggs were removed from the foam and sunk into the water. The three groups were kept at different constant temperatures (13, 21 and 29°C). Developing embryos were inspected every day. Halted or impaired development in the embryos was indicated by malformation, discoloration, fungal infestation or any combination of the above factors, and we counted dead embryos and hatchlings. When dead embryos and hatchlings were found in the petri dishes, they were removed.

Since foam nests had, on average, 533 eggs (SD=133, $n=24$) in the study pond, many eggs remained within the nests even after 60 eggs were taken. The foam nest used in the experiment was therefore returned to the pond and attached to small branches on the shore. A large bucket (volume 20 l) filled with pond water was placed beneath the nest to collect hatchlings dropping down from the nest. When hatchlings began to emerge, the nest was collected again, and dead embryos and hatchlings were counted to determine hatching success in the field. We repeated the procedures for a total of five nests during the breeding season of 2001.

NUTRITIONAL EFFECTS OF THE FOAM

We visited the study pond at least once a day during the breeding season of *R. arboreus*, and searched for newly constructed foam nests. When such nests were

found, their positions were recorded on a map and monitored until the hatchlings emerged from the nests. From those nests constructed in 2000, we collected a total of four nests just after the hatchlings began to emerge from the nests. From each nest, 30 hatchlings (stage 22; Gosner, 1960) were collected randomly, and their total lengths and snout-vent lengths (SVL) were measured to the nearest 0.1 mm with a vernier calliper. They were divided into three treatment groups (10 hatchlings per group). Hatchlings of each group were placed in a water bath (17 cm x 27 cm x 17 cm), which was filled with 5 l of tap water purified by water filter. Different nutritional conditions were assigned to three treatment groups: (1) water only (no food); (2) an *ad libitum* amount of foam mass that was taken from their nest; and (3) an *ad libitum* amount of boiled lettuce. Hatchlings were reared at a constant temperature of $23\pm 0.5^\circ\text{C}$ with 14L:10D photoperiod for one week. Water in the baths was not changed until the end of the experiment. After the experiment, all tadpoles were anaesthetized and killed with MS222, their total lengths and SVLs were measured, and the developmental stages were recorded according to Gosner (1960). Dry body masses of individual tadpoles were determined to the nearest 0.01 mg by an electronic reading balance (Mettler AT201) after they had been dried at 55°C for 24 hours.

In order to determine the initial body masses of hatchlings, 10 additional hatchlings were also collected at random from each nest, and their dry masses were determined in the same way as described above.

STATISTICAL ANALYSIS

Statistical analyses were performed with the Statistical Analyses Software version 6.12 (SAS Institute Inc., 1990). Difference in temperatures inside and outside the foam nests was tested using paired *t*-tests for each nest examined. The effects of temperature and nests on hatching success were examined using two-way analysis of variance (ANOVA) without replication, after the rate of the number of hatchlings to the total number of eggs (hatching success) was arcsine transformed. Pairwise comparisons were also conducted between different temperatures following the procedure of the Tukey test (Zar, 1996). The significance level in all tests was $P<0.05$.

For each nest, pairwise comparisons of dry body masses of larvae at the end of the experiment were conducted between nutritional conditions using Welch's test, because of heterogeneity of variances (Zar, 1996). Acceptance levels for simultaneous statistical tests were adjusted by the sequential Bonferroni procedure (Rice, 1989). Results where the adjusted *P*-value was less than 0.05 were judged statistically significant.

RESULTS

THERMAL EFFECTS OF THE FOAM NESTS

The temperatures inside and outside the nests were monitored concurrently for eight nests using a data log-

TABLE 1. Data on air temperature at the study site during the breeding season of *R. arboreus*. Data on monthly rainfall obtained at the nearest AMEDAS weather station (8 km north-west of the study site) is also shown (Japan Meteorological Agency, 2005).

