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Behavioral Ecology of Anuran Tadpoles: The Indian Scenario

S K SAIDAPUR*
Department of Zoology, Karnatak University, Dharwad 580003

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The study of behavioral ecology of amphibian tadpoles is in its infancy in India. Available descriptions of tadpoles that are limited to less than 25% of 218 known anurans in India are sketchy, incomplete and inadequate. Good descriptions and photographs of specimens in life that enable researchers to identify tadpoles are needed for all 218 species of amphibians living in our country. Recent studies, especially from our laboratory have revealed microhabitat choice and its ecological correlation, diversity in morphological characteristics, kin recognition ability, effect of kinship and density on larval growth and metamorphic traits and so on. The study of anuran tadpoles offers a unique opportunity to elucidate many complex biological phenomena and evolutionary strategies associated with their survival, growth and transition from purely aquatic to terrestrial mode of life. This report summarizes our gains and lacunae in our present knowledge of behavioral ecology of the tadpoles inhabiting India.

Key Words: Anura, Behavioral Ecology, Effect of Density and Kinship, Kin Recognition, Microhabitat Choice, Morphology, Tadpoles

Introduction

The tadpoles of anuran amphibians are the seemingly odd organisms with a composite head and body, a muscular tail without vertebrae and dorsal and ventral fins that lack bony supports. They possess a pair of eyes and usually external nares. A spiracle (s) that provides an exit for water pumped through the respiratory and food-trapping structures may occur in assorted positions in different species. Neuromast cells occur in specific patterns over a skin rich in mucous glands. The intestine is generally long and arranged in a spiral manner. The liver is large. These two organs are the major components of the viscera and often visible from the ventral side. A structurally variable and evolutionarily unique oral apparatus typically composed of soft and keratinized parts facilitates the harvesting of a myriad of food sources. Numerous morphological variations encountered not only reflect adaptations to diverse habitats such as puddles, ponds, stagnant or gently flowing water bodies and even fast flowing streams but also phylogeny (Duellman & Trueb 1986, McDairmid & Altig 1999).

**E-mail:* saidapur@hotmail.com

Small size, general abundance, low trophic position, relatively short life span, absence of sexual behavior, and ease of culture make tadpoles particularly good subjects to investigate many complex biological processes and interactions. Furthermore, their considerable developmental plasticity and complex life cycles provide an opportunity to investigate intriguing aspects of environmental and community influences on morphology, growth, behavior, larval duration and metamorphosis.

The recent alarming declines in amphibian populations worldwide and the suitability of amphibians for use in research in disciplines as diverse as molecular systematics, animal behavior, ecology and evolutionary biology have led our focus on tadpoles, the fascinating creatures, about which so little is known. In recent years, there has been a spurt of interest in the study of Indian amphibians especially with regard to faunal diversity, reproduction, development and behavior. Likewise, anuran tadpoles have attracted the interest of biologists and many interesting phenomena such as kin recognition, effects of kinship and density on growth and metamorphosis, foraging strategies, microhabitat choice and social aggregation are being discovered. The present status report attempts to summarize studies on the behavioral ecology of tadpoles harboring the Indian waters.

Morphological Diversities

The anuran tadpoles are highly plastic and therefore depending upon the ecological conditions the morphological features, habitat, time of the year when they are found in different geographical locations, duration of metamorphosis and size at transformation vary greatly within and between the species (table 1). Body shapes and fin configurations vary across taxa (figure 1). The diversity in oral apparatus is also extraordinary (figure 2). The complexity of oral apparatus and buccopharyngeal structures of tadpoles are diverse on both micro- and macromorphological scales. However, inter-specific, ontogenetic and geographical patterns of variations of the oral disc have not been studied adequately.

In general, the morphological variations are ecologically correlated. For instance, habitat selection and body form, foraging behavior and oral armature are interrelated. Lentic forms have weak tail musculature than the lotic forms, and the smallest muscles are associated with the largest fins (McDairmid & Altig 1999). The benthic forms typically possess a dorsoventrally flattened body, dorsal eyes and low fins whether in lentic or lotic environments. On the other hand, lentic (pond), nektonic (rarely lotic) forms may have compressed, depressed or equidimensional bodies and they live in different parts of the water column. A surface dweller, on the other hand, will typically have a laterally compressed body and a well developed ventral fin. The burrowing forms and those that live in confined spaces are vermiform with depressed bodies, dorsal eyes and low fins. Semi-terrestrial tadpoles have elongate bodies, narrow tail muscles with abbreviated fins, large eyes that bulge above the surrounding body surface, and hind limbs that develop precociously (McDairmid & Altig 1999). Tadpoles that live in slower reaches of streams resemble lentic-benthic forms except for a typical increase in the number of tooth rows, and the number of upper tooth rows is often larger than the lower. Lotic forms use the oral disc to maintain position as well as to feed in flowing water. They possess complete marginal papillae and frequently have more tooth rows and higher tooth

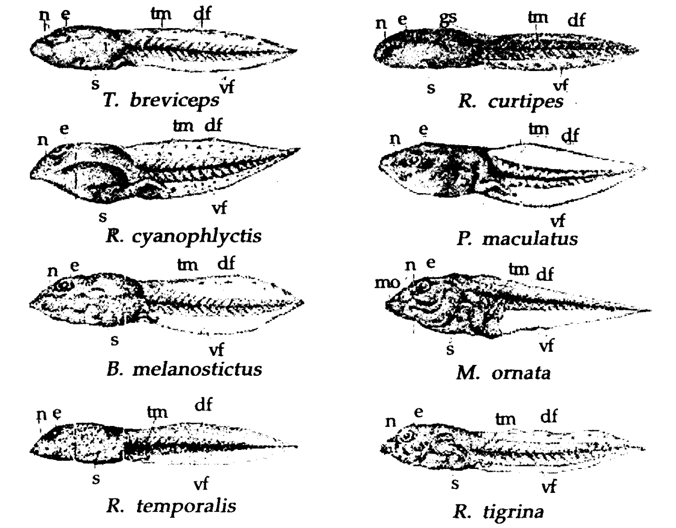

Figure 1 Representative body and tail configurations among anuran tadpoles found in Dharwad and Western ghat area. Note the diversity in morphological features of body, spiracle, tail, tail-fins and its musculature among the different species. *df,* dorsal fin; *e,* eye; *mo,* mouth; *n,* naris; *s,* spiracle; *tm,* tail muscle; *vf,* ventral fin.

