- Bhattacharyya, A., Palaeogeol. Palaeoclimatol. Palaeoecol., 1989, 73, 25–38.
- 7. Bhattacharyya, A., Pollen Spores, 1988, 30, 417-427.
- Mazari, R. K., Bagati, T. N., Chauhan, M. S. and Rajagopalan, G., Proc. IGBP-PAGES/PEP-II Symp., Nagoya, Japan, 1997, pp. 262– 269
- Bhattacharyya, A. and Chauhan, M. S., Curr. Sci., 1997, 72, 408–412.
- Rajagopalan, G., Vishnu-Mittre and Sekar, B., Radiocarbon, 1978, 20, 398–404.
- 11. Erdtman, G., An Introduction to Pollen Analysis, Waltham, USA, 1943
- 12. Lamb, H. H., Climate: Past, Present and Future, Methuen, London, 1977.
- 13. Berger, A., Climatic Variations and Variability: Facts and Theories, D. Reidel, Dordrecht, 1981.

ACKNOWLEDGEMENTS. We are grateful to the Directors of BSIP and WIHG for providing the necessary facilities to carry out this work.

Received 4 April 2000; accepted 8 June 2000

## Courtship and nesting behaviour of the Malabar gliding frog, *Rhacophorus* malabaricus (Jerdon, 1870)

**Girish G. Kadadevaru and Ravishankar D. Kanamadi\***Department of Zoology, Karnatak University, Dharwad 580 003, India

Rhacophorus malabaricus is endemic to the Western Ghats of India. Courtship and nesting behaviour of this tree frog have been studied. Males emit advertisement calls after three or four heavy monsoon showers. Females approach calling males and axillary amplexus is effected. Females chose the leaf of a tree overhanging a water body for spawning. During spawning, the female rubs the back of the male by reversing her hind limbs. The male releases seminal fluid and agitates it to form the foam. Later the female covers the foam with leaves. R. malabaricus, in altered environmental conditions, constructs terrestrial foam nests. Females choose the slope towards the water body for spawning and use leaf litter to cover the foam. Modification of the reproductive mode from arboreal to terrestrial may be an adaptation to the changed environmental conditions.

A majority of anuran amphibians have external fertilization and they exhibit great diversity in reproductive modes. The most common and widespread site of oviposition is in free flowing or standing water. In some groups the eggs are terrestrial or arboreal while in others the eggs are retained in the oviduct<sup>1</sup>. Amongst the 179 anuran amphibians reported so far from India<sup>2</sup>, information on reproductive modes other than the species having aquatic eggs is scarce. In India, family Rhacophoridae includes 52 species<sup>2</sup>, many of which lay their eggs in the foam nests and others exhibit direct development<sup>3,4</sup>. *Rhacophorus malabaricus* is a large-sized frog endemic to the Western Ghats of India. Adult *R. malabaricus* is bright green coloured. It inhabits evergreen, and semi-evergreen forests and builds arboreal foam nests<sup>5</sup>. Except for preliminary observations on the developmental stages<sup>6</sup>, studies on this species are limited to distribution records. In the present work, we describe the courtship and nesting behaviour of *R. malabaricus*.

Field observations were carried out in different parts of the Western Ghats between 1996 and 1999, to study the breeding behaviour of R. malabaricus. Courtship and nesting behaviour was observed in 15 pairs. Calling activity in the frog begins after 3 to 4 heavy monsoon showers (June/July). Several calling males were located in Anashi Ghat near Karwar (14°48'N, 74°11'E). Males emit advertisement calls by sitting on the tree branches near a water source. As the female approaches the calling male, it is suddenly grasped by the male, resulting in axillary amplexus (Figure 1 a). For spawning, the females choose leaves of a tree branch overhanging the water body. During spawning, the female stretches its hind limbs and reverses them on to the back of the male. This brings the vent of the male closer to that of the female. Soon spawning begins and lasts for a few minutes. During spawning, simultaneously the female squeezes the back of the male and the male releases seminal fluid. The process continues for 15 to 20 minutes, then the female withdraws its hind limbs. The male whips the seminal fluid with its hind limbs, which results in the formation of foam. Then it leaves the female and moves away. Thus the amplexus lasts for 2 to 3 h. Later the female holds the leaf containing the foam nest with its fore limbs and starts collecting leaves one after another from the surroundings by stretching its hind limbs to cover the foam from all the sides. The collected leaves are held together between the limbs for a few seconds (Figure 1 b) to ensure proper binding. Foam itself acts as an adhesive for binding the leaves. The free end of the leaf holding the foam nest is folded by the frog to seal it from the lower end (Figure 1 c). Fourteen such nests were observed in a tree. Some of the nests were opened to see the eggs and clutch size. Eggs were spherical, cream coloured (Figure 1 d) and measured 2.62 mm ( $\bar{x}$ , n = 10). Heavy showers in due course not only washed the binding material between the leaves to open the foam nest, but also acted as a vehicle for the developing embryos to drop into water (Figure 1 e).