Month	Air temperature (°C)			Rainfall (mm)
	Mean	Min	Max	
2001				
May	17.2	6.5	25.5	158.1
June	20.5	14.9	28.8	76.3
July	25.9	19.8	33.9	231.7
2002				
May	15.8	9.7	26.1	130.9
June	18.9	13.0	28.4	100.1
July	25.1	19.9	31.2	141.4

ger; each nest was monitored for, on average, 4.4 days (SD=1.7, Table 2). We also monitored air temperature at the shore of the pond, and Table 1 shows climatic conditions of the pond during the study period.

Fig. 1 shows diel changes of both temperatures for nest No.12. From the middle of the night to early the next morning, the nest temperature was almost equal to the ambient air temperature, but as the air temperature rose gradually, the difference in temperature increased. When the air temperature rose above 25°C in the afternoon, the nest temperature was maintained at about 3–4°C lower than the ambient air temperature. For most of the other nests, similar relationships were observed between nest and air temperatures. The mean tempera-

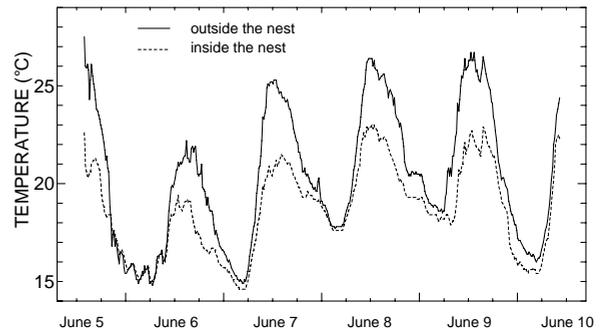


FIG. 1. Daily fluctuations of temperature inside a foam nest (No.12) during June 5–10 in 2002 (dashed line). Air temperature just above the outer surface of the nest is shown by the solid line.

ture was significantly lower inside the nests than outside in almost all nests (six out of eight), although the opposite result was observed in nest No.2 in 2001 (Table 2). At present, we do not know the reasons for this result in nest No.2.

When the air temperature was low (<20°C), the difference in temperature inside and outside the nests was comparatively small. As the air temperature rose gradually, the difference in temperature increased, because the temperature inside the nests did not rise at the same rate as the air temperature (Fig. 2). At air temperatures higher than 25°C, the difference in temperature between the centre of foam nests and the ambient air reached a maximum of 6°C. This result demonstrates thermal

TABLE 2. Mean air and nest temperatures in the foam nests of *R. arboreus*. Air temperatures just above the outer surface of the nest and nest temperatures at the centre of the foam nests were monitored at intervals of 15 minutes using a data logger.

Nest	Period	Temperature (°C)		Paired <i>t</i> -test	
		air	nest	<i>n</i>	<i>P</i>
2001					
No.1	May 17–21	19.00±3.94 (11.9–28.4)	17.85±2.84 (12.1–24.6)	395	<0.0001
No.2	May 21–25	18.3±1.42 (16.0–23.4)	18.52±1.46 (16.3–24.0)	386	<0.0001
No.9	May 29–30	17.84±1.62 (14.1–22.2)	17.64±2.22 (15.1–20.4)	99	0.072
No.10	May 25–29	18.68±2.48 (13.9–26.30)	18.22±1.80 (14.4–22.6)	369	<0.0001
2002					
No.2	May 16–20	13.99±2.31 (11.3–22.6)	13.37±2.00 (10.8–19.2)	381	<0.0001
No.7	May 30–Jun 6	20.33±2.83 (15.9–27.7)	19.48±2.55 (15.7–28.2)	572	<0.0001
No.12	Jun 5–10	20.36±3.45 (14.8–27.5)	18.64±2.31 (14.6–23.0)	467	<0.0001
No.17	Jun 21–28	16.45±2.10 (14.2–25.3)	16.08±1.70 (14.1–22.3)	669	<0.0001

regulation by the foam mass; the inside of nests was maintained cooler to some extent by the foam masses when the ambient temperature was high.