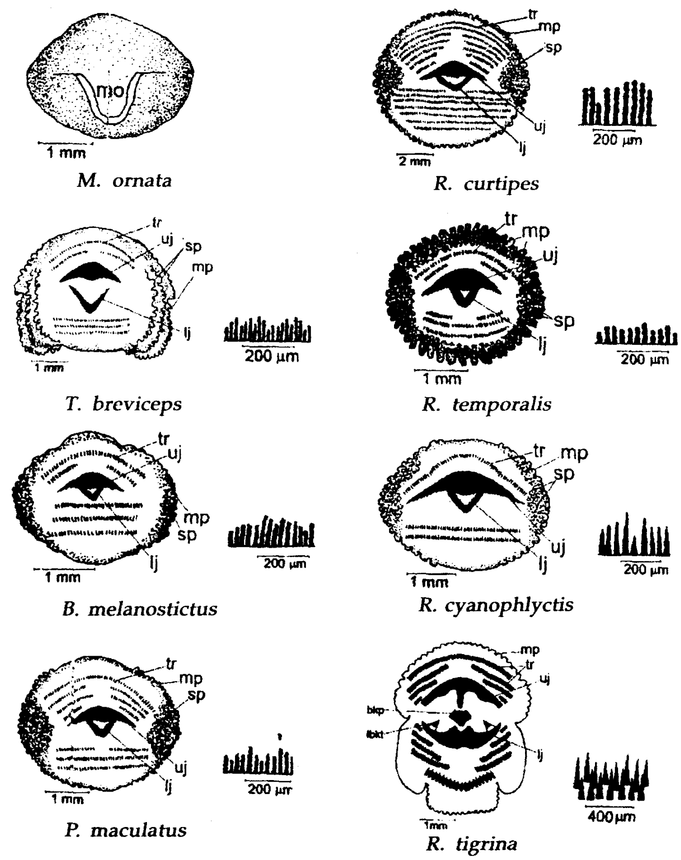

Figure 2 Representative oral disc configurations of tadpoles shown in Fig.1 reflecting diversities in their foraging capabilities. Note the variation from a most simplified (*M. ornata*) to a most robust (*R. tigrina*) oral apparatus. *bkp,* buccal keratinized plate; *lbkt,* lateral buccal papillae with keratinoized tip; *lj,* lower jaw sheath; *mp,* marginal papillae; *sp,* submarginal papillae; *tr,* tooth row; *uj,* upper jaw sheath.

Table 1 *Record of tadpoles, larval duration and size at metamorphosis of some anurans in India*

Species	Location of study	Occurrence of tadpoles	Type of Habitat	Larval duration (days)	Size (mm) at metamorphosis
1. *Amolops afghanus*	Meghalaya[1]	_	Rapid streams	_	_
2. *Bufo melanostictus*	Meghalaya[1]	_	Temporary Ponds and Puddles	_	_
	Dharwad[2]	Feb - Nov	"	25 - 35	8 - 12
	UP[3]	_	_	_	_
3. *Bufo stomaticus*	South India[4] UP[3]	_	_	_	10
4. *Callula obscura*	Trivandrum[5]	July	_	_	_
5. *Leptobrachium hasselti*	Meghalaya[1]	_	Slow streams	_	_
6. *Leptobrachium nigrops*	Meghalaya[1]	_	"	_	_
7. *Microhyla ornata*	Dharwad[2]	June - Nov	Temporary Ponds and Puddles	30 - 40	8 - 11
	UP[3] Orissa[6] Bubaneswar[7]	_	"	29	_
	Assam[1]	_	"	_	_
8. *Microhyla rubra*	Trivandrum[5]	June - Nov	_	_	_
9. *Megalophrys parva*	Meghalaya[8]	_	Streams	_	_
10. *Nyctibatrachus major*	Western ghats Tamil Nadu[9]	_	_	_	_
11. *Nyctibatrachus humayuni*	Western ghats[10]	_	_	_	_
12. *Nyctibatrachus sanctipalustris*	Western ghats[11]	_	_	_	_
13. *Philautus cherrapunjiae*	Meghalaya[1]	_	Slow streams	_	_
14. *Polypedates maculatus*	Dharwad[2] UP[3]	June - Oct	Temporary Ponds and Puddle	50 - 70	21 - 23
15. *Ramanella variegate*	Bubaneswar[12]	_	_	32	_
16. *Rana alticola*	Meghalaya[1]	_	Streams and Permanent Ponds	_	_
17. *Rana crassa*	Bubaneswar[13] UP[3]	June - Aug	_	31	_
18. *Rana curtipes*	Western ghats[14]	Year round	Streams	180 - 600	24 - 44
	Karnataka[15]	_	_	_	_
19. *Rana cyanophlyctis*	Dharwad[2] UP[3]	Year round	Temporary and Permanent Ponds	60 - 90	20 - 27
	Bubaneswar[16]	_	_	15 - 60	_
	Meghalaya[1]	_	Temporary ponds	_	_
	Trivandrum[5]	_	_	_	_
20. *Rana danieli*	Meghalaya[1]	_	Swamp streams	_	_