During our field observations in 1998, in a location marked near Sagar (16°37′N, 76°51′E), the habitat was disturbed. Many trees and bamboo vegetation were removed to utilize the land for agricultural activities. Late

<sup>\*</sup>For correspondence. (e-mail: karuni@bgl.vsnl.net.in)



Figure 1 a-d. Arboreal nesting behaviour. a, Axillary amplexus of R. malabaricus; b, Female frog holding the leaf containing the foam nest between its limbs; c, Female R. malabaricus moving away from the foam nest after covering it with from all the sides with the leaves and sealing it from the lower end; d, Foam nest showing large cream-coloured egg; e. Falling of the water droplet from the arboreal foam nest overhanging the water body, which has been exposed due to heavy rains.

in the evening, calls of R. malabaricus were heard. The males were emitting calls by sitting on the cut shoots of bamboo beside the stream. In an observation, a female approached the calling male that resulted in axillary amplexus. The amplexed pair moved towards the stream. On the bank of the stream, four amplexed pairs were found on land partially hiding between the litter (Figure 2 a). Spawning occurred on land. After the foam was formed, the male moved away from the site leaving the female and the foam (Figure 2 b). Immediately the female started collecting the dead leaves from the surrounding to cover the foam by stretching her limbs (Figure 2 c). Soon the foam nest was completely covered with litter (Figure 2 d). The site chosen to form the foam nest was always the slope towards the stream and was about 1 to 3 m away from the water. When we visited the same spot after five days, it

was filled with water due to heavy rains and the excess water was flowing towards the stream. The overflowing water from the agricultural land washed the foam nests and the developing embryos to the stream. The nests that were deposited near the stream were found floating due to rise in the water level.

Two amplexed pairs were brought to the laboratory and kept in the aquarium containing water, leaves and litter. The frogs constructed a foam nest on the side walls of the aquarium (Figure 3) and it was not covered. The embryonic development began in the foam nest and on the fourth/fifth day of spawning the eggs hatched. The clutch size varied between 160 and 192 and the hatching percentage varied from 86.24 to 91.97 (n = 4).

Reproductive strategies are as significant to the survival of species, as are the physiological and morphological

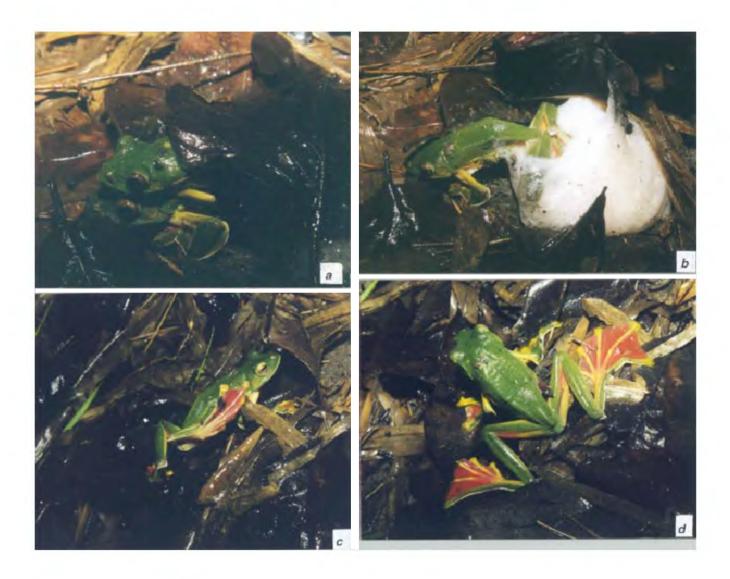


Figure 2. Terrestrial nesting behaviour. a, Amplexed pair on land, hiding between the leaf litter; b, Female frog along with the foam; c, Female frog covering the foam with litter by stretching its hind limbs; d, Completely covered foam nest.