Embryos kept at different temperatures required from three days to three weeks to hatch (stage 22). Many dead embryos halted their developments before stage 10 (gastrulation) without fungal infection at 13°C, but most dead embryos reached later developmental stages and showed fungal infection at higher temperatures, especially at 29°C. Hatching success varied greatly from 0 to 0.8 under constant temperatures, and from 0.51 to 0.91 in the field (Fig. 3). Effects of temperature and nest on hatching success were examined using two-way ANOVA after arcsine transformation, and the results showed a significant effect of temperature ($F_{3,12}=17.54$, $P<0.0001$) as well as nest ($F_{4,12}=5.17$, $P=0.0118$). Hatching success was significantly lower at 13 and 29°C

than in the field, but the difference between 21°C and field conditions was not significant. This result shows that the embryos of *R. arboreus* were vulnerable to both low and high temperatures, and high temperatures (near 30°C) in particular were lethal to the embryos.

NUTRITIONAL EFFECTS OF THE FOAM

Four nests (Nos. 2, 3, 5, and 8) were used for the experiment on hatchling growth under different nutritional conditions. Although six larvae from nest No.2 died during the experiment, all the larvae from the other three nests survived until the end of the experiment. By the end of the experiment, hatchlings (stage 22) had reached different stages for different food conditions (Kruskal-Wallis test, $\chi^2=22.71$, $P<0.001$): the median stage was 26 (range 25–28) for no food, 28 (26–28) for foam, and 28 (26–29) for lettuce. The developmental rate of