Table 1 *(contd...)*

Species	Location of study	Occurrence of tadpoles	Type of Habitat	Larval duration (days)	Size (mm) at metamorphosis
21. *Rana hexadactyla*	Trivandrum[5]	–	–	–	–
22. *Rana limnocharis*	Meghalaya[1] UP[3]	–	Temporary ponds and Puddles	–	–
	Trivandrum[5]	July	–	–	–
23. *Rana malabarica*	Bombay area[17]	–	–	78	–
24. *Rana temporalis*	Western ghats[18]	Oct - Mar	Streams	90 - 120	11- 14
25. *Rana tigrina*	Bubaneswar[19]	–	–	33	–
	Dharwad[2]	Apr - Sept	Temporary Ponds and Puddles	45 - 60	20 - 25
	Trivandrum[5]	–	–	–	–
26. *Rhacophorus maculates*	Trivandrum[5]	–	–	–	–
27. *Rhacophorus malabaricus*	Trivandrum[5] Goa[20]	June - Nov	Temporary ponds	68	21
28. *Rhacophorus nigropalmatus*	Meghalaya[1]	–	Temporary ponds	–	–
29. *Rhacophorus leucomystax*	"	–	Temporary ponds	–	–
30. *Tomopterna (Rana) breviceps*	Dharwad[2] Bubaneswar[21] UP[3]	July - Sept	Temporary Ponds and Puddles	45 - 60	10 - 12
	Trivandrum[5]	–	–	–	–
31. *Uperodon globulosum*	Bombay area[22]	Monsoon	–	–	–
32. *Uperodon (Cacopus) systoma*	UP[3] Trivandrum[5] Bubaneswar[23]	–	–	–	–

[1] Sahu 1994; [2] Saidapur *et al.* (unpublished); [3]Ray & Tilak 1994; [4]Abdulali and Daniel 1956; [5]Ferguson 1904; [6]Dei *et al.* 1994; [7]Mohanty-Hejmadi et al. 1980; [8]Hora 1922; [9]Pillai 1978; [10]Bhaduri & Kripalani 1955; [11]Rao 1920; [12]Dutta *et al.* 1991; [13]Dutta et al. 1994; [14]Hiragond et al.2001; [15]Sekar 1990; [16]Mohanty-Hejmadi & Dutta1978; [17]Chari1962; [18] Hiragond & Saidapur 1999; [19] Dutta & Mohanty-Hejmadi 1976; [20] Sekar1990; [21] Mohanty-Hejmadi *et al.* 1979; [22]Bhaduri & Daniel1956; [23]Mohanty-Hejmadi et al. 1979.

density; larger numbers of tooth rows presumably signal faster water habitats. A carnivorous tadpole will have pointed and keratinized teeth. Those foraging on detritus possess blunt teeth that are not so much keratinized. A suspension feeder may have a highly simplified oral apparatus that is devoid of teeth and oral papillae. In short, each species exhibits its own unique characteristic features.

Although description of the tadpoles of the Indian anurans dates back to almost a century (Ferguson 1904, Annandale & Rao 1918, Boulenger 1920) we still have scanty information, that is limited to less than 25% of anurans found in the country (table 1). A typical description of tadpoles should include general morphology, color, shape, size with respect to the developmental stage (preferably as per Gosner 1960), minute details of oral apparatus (position of the mouth, dental formula, nature of teeth, lips, papillae etc.) position of eyes, nares, internaral and interorbital distances, peculiarities of the spiracle (sinistral or dextral, lateral or median, attachment to body etc.,) and vent openings, tail musculature, dorsal and ventral fins and the morphometric features of the body (e.g. snout-vent length), and the tail. Unfortunately, the previous descriptions of the tadpoles are by and large inadequate, incomplete and often are of little value in identifying the species. Inadequate tadpole descriptions are common (table 1). Furthermore, the descriptions generally do not include all stages of development and therefore ontogenetic variations, if any are not revealed by these studies. The dental formula and descriptions of the oral disc are often missing. Invariably the tadpole figures are of poor quality. Good descriptions are however, available for a few species that include *Rana* *malabarica* (Chari 1962), *Uperodon globulosum* (Bhaduri & Daniel 1956), *Nyctibatrachus major* (Pillai 1978), *Tomopterna (Rana) breviceps* (Mohanty-Hejmadi et al. 1979a), *Rhacophorus malabaricus* (Sekar 1990a), *Rana temporalis* (Hiragond & Saidapur 1999) *Rana curtipes* (Sekar 1990b, Hiragond et al. 2001), *Bufo melanostictus, Rana tigrina* (changed to *Rana tigrerina, Hoplobatrachus tigerinus in recent years*), *Rana cyanophlyctis* (changed to *Oxidozyga cyanophlyctis and Euphlyctis cyanophlyctis recently*), *Microhyla ornata, Polypedates maculatus* (table 2). Sahu (1994) provided identification keys for 12 species from North Eastern India. However, his descriptions of tadpoles are rather brief. The representative morphological variations (body shapes and fins) among the tadpoles from southern India are shown in figure 1. The specific details of different tadpoles may be found in the original articles cited above. In general, the head shape and size vary greatly. The snout varies from being pointed to rounded shape. The body may be laterally or dorsoventrally compressed. It may even be equidimensional. Likewise, the tadpole tail, tail musculature (thickness and height) and its dorsal/ventral fins exhibit great variations in their shape and size across taxa (figure 1). The tail musculature of bufonids is generally weak. On the other hand, the tail musculature in stream dwelling and active swimmers is strong. The traits related to tail musculature have a bearing on the microhabitat choice of the tadpoles and swimming capabilities.

Das (1994) described in detail the internal oral morphology of some anurans using SEM and correlated these features with the feeding habits of the tadpoles. The oral papillae (submarginal and marginal) whose distribution and density vary greatly in different tadpoles are believed to serve as chemosensory and tactile receptors (McDiarmid & Altig 1999). They are also considered to help in the control of water flow, attachment to substrates, alter the shape of oral disc during feeding, and manipulate food and substrate particles. The labial teeth also show wide variations in their occurrence and morphology with respect to shape, size and keratinization (figure 2). These may be absent in some species. In others, these may be blunt, pointed and with or without cusps. A functional difference in the morphology of labial teeth is unknown. Probably they serve as broom, for current generation, for breaking up mucilaginous layers, sieving particles, combing strands into alignment for easier cutting, piercing plant cells, rasping food particles from a substrate, attaching to a substrate, and trapping food. Likewise, the jaw sheaths also show variations across taxa. The functional aspect of jaw sheath is not clear. Probably they serve as gouging, biting and/or scrapping structures. However, their striking differences across taxa indicate innumerable variety of performance abilities. The representative configurations of oral disc including labial teeth and papillae in different species are shown in figure 2. Understanding morphology, especially that of the oral disc is crucial to comprehending the feeding ecology of tadpoles. The functional morphology of the oral apparatus of tadpoles is largely unknown at present. Hence, little is known about how the mouth-parts work.