**Figure 3.** Nesting behaviour in the laboratory. Foam nest on the side wall of aquarium with arrow marks showing the eggs.

adaptations to the environment. Patterns of reproduction are modified by natural selection so as to produce high fitness and they reflect a trade-off amongst many selective pressures. The diversity of reproductive modes in amphibians is much greater than that observed in any other groups of vertebrates. In each of the living orders there are trends towards terrestriality. The varieties of these trends are more in anurans<sup>1</sup>. Terrestrial foam nests are known in *myobatrachids*<sup>7</sup>, *Lepidodactylus fuscus* group<sup>8</sup>, *Polypedatus bambisicola*<sup>9</sup> and *P. maculatus*<sup>10</sup>. Asiatic rhacophorids belonging to the genus *Philautus*<sup>11</sup>, various species of *Polypedatus*<sup>9,12,13</sup> and *Rhacophorus*<sup>13,14</sup> construct foam nests in trees and bushes over the ponds. Many African frogs construct foam nests over ponds<sup>15</sup>. The courtship pattern observed in the frog R. malabaricus is unique among Indian anurans where the female reverses its hind limbs on the back of male, which is similar to the reverse clasping observed in the frog Eleutherodactylus coqui<sup>16</sup>. However in E. coqui, there is internal fertilization and direct development. Rubbing the back of the male by the female in R. malabaricus may act as a stimulus for the male to release the seminal fluid at the right time. Foam nests provide protection against desiccation: the upper surface exposed to air becomes viscous and even dries to form a thin crust, while the interior remains moist<sup>1</sup>. Covering the foam nest with leaves/leaf litter in *R. malabaricus* not only helps to maintain the humidity and moisture for a longer time but also camouflage the nest to protect it from predators. Construction of the terrestrial foam nest by *R. malabaricus* in altered environmental conditions by selecting the slope towards the stream and utilizing the litter from the surroundings to cover it, appears to be a modification in its reproductive strategy. It may be a product of natural selection under selective pressure and a trend towards the terrestriality as suggested by Duellman and Trueb<sup>1</sup>.

- Duellman, W. E. and Trueb, L., Biology of Amphibians, McGraw-Hill, New York, 1986.
- 2. Dutta, S. K., Hamadryad, 1992, 17, 1-13.
- 3. Daniels, R. J. R., Cobra, 1997, 29, 1-13.
- 4. Patil, N. S. and Kanamadi, R. D., Curr. Sci., 1997, 73, 697-701.
- Inger, R. F. and Dutta, S. K., J. Bombay Nat. Hist. Soc., 1986, 83, 135–146.
- 6. Sekar, A. G., J. Bombay Nat. Hist. Soc., 1990, 87, 223-226.
- Lee, A. K., Aust. J. Zool., 1967, 15, 367–439.
- 8. Heyer, W. R., Evolution, 1969, 23, 421-428.
- 9. Liu, C. C., Fieldiana, Zool. Mem., 1950, 2, 1-400.
- Kanamadi, R. D. and Jirankali, C. S., Zool. Anz., 1991, 266, 149– 162
- 11. Inger, R. F., Fieldiana, Zool., 1966, 52, 1-402.
- 12. Pope, C. H., Bull. Am. Mus. Nat. Hist., 1931, 61, 397-611.
- 13. Alcala, A. C., Copeia, 1962, 1962, 679–726.
- 14. Okada, Y., Biogeo. Soc. Jpn., 1966.
- 15. Amiet, J. L., Ann. Fac. Sci., Univ. Cameroun, 1974, 17, 121-130.
- Towensend, D. S. and Stewart, M. M., Herpetologica, 1986, 42, 165–170.

ACKNOWLEDGEMENTS. The study was supported by a grant from DST (No. SP/SO/C-23/93) awarded to R.D.K. and partly by the SAP-II UGC grant, New Delhi. G.K. thanks M. S. Bisnal and N. S. Patil for their help during the fieldwork.

Received 27 April 2000; revised accepted 31 May 2000