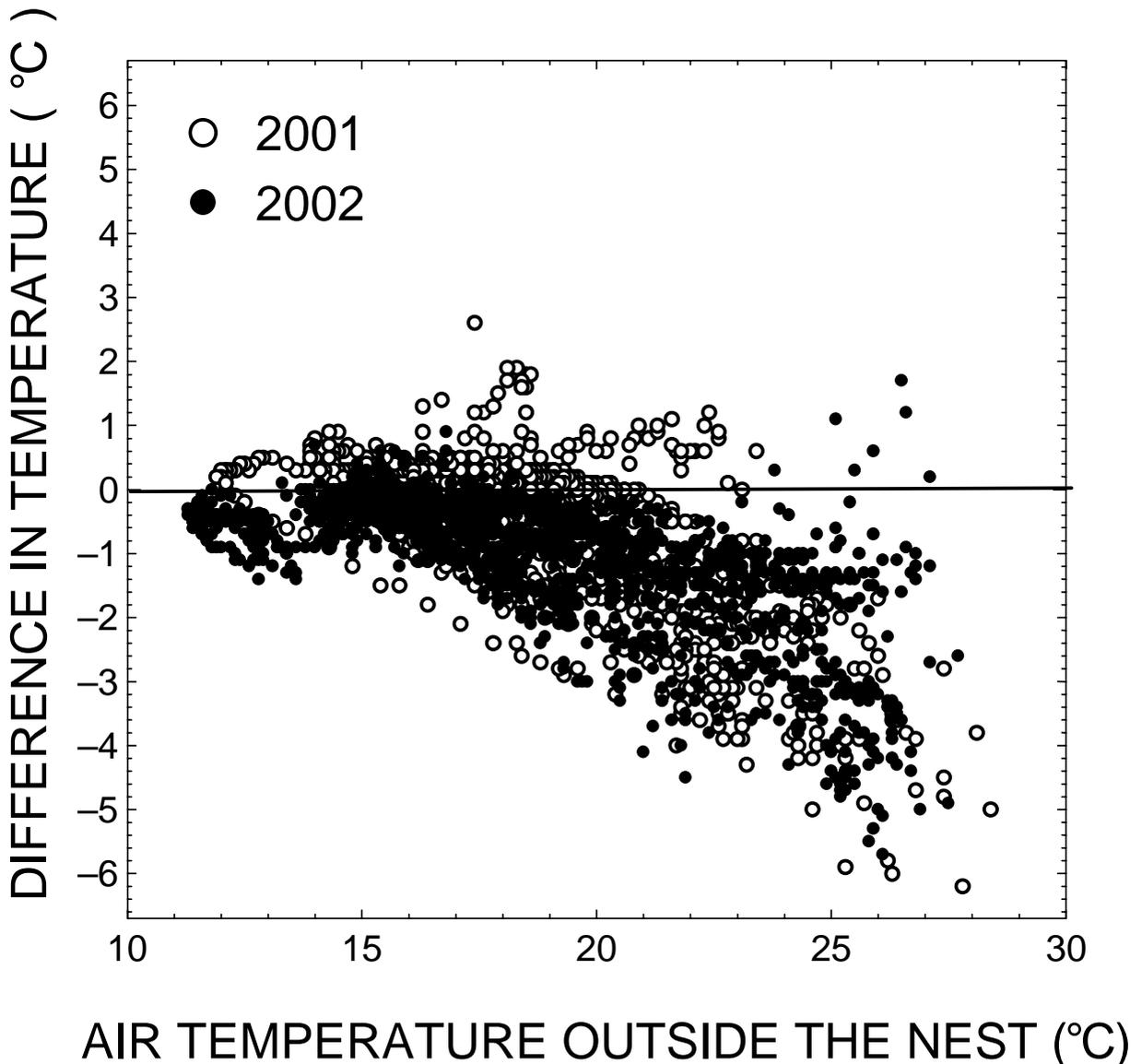


FIG. 2. Relationship between nest and air temperatures. Nest and air temperatures were measured at an interval of 15 min at the centre of the foam nests and 1 cm away from the surface of the nests, respectively. Differences in temperature (nest minus air) are plotted against air temperature. Data from a total of eight nests for 35 days were plotted ($n=3338$).

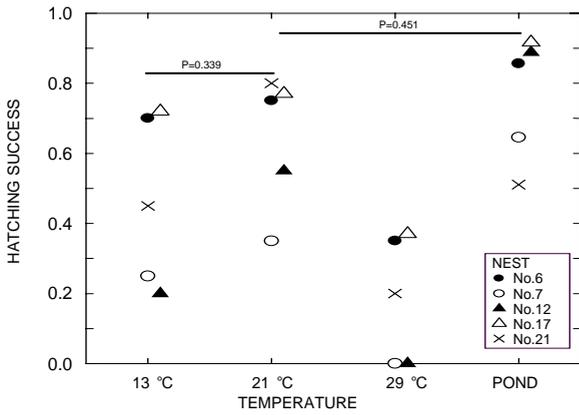


FIG. 3. Effects of temperature on hatching success of the embryos. Embryos from five nests were kept at three different constant temperatures (13, 21, and 29°C) and under field (pond) conditions. Mean air temperatures during the field incubation periods were 19.1 (nest No.6), 18.8 (No.7), 18.7 (No.12), 19.0 (No.17), and 24.6°C (No.21), respectively. Horizontal bars indicate non-significant differences ($P > 0.05$) between temperatures (Tukey's test after arcsine transformation).

hatchlings was significantly reduced when no food was supplied (Newman, 1998), but development was similar in the foam and lettuce food conditions.

Dry body masses of hatchlings and larvae at the end of the experiment are shown in Fig. 4. Mean body masses of hatchlings varied slightly from 4.28 to 4.76 mg among the nests, and mean body masses of larvae at the end of the experiment varied markedly from 4.49 to 26.29 mg among treatment groups. Pairwise compari-