Identification of tadpole species is not easy (Daniels 1997abc, McDairmid & Altig 1999). Besides, related species often exhibit close resemblance. For instance, *U. globulosum* and *U (cacopus). systoma* tadpoles resemble very closely. Likewise, *N. major, Nyctibatrachus pygmaeus* and *Nyctibatrachus humayuni* show close similarities (Bhaduri & Kripalani 1955). Hence, a wrong identification is not uncommon. Ferguson (1904) seems to have mistaken *M. ornata for Microhyla rubra*. Boulenger (1920) described *R. curtipes* tadpoles but called them *Rana malabarica* (see Chari 1962). Annandale's description of *Philautus variabilis* is now identified as *N. pygmaeus* by Pillai (1978). Whether, *P. variabilis* has a tadpole stage is itself doubtful. Obviously, a careful investigation covering all stages of the development (Gosner stages 25-46) along with the morphometric features is needed for all the 218 species of anurans inhabiting the country. Such studies are urgently needed in order to develop the identification keys and diagnostic features of different species of tadpoles as shown in table 2 for some recently studied species from south India.

Factors Affecting Growth and Metamorphosis

The growth rates of anuran tadpoles are known to depend upon various factors such as density and inter- and intra-specific competition for food and space and other resources (Dash & Hota 1980, Hota & Dash 1981, Hokit & Blaustein 1997, Girish & Saidapur 1999, Saidapur & Girish 2001). The duration of different stages of larval development vary with the species and also depending upon various factors such as

Table 2 *Diagnostic Characteristics of Some Anuran Tadpoles from South India*

Species (size range in mm)	Color		Snout	Spiracle	Intestine	Tail Fin	Mouth	Teeth	Denial Formula
	Dorsal	Ventral							
1. R. curtipes[1] (23.5-87.5)	Light brown/ Black	Ash	Semicircular	Sinistral, Lateral	Visible in light brown tadpoles	DF>VF	Ventral	Blunt	7 (3-7) / 7 (1)
2. R. cyanophlyctis[2] (19.5-55.0)	Light/dark Brown	White	Triangular	Sinistral, Lateral	Not visible	DF>VF	Ventral	Pointed	1 / 2
3. R. tigrina[2] (12.5-52.0)	Olive or buddy brown	White	Triangular	Sinistral, Lateral	Not visible	DF>VF	Antero-ventral	Pointed	4(3-4) / 5(1-4)
4. R. temporalis[3] (9.5-32.0)	Muddy green/ White/ Yellowish or Olive brown	Muddy	Triangular	Sinistral, Lateral	Not visible	DF>VF	Ventral	Blunt	2 (2) / 3 (1)
5. B. melanostictus[2] (12.5-22.0)	Black	Ash	Semicircular	Sinistral, Lateral	Visible	DF>VF	Antero-ventral	Blunt	2 (2) / 3
6. M. ornata[2] (13.5-27.0)	Transparent	Trans-parent	Semicircular	Median Ventro-Posterior	Visible from ventral and lateral sides	DF<VF	Antero-dorsal	Absent	–
7. P. maculatus[2] (16.5-50.0)	Dull green or Muddy dark	White	Semicircular	Sinistral, Ventrolateral	Not visible	DF≅VF	Antero-ventral	Blunt	4 (2-4) /3 (1)
8. T. breviceps[2] (28.0-32.0)	Dark/muddy Brown	Muddy	Semicircular	Sinistral Lateral	Not visible	DF>VF	Ventral	Blunt	2 (2) / 3

Size range (total length) is shown for stages 25-42 except for *T. breviceps* (stages 34-42). DF- Dorsal fin; VF- Ventral fin.
[1]**Hiragond et al. 2001;** [2] S K Saidapur, N C Hiragond and B A Shanbhag, unpublished; [3]Hiragond and Saidapur 1999

temperature, food availability, aeration, crowding and kinship. Consequently, the duration of metamorphosis also varies. In general those that exhibit a rapid development metamorphose early and emerge as adult morphotypes at a smaller size while those having a prolonged larval life emerge as froglets at a larger size (table 1). The factors affecting growth and metamorphosis are studied in a few species among the Indian anurans.

Effect of Food Availability

Most anurans breed in ephemeral ponds and puddles of diverse nature that support the growth and abundance of different species of algae, diatom and plankton. Consequently, the type of food consumed by the tadpoles depends on the availability of food (type and abundance) in a given water body. A majority of anuran tadpoles are herbivorous or omnivorous while a few of them are carnivorous and even cannibals (Kamat 1962, Costa & Balasubramaniam 1965, Sabnis & Kolhatkar 1977, Sabnis & Kuthe 1980, Sekar 1992). In my laboratory, we have been able to maintain tadpoles of several herbivorous species on spinach. They show good growth and timely metamorphosis.

There are a few experimental studies dealing with the influence of food availability on growth and metamorphosis of tadpoles. Dash and Hota (1980) opined that increased competition for food at high density delays metamorphosis in *R. tigrina*. Later, Hota and Dash (1981) showed that both food and density act independently in affecting growth and metamorphosis. In *B. stomaticus* a mixed diet of animal and plant protein, fat and carbohydrate promoted the best larval growth especially at intermediate food levels. When only goat meat was provided to these tadpoles there was a decline in growth rate and a delay in metamorphosis. The *B. melanostictus* larvae grew equally well when hey were provided with spinach plus chironomous larvae or only spinach. But when they were provided with only the chironomous larvae the growth was stunted and metamorphosis was delayed (N C Hiragond & S K Saidapur, unpublished). Most bufonid larvae are herbivorous and therefore their growth is affected when they are maintained only on animal diet.

Effect of Aeration

There are only two studies that deal with the effect of aeration on larval growth. In *R. tigrina* aeration of water enhanced growth and rate of metamorphosis (Mohanty & Dash1986).Likewise, in *B. stomaticus*, aeration had a significant effect on larval growth and metamorphosis, by enhancing the food consumption of the tadpoles. Interestingly, aeration of the culture medium for one hour per day produced maximum larval growth, while a longer aeration period (2-4 hr) led to negative effect on growth rate (Mahapatro & Dash1990). It is interesting to see whether the effect sof aeration reported in the two species is also true for other species.

Effect of Temperature

Although experimental studies on Indian tadpoles are lacking the circumstantial evidences support the notion that higher ambient temperature usually accelerates growth and hastens metamorphosis. For instance, the duration of metamorphosis reported for anurans inhabiting Orissa (Bubaneshwar, Sambhalpur) is shorter (table 1) than those living in Karnataka (Dharwad) that experiences temperatures lower than in Orissa. The effect of temperature on pre and postembryonic development may also vary. For instance in *R. limnocharis*, at Shillong, exposure to constant 5^0C delayed development, induced abnormalities and heavy mortality of embryos. On the other hand, exposure to constant 28^0C enhanced growth rates of embryos but inhibited postembryonic growth (Roy & Khare 1979). The effect of temperature on growth and metamorphosis needs a careful investigation involving more species.

Effect of Density and Kinship

Density can influence growth and metamorphosis of tadpoles of many species of anurans (Wilber 1977) including the Indian bullfrog, *R. tigrina* (Dash & Hota 1980, Hota & Dash 1981), the bronze frog *R. temporalis* (Girish & Saidapur 1999) and the toad *B. melanostictus* (Saidapur & Girish 2001). These studies showed that generally growth rates, measured in terms of body mass, vary inversely with population density, and slowly growing individuals metamorphose at smaller sizes than their larger conspecifics(figures3-4). In *R. temporalis*, growth and size at metamorphic climax were inversely correlated to density of rearing. The crowding also significantly lowered the median developmental stage in the bronze frog. Interestingly, presence of kin and non-kin (intra-specific competition) also affect larval

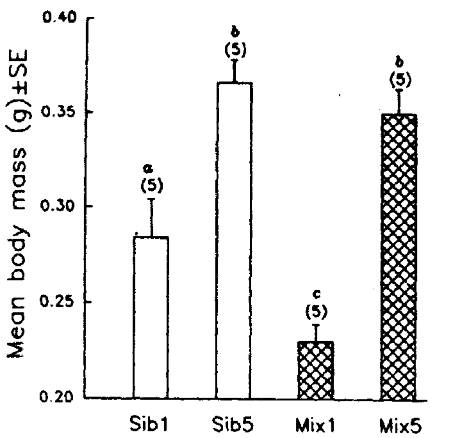

Figure 3 Effect of different rearing conditions on mean body mass of *Rana temporalis* at metamorphic climax. (5) indicates number of replicates. Non-identical labels (a,b,c) indicate significant ($P < 0.05$, ANOVA) differences from each other. Note the context dependent (i.e. crowding) effect of mixed rearing. (*From Girish and Saidapur, 1999*)

Sib 1 = ten siblings reared in 1L water; Sib 5 = ten siblings reared in 5L water; Mix 1 = mixed rearing consisting of two tadpoles from each of the 5 parental lines in 1L water; Mix 5 = mixed rearing consisting of two tadpoles from each of the 5 parental lines in 5L water

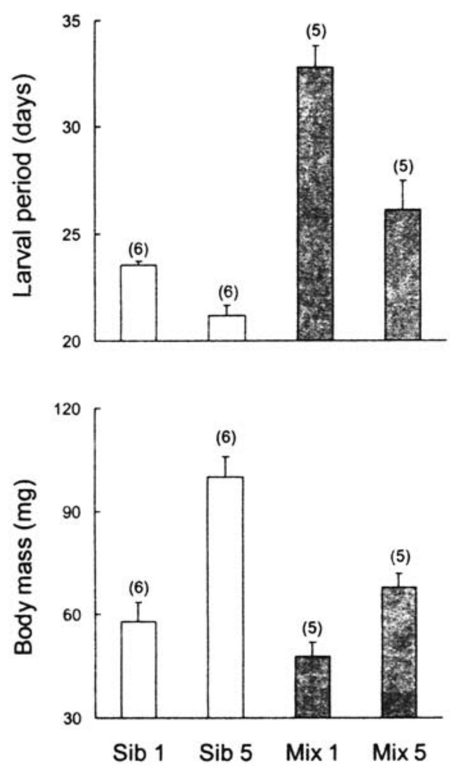

Figure 4 The effect of different rearing conditions on body mass and larval period in *Bufo melanostictus* at metamorphosis (Mean ± SE). Figures in parenthesis indicate number of replicates. Both density and kinship affect growth and duration of tadpole metamorphosis. Non identical labels (a, b, c, d) indicate a significant difference ($P < 0.05$, Two-way ANOVA) from each other. (*From Saidapur and Girish, 2001*)

growth and metamorphosis. For instance, in *R. temporalis* larval growth rates were significantly greater when reared with siblings (crowded or uncrowded) compared to those reared with non-kin (Girish & Saidapur 1999). Also, in pure groups individuals were less variable in size than those in mixed groups. In mixed groups the spectrum of developmental stages was broad but in pure groups it was narrow. Kinship was thus beneficial in regulating the growth rates in *R. temporalis* tadpoles, at least in the laboratory. Moreover, a genotypic heterogeneity in conjunction with crowding resulted in the production of a greater number of smaller individuals than in the genetically homogenous or sibling group. Interestingly, though both crowding and mixing affected the larval growth in *R. temporalis*, the latter had effect only under the crowded condition indicating a context dependent effect of the crowding.