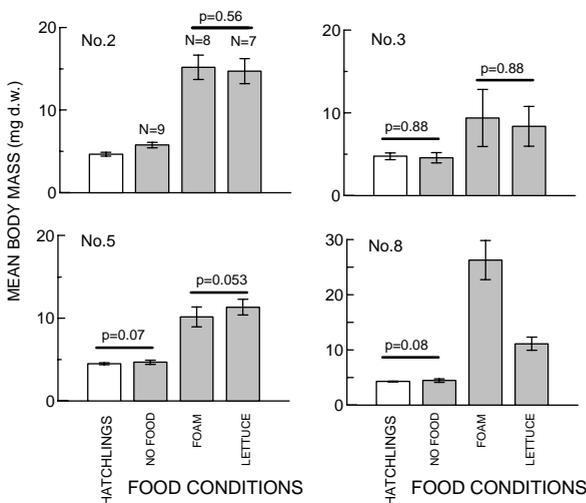


FIG. 4. Growth of hatchlings under different nutritional conditions. Hatchlings were taken from four nests, and reared at a constant temperature (23°C) for a week. Grey and clear histograms indicate mean dry body masses of larvae at the end of the experiment and those just after hatching, respectively. Vertical bars indicate 1 SD. Sample sizes (N) are all 10 except for where N is explicitly indicated (data on six dead larvae of nest No.2 were excluded from analysis). Horizontal bars indicate non-significant differences, but other comparisons are all significant ($P < 0.05$, Welch's test, sequential Bonferroni adjustment).

sons were made between different food conditions within the nests. Larvae showed no significant growth without food, but they grew to be 2–5 times heavier than hatchlings when supplied with foam mass or boiled lettuce as food (Fig. 4). Larval growth when foam mass was supplied was equal to, or even higher than, that when boiled lettuce was supplied. Mean body mass of the larvae supplied with foam mass was more than twice that of the larvae supplied with lettuce for nest No.8. The effect of food conditions on growth in SVL was quite similar to that on growth in dry body mass. These results show that foam mass of *R. arboreus*, as well as boiled lettuce, is an effective food resource for hatchlings.

DISCUSSION

TEMPERATURE REGULATION

The thermal advantage of foam nests has been examined by a number of researchers, but their results are not consistent with each other. Gorzula (1977) measured the temperature of foam nests of *Physalaemus enesefae*, and found that nest temperature was almost 5°C less than that of adjacent water. He suggested that foam keeps eggs cool to prevent thermal damage. However, Dobkin & Gettinger (1985) measured the temperature of foam nests of *P. pustulosus* and obtained the opposite result. Absorption of solar radiation by nests resulted in temperatures up to 8.2°C above ambient air temperature, allowing more rapid development. Downie (1988) examined the thermal properties of foam nests more completely than the previous authors, using *P. pustulosus*, and his data supported neither study. Foam temperature was very similar to ambient water or air temperatures, and time to hatching did not differ whether in foam or floating on water. No thermal effect of the foam was detected.

We monitored long-term temperature fluctuations of arboreal foam nests of *R. arboreus* using a data logger. The observation lasted for a total of 35 days using eight foam nests. Our data on the fluctuation of temperatures inside and outside the nests shows a significant thermal effect of the foam (Table 2 and Fig. 2). The inside of nests was maintained up to 6°C lower by the foam masses when the ambient temperature was high, which suggests that temperature is regulated by the foam. The white foam of nests may reflect solar radiation, and evaporation from the foam may cool down egg temperatures (but see Dobkin & Gettinger, 1985). The temperature regulation is, however, considered to be chiefly due to the insulation effect of the foam masses. Our result is consistent with that of Gorzula (1977). There may well be differences in thermal properties between foam nests which float on water and those surrounded by air and attached to branches.

The effect of temperature on hatching success was examined, and we detected a significant effect. Both high and low temperatures had detrimental effects on embryos, and especially at high temperatures (near

30°C), most of the embryos did not survive to hatching (Fig. 3). If the insulation effect of the foam prevents the nests from overheating (near 30°C), foam nests must be adaptive for *R. arboreus*, since embryonic mortality is kept low.

FOAM AS A POTENTIAL NUTRITIONAL RESOURCE

Foam could be a food source for hatchlings, either directly or by offering a substrate for microorganisms (Downie, 1988). Tanaka & Nishihira (1987) examined this possibility using *R. viridis*, which makes terrestrial foam nests at pond edges, and demonstrated that the foam mass can promote hatchling growth effectively. The present study showed a similar result in *R. arboreus* (Fig. 4). At present, however, we do not know what produces the nutrient effect: the foam itself or microorganisms involved in foam breakdown.