The toad *B. melanostictus*, tadpoles reared as siblings metamorphosed in 25 days, whereas those reared with non-siblings metamorphosed between 30-35 days (Saidapur & Girish 2001). The largest mean body mass at metamorphosis was for sibling groups reared in lower densities. Rearing with siblings resulted in a uniform growth, production of bigger toadlets, and a narrow spectrum of size classes. In contrast, mixed rearing retarded growth rates, increased larval duration, and produced smaller individuals at metamorphosis, resulting in extreme variability in size classes, especially under crowded conditions. These findings show that both kinship and density affect larval duration and size at metamorphosis in *B. melanostictus*. Also, they signify the importance of social aggregation phenomenon seen in the two species, *R. temporalis* and *B. melanostictus* in both of which association with siblings (genetic homogeneity) enhances larval growth and metamorphosis, while mixed rearing (genetic heterogeneity) affects the larval growth adversely.

In *R. tigrina, P. maculatus* and *B. stomaticus* also crowding affected larval growth (Dash & Hota 1980, Hota & Dash 1981, Mishra & Dash 1984, Mahapatro & Dash 1987). However, in these studies pure groups were not used. Instead, the authors used only mixed groups. Therefore, the individual impact of non-kin and density on larval development in these species is unclear.

Behavior of Tadpoles

Anuran larvae are the major components of ephemeral pond ecosystems. In southern India, following southwest monsoon rains many anuran species co-breed in ephemeral ponds and puddles (Saidapur 1989). Hence, tadpoles of different species that live together are subjected to severe competition (intra- and interspecific) for food and space and to predation pressures due to aquatic insects as well as carnivorous tadpoles of other species. Some species of tadpoles also exhibit cannibalism. Among many possible ways, one way to avoid such competitions is to select proper microhabitat *vis-à-vis* adaptation to appropriate strata within a given water body. Indeed, the tadpoles of different anuran species living sympatrically exhibit diversity in their microhabitat choice (Hiragond & Saidapur 2001). In addition, anuran tadpoles exhibit many interesting behavioral patterns such as kin discrimination, ideal free distribution, social aggregation and so on. The studies relating to these aspects are summarized below.

Microhabitat Choice

Microhabitat selection is an important strategy of anuran larvae as it plays a key role in ensuring their survival and growth. However, experimental studies on the microhabitat choice of anuran larvae are scanty. Recently, the microhabitat habitat choice of tadpoles of seven anuran species with respect to light and dark phases was studied using a choice tank with a simulated pond edge (Hiragond & Saidapur 2001). In each trial, which lasted for 12 hrs, twenty freshly collected tadpoles (Gosner stage 32-38) of a given species were used. After introducing tadpoles into the choice tank, their number at the *surface, column,* and *substrate* was recorded at half-hour interval. Four trials each for day and night were conducted for each species. Tadpoles of *R. curtipes, R. cyanophlyctis,* and *R. temporalis,* which possess a ventral mouth, predominantly occupied substrate zone, whereas those of *B. melanostictus, P. maculatus,* and *R. tigrina,* which have an antero-ventral mouth, utilized both substrate and column zones but with a clear preference for substrate zone. Within the substrate zone, the number of tadpoles of *B. melanostictus, P. maculatus, R. temporalis,* and *R. tigrina* was greater in the night hours than in the daytime, whereas the opposite was true for *R. curtipes.* Of these five species response for day-night changes was prominent in *P. maculatus.* It is unclear whether diurnal/nocturnal variation in the number of tadpoles is due to changes in the light intensity or temperature or oxygen levels. The tadpoles of *R. cyanophlyctis* did not show any response to day-night changes. On the other hand, the tadpoles of *M. ornata,* which possess an antero-dorsally placed and highly simplified mouth (devoid of teeth) preferred surface (64%) and column (28%) zones in both light and dark phases. The tadpoles of *M. ornata* are not easily spotted despite their surface occupancy due to their transparent appearance. The study shows the diversity in the microhabitat choice of anuran tadpoles that correlates well with their morphological characteristics.

Social Aggregation

The tadpoles of some anurans are gregarious while those of the other are solitary. The tadpoles of *B. melanostictus, R. temporalis* and *R. curtipes* show social aggregation phenomenon. On the other hand, the tadpoles of *R. tigrina* are solitary. However, experimental studies are needed to establish the nature of social aggregation and its significance. Similarly, benefits of solitary living need to be studied.

Kin Recognition

Kin recognition is a widespread phenomenon in organisms as diverse as social insects, fishes, amphibians, birds, and mammals and even plants (Waldman 1991, Blaustein & Waldman 1992, Pfennig & Sherman 1995) though its significance is not well understood in most cases. Recently, the ontogeny of kin recognition and influence of social environment on the development of kin recognition behavior was experimentally investigated in tadpoles of the toad *B. melanostictus* that live in social aggregations and show a low larval dispersion (Saidapur & Girish 2000). In this study, the embryos and tadpoles of the toad from separate parental lines were reared as (i) kin only, (ii) with kin and non-kin (separated by a mesh screen), and (iii) in isolation. They were then tested for the ability to discriminate between (i) familiar siblings and unfamiliar non-siblings, (ii) familiar siblings and familiar non-siblings, and (iii) unfamiliar siblings and unfamiliar non-siblings. All tadpoles were fed on boiled spinach before conducting trials. Preference of test tadpoles to associate near the end compartments whether empty or containing members of specific stimulus groups was assessed using a specially designed rectangular choice tank. When tested in tanks with empty end compartments, the test tadpoles showed random distribution and thus no bias for the apparatus or the procedure. In the presence of kin/non-kin in the end compartments a significantly greater number of test tadpoles spent the majority of the time near familiar or unfamiliar kin rather than near familiar or unfamiliar non-kin. Kin discrimination ability persisted throughout larval development. Further, the study showed that familiarity with siblings is not required for discriminating kin from non-kin (table 3), and kin discrimination ability is not modified following exposure to non-kin. Also, involvement of dietary cues is unlikely to be the prime mechanism of kin recognition in *B. melanostictus* unlike in some other anurans (Waldman 1991, Blaustein & Waldman 1992). The kin recognition behavior of *B. melanostictus* and *R. temporalis* tadpoles seems to be associated with growth regulation as they perform better in growth and metamorphosis when reared with siblings than with non siblings (Girish & Saidapur 1999, Saidapur & Girish 2001). However, more studies involving more species are needed in order to elucidate the kin discrimination ability across taxa and its significance.