A chemical analysis of the freshly produced foam of *Polypedates leucomystax* showed that dried foam substances consist of protein (93.7%) and antronpositive sugars (6.3%), and that among the 17 amino acids detected, asparagine, lysine and glutamate are relatively abundant (Kabisch *et al.*, 1998). Promotion of hatchling growth by foam mass might be attributable to these components, although the chemical composition of the foam mass of *R. arboreus* is not yet known.

One or two weeks after nest construction, foam nests with hatchlings dissolve by themselves when they are exposed to high humidity or rain drops. Most of the hatchlings that escape from foam nests still have yolk supplies in the abdomen. However, hatchlings may not be able to escape from the nests when the outer layers of foam nests become dry and hardened during droughts (e.g. Downie, 1993). It is possible that in such situations, hatchlings use the foam masses as their food sources within the nests (Tanaka & Nishihira, 1987). In addition, the tadpoles of *R. arboreus* were observed to gather around the foam masses that had dropped down on the water surface to feed on the foam (personal observation). Females of *R. arboreus* sometimes construct foam nests above small temporary water bodies, such as side ditches or wheel ruts in forest roads (personal observation). Foam masses may be an effective nutritional resource for tadpoles, especially in such small water bodies. The foam masses can, therefore, be a potential food resource for hatchlings both inside and outside the nests.

OTHER FUNCTIONS

Two of five suggested functions of foam nests were examined in detail, as mentioned above. The remaining functions may be also effective in *R. arboreus*: prevention of desiccation of eggs and larvae (Dobkin & Gettinger, 1985; Downie, 1988, 1993), protection against egg predation (Heyer, 1969; Magnusson and Hero, 1991; Downie, 1988, 1990) and gas exchange (Seymour & Loveridge, 1994). Of these suggested functions, prevention of desiccation is the most likely to be an actual function of the foam nests of *R. arboreus*.

In *R. arboreus*, arboreal spawning occurs. If foam nests are not constructed and eggs are deposited directly on leaves or branches of trees without foam mass, the eggs would surely dry up quickly. Hence, it is highly likely that the foam must prevent eggs from becoming desiccated.

In a laboratory experiment using foam nests of *P. pustulosus*, Downie (1990) showed that a much higher proportion of floating eggs presented as individuals were predated by *Leptodactylus fuscus* tadpoles than as groups embedded in foam, and demonstrated that *P. pustulosus* eggs are somewhat protected from predation by being surrounded in foam. In the population studied, the most important predator of eggs was a snake, *Amphiesma vibakari*, which was sometimes observed to eat eggs by crashing the head into the foam nests (personal observation). Foam nests are not effective as a protective device against large vertebrate predators such as snakes, but may be effective against predation by small invertebrates. We observed in detail a total of 24 foam nests during the 2000–2002 breeding seasons, and only one of them was attacked by invertebrate predators: dipteran larvae (not identified, see Vonesh, 2000). This fact may indicate significant anti-predator effects of foam nests, but we do not have any definite evidence at present.

The foam of terrestrial nests may also be advantageous, as it allows the depositing of a clutch much larger than would be possible were the eggs surrounded by jelly alone. The bubbles in the foam not only facilitate oxygen diffusion into the egg mass but also provide a capacious oxygen store for immediate use by embryos, without the need for diffusion over long distances (Seymour & Loveridge, 1994). Female *R. arboreus* construct a large spherical foam nest, 10–15 cm in diameter, including 300–800 eggs above pond waters (Maeda & Matsui, 1999). If the respiratory role of the foam is not effective, production of such a large clutch may be impossible (see Seymour & Loveridge, 1994). But at present we have no data on the respiratory role of the foam in *R. arboreus*, and further studies are needed to investigate this.

ACKNOWLEDGEMENTS

We thank Yoshitaka Kamimura and Mitsuhiro Toda for their valuable advice, and members of the Laboratory of Animal Ecology of Tokyo Metropolitan University for their assistance in the laboratory and field experiments.