Predatory Behavior

Anuran tadpoles are known to exhibit herbivory (e.g. *B. melanostictus*) carnivory (e.g. *R. tigrina*), omnivory (e.g. *R. cyanophlyctis*) and also cannibalism (e.g. *R. tigrina and Rana crassa*). The tadpoles of *R. tigrina* predate (Mohanty-Hejmadi & Dutta 1981, Hota & Dash 1983) upon small worms, guppies and tadpoles of other sympatric anurans. However, very little is known about the predatory tactics of these tadpoles.

Table 3 *Shows that Bufo melanostictus tadpoles (stage 30-34) reared in isolation (from Gosner stage 12 onwards) recognize unfamiliar siblings over unfamiliar non-siblings.* I_1-I_5 *represent test tadpoles from 5 different parental line*

Group Tested	Number spending most[a] time near		Time (sec) spent in zones [b] (Mean ± SE)	
	Unfamiliar Siblings	Unfamiliar Non- siblings	Unfamiliar Siblings	Unfamiliar Non- siblings
I_1	15*	3	342 ± 27*	109 ± 30
I_2	20*	0	369 ± 27**	103 ± 22
I_3	17*	3	381 ± 30*	110 ± 27
I_4	16*	2	323 ± 26**	117 ± 27
I_5	15*	3	279 ± 43*	158 ± 31

a = Compared using Binomial test. b = Time spent in sibling zone was compared with a random expectation using Wilcoxon signed rank test. * = $p < 0.05$; ** = $p < 0.01$ *Fisherm procedure of combining probabilities for overall result:*

$-2\Sigma \ln p = 54.48$; $\chi^2_{(10)}$: $p < 0.0001$ *(Number data),*

$-2\Sigma \ln p = 64.42$; $\chi^2_{(10)}$: $p < 0.0001$ *(Time data).*

Source: Saidapur and Girish 2000

Cannibalism

The tadpoles of a few species (e.g. *R. tigrina, R. crassa*) seem to exhibit cannibalism especially under crowded conditions (Dutta et al. 1994). However, systematic studies are needed to elucidate the predatory tactics and circumstances (e.g. starvation, crowding) leading to cannibalism and its evolutionary significance.

Ideal Free Distribution

Ideal free distribution (IFD) is an interesting foraging strategy of many species which involves distribution of the groups of animals according to the patch profitability so that each individual has the same chance of obtaining food (Krebs & Davies 1993). Recently, this phenomenon was tested in tadpoles of *B. melanostictus* (S K Saidapur & N C Hiragond, unpublished) using a choice tank similar to that used in kin recognition studies. The food (boiled spinach) was provided in different ratios/or quantities at the end compartments (e.g. 1:2, 1:4, 2:4, 4:8 and so on). Thirty tadpoles were then placed in the center of the choice tank using an open-ended cylinder. After 5 min the cylinder was lifted gently allowing the tadpoles to choose the end compartments with differential food quantity. It is astonishing to note that the tadpoles distributed among themselves, in less than 10 min, in the ratio of food. These studies demonstrate the phenomenon of IFD by the toad tadpoles. The mechanism of IFD is however far from clear.

Conclusions

The recent alarming declines in amphibian populations worldwide and the suitability of amphibians for use in research in disciplines as diverse as molecular systematics, animal behavior, ecology and evolutionary biology have led biologists to focus their attention on tadpoles, the interesting creatures about which so little is known. In recent years, there has been a spurt of interest in the study of anuran tadpoles and many interesting phenomena such as kin recognition, effects of kinship and density on growth and metamorphosis, foraging strategies, microhabitat choice and social aggregation are being discovered. However, behavioral ecology of anuran tadpoles is still in its infancy in India. The tadpoles of more than two-thirds of Indian anurans are still undescribed. The available descriptions of a few species are sketchy, incomplete and inadequate. Also, the journals in which such descriptions appear are often not easily accessible. Hence, detailed descriptions, diagnostic features, identification keys and photographs of live/unpreserved specimens are urgently needed for all the species found in the country. The study of anuran tadpoles offers a unique opportunity to elucidate many complex biological phenomena and evolutionary strategies associated with their survival, growth and transition from purely aquatic to terrestrial mode of life. The study of behavioral ecology of anuran tadpoles is both challenging and fascinating. Such studies if pursued systematically and extended to many more species, will shed light on factors contributing to the evolution and maintenance of the tadpole stage in the life history of a frog, primitive or derived state of various traits. A sound knowledge of behavioral ecology of tadpoles will also help us appreciate fully the morphological variations and their ecological significance.

References

Annandale N and Rao C R N 1918 The tadpoles of the families Ranidae and Bufonidae found in the plains of India; *Rec. Indian Mus. Calcutta* 15 25-40

Abdulali H and Daniel J C 1956 Notes on *Bufo stomaticus* Lütken in Bombay; *J. Bom. Nat. Hist. Soc.* 53 716-717

Bhaduri J L and Daniel J C 1956 The tadpoles of *Uperodon globulosum* (GÜNTH.); *J. Zool. Soc. India* 53 713-716

Bhaduri J. L and Kripalani M 1955 *Nyctibatrachus humayunii*, a new frog from Western ghats, Bombay; *J. Bom. Nat. Hist. Soc.* 52 852-859

Blaustein A R and Waldman B 1992 Kin recognition in anuran amphibian larvae; *Anim. Behav.* 44 207-221

Boulenger 1920 A monograph of the south Asian, Papuan, Malayesian and Australian frogs of the genus *Rana*; *Rec. Indian. Mus. Calcutta* 1-226

Chari V K 1962 A description of the hitherto undescribed tadpole of, and some field notes on the fungoid frog, *Rana malabarica*; *J. Bom. Nat. Hist. Soc.* 59 71-76

Costa H H and Balasubramaniam S 1965 The food of the tadpoles of *Rhacophorus cruciger* (Blyth) Ceylon; *J. Biosci.* 5 105-109