REFERENCES

- Dobkin, D. S. & Gettinger, R. D. (1985). Thermal aspects of anuran foam nests. *Journal of Herpetology* **19**, 271–275.
- Downie, J. R. (1988). Functions of the foam in the foam-nesting Leptodactylid *Physalaemus pustulosus*. *Herpetological Journal* **1**, 302–307.
- Downie, J. R. (1990). Functions of the foam in foam-nesting Leptodactylids: anti-predator effects of

- Physalaemus pustulosus* foam. *Herpetological Journal* **1**, 501-503.
- Downie, J. R. (1993). Functions of the foam in foam-nesting Leptodactylids: the nest as a post-hatching refuge in *Physalaemus pustulosus*. *Herpetological Journal* **3**, 35-42.
- Duellman, W. E. & Trueb, L. (1994). *Biology of Amphibians*. Baltimore: Johns Hopkins University Press.
- Gorzula, S. (1977). Foam nesting in Leptodactylids: a possible function. *British Journal of Herpetology* **5**, 657-659.
- Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identifications. *Herpetologica* **16**, 183-190.
- Heyer, W. R. (1969). The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* **23**, 421-428.
- Japan Meteorological Agency (2005). Meteorological data reference room. URL <http://www.data.kishou.go.jp>
- Kabisch, K., Herrmann, H.-J., Klossek, P. & Brauer, K. (1998). Foam gland and chemical analysis of the foam of *Polypedates leucomystax* (Gravenhorst 1829) (Anura: Rhacophoridae). *Russian Journal of Herpetology* **5**, 10-14.
- Kasuya, E., Hirota, M. & Shigehara, H. (1996). Reproductive behavior of the Japanese treefrog, *Rhacophorus arboreus* (Anura: Rhacophoridae). *Researches on Population Ecology* **38**, 1-10.
- Kato, K. (1955). Ecological notes on the green frogs during the breeding season. I. *Japanese Journal of Ecology* **5**, 70-73. (In Japanese, with English summary)
- Kato, K. (1956). Ecological notes on the green frogs during the breeding season. II. Breeding habits and others. *Japanese Journal of Ecology* **6**, 57-61. (In Japanese, with English summary)
- Kusano, T. (1998). A radio-tracking study of post-breeding dispersal of the treefrog, *Rhacophorus arboreus* (Amphibia: Rhacophoridae). *Japanese Journal of Herpetology* **17**, 98-106.
- Maeda, N. & Matsui, M. (1999). *Frogs and Toads of Japan*, 2nd ed. Bun-Ichi Sogo Shuppan, Tokyo. (In Japanese, with English abstract)
- Magnusson, W. E. and Hero, J.-M. (1991). Predation and the evolution of complex oviposition behaviour in Amazon rainforest frogs. *Oecologia* **86**, 310-318.
- Newman, R. A. (1998). Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia* **115**, 9-16.
- Rice, W. R. (1989). Analysing tables of statistical tests. *Evolution* **43**, 223-225.
- SAS Institute Inc. (1990). *SAS/STAT User's Guide, Version 6, Vols. 1 and 2*, 4th ed. Cary: SAS Institute Inc.
- Seymour, R. S. & Loveridge, J. P. (1994). Embryonic and larval respiration in the arboreal foam nests of the African frog *Chiromantis xerampelina*. *Journal of Experimental Biology* **197**, 31-46.
- Tanaka, S. & Nishihira, M. (1987). Foam nest as a potential food source for anuran larvae: a preliminary experiment. *Journal of Ethology* **5**, 86-88.
- Toda, M. (1989). *The Life History of Japanese Forest Frog, Rhacophorus arboreus in the Kanazawa Castle* (Master's Thesis). Kanazawa: Kanazawa University. (In Japanese)
- Vonesh, J. R. (2000). Dipteran predation on the arboreal eggs of four *Hyperolius* frog species in western Uganda. *Copeia* **2000**, 560-566.
- Zar, J. H. (1996). *Biostatistical Analysis*, 3rd ed. Upper Saddle River: Prentice-Hall.

Accepted: 12.7.05