Daniels R J R 1997a A field guide to the frogs and toads of the Western ghats, India: Part I *Cobra* 27 1-25

Daniels R J R 1997b A field guide to the frogs and toads of the Western ghats, India: Part II *Cobra* 28 1-24

Daniels R J R 1997c A field guide to the frogs and toads of the Western ghats, India: Part III *Cobra* 29 1-13

Das I 1994 The internal morphology of some anuran larvae from south India: a scanning microscopic study; *Amphibia-Reptilia* 15 249-256

Dash M C and Hota A K 1980 Density effects on the survival, growth rate, and metamorphosis of *Rana tigrina* tadpoles; *Ecology* 6 1025-1028

Dei C Mishra P K and Dash M C 1994 Larval stages, growth and metamorphosis of *Microhyla ornata* (Dum. & Brib.); *J. Freshwater Biol.* 6 269-273

Duellman W E and Trueb L 1986 Biology of amphibians (New York: McGraw Hill)

Dutta S K and Mohanty-Hejmadi P 1976 Breeding and life history of the Indian bull frog, *Rana tigerina* (Daudin); *Prakruti Utkal University Journal-Science* 13 51-59

Dutta S K Jena S and Mohanty-Hejmadi P 1994 Breeding and development of *Ramanella variegata* (Anura: Microhylidae); *J. Zool. Soc. India* 42- 43 55-76

Ferguson H S 1904 A list of Travancore batrachians; *J. Bom. Nat. Hist. Soc.* 15 409-509

Girish S and Saidapur S K 1999 The effects of density and kinship on growth and metamorphosis of the bronze frog (*Rana temporalis*) tadpoles; *Acta. Ethol.* 2 61-66

Gosner K L 1960 A simplified table for staging anuran embryos and larvae with notes on identification; *Herpetologica* 16 183-190

Hiragond N C and Saidapur S K 1999 Description of tadpole of *Rana temporalis* from South India; *Curr. Sci.* 76 442-444

_____ and Saidapur S K 2001 Microhabitat choice of tadpoles of seven anuran species; *Curr. Herpetol.* 20 51-60

Hiragond N C Saidapur S K and Shanbhag B A 2001 Description of the tadpole of a stream breeding frog, *Rana curtipes*; *J. Herpetol.* 35 166-168

Hokit D G and Blaustein A R 1997 The effects of kinship on interaction between tadpoles of *Rana cascadae*; *Ecology* 78 1722-1735

Hota A K and Dash M C 1981 Growth and metamorphosis of *Rana tigrina* larvae: Effects of food level and larval density; *Oikos* 37 349-352

Hota A K and Dash M C 1983 Evidence of interspecific predation among larval anurans: Predation of *Rana tigrina* larvae on *Bufo melanostictus* larvae; *Biol. Bull. India* 5 54-55

Hora S. L 1922 Some observations on the oral apparatus of the tadpoles of *Megalophrys parva* Boul.; *J. Proc. Asiatic Soc. Bengal* 18 9-15

Kamat N D 1962 On the intestinal contents of the tadpoles and algae of small ponds; *Curr. Sci.* 31 300-301

Krebs J R and Davies N B 1993 An introduction to behavioral ecology (London: Blackwell Scientific Publications)

McDiarmid R. W and Altig R 1999 Tadpoles: The biology of anuran larvae (Chicago: The University of Chicago Press)

Mahapatro B K and Dash M C 1987 Density effect on growth and metamorphosis of *Bufo stomaticus* larvae; *Alytes* 6 88-98

Mahapatro B K and Dash M C 1990 Aeration effect on growth and metamorphosis of *Bufo stomaticus* larvae; *J. Zool. Soc. India* 41 99-105

Mishra P K and Dash M C 1984 Metamorphosis of *Polypedates maculatus* (Gray, 1830): an analysis of crowding effect; *Alytes* 3 163-172

Mohanty-Hejmadi P and Dutta S K 1978 Breeding and development of *Rana cyanophlyctis* Schneider; *J. Bom. Nat. Hist. Soc.* 76 291-296

Mohanty-Hejmadi P Dutta S K and Parida S 1979a Life history of the Indian frogs I: The burrowing frog *Rana breviceps* Schneider; *J. Zool. Soc. India* 31 29-37

Mohanty-Hejmadi P Dutta S K and Mallick S C 1979b Life history of Indian frogs II: The marbled ballon frog *Uperodon systoma* Schneider; *J. Zool. Soc. India* 31 65-72

Mohanty-Hejmadi P Dutta S K and Khan I 1980 Life history of Indian frogs III: The ornate frog *Microhyla ornata*; *J. Zool. Soc. India* 33 43-48

Mohanty-Hejmadi P and Dutta S K 1981 Inter and intraspecific predation by *Rana tigerina* tadpoles; *Pranikee* 2 51-55

Mohanty S N and Dash M C 1986 Effects of diet and aeration on the growth and metamorphosis of *Rana tigrina* tadpoles; *Aquaculture* 51 89-96

Pfenning D W and Sherman P W 1995 Kin recognition; *Sci. Am.* (June) 68-73.

Pillai R S 1978 On *Nictybatrachus major* Boul. (Ranidae) with a description of its tadpole; *Bull Zool. Surv. India* 1 135-140

Rao C R N 1923 Notes on a collection of batrachia from south Waziristan; *J. Bom. Nat. Hist. Soc.* 29 131-135

Ray P and Tilak R 1994 Fauna of conservation area 5: Rajaji national Park: Amphibia; *Zool. Surv. India* 55-75

Roy D and Khare M K 1979 The influence of embryonic limiting temperatues on the development of Rana limnocharis. Wiegman; Biol. J. Linn.Soc. 11 279-289

Sabnis J H and Kolhatkar B L 1977 Observations on the food preferences of *Rana cyanophlyctis* tadpoles; *Comp. Physiol. Ecol.* 2 232–233

Sabnis J H and Kunthe K S 1980 Observations on the food and growth of *Bufo melanosticus* tadpoles *J. Bom. Nat. Hist. Soc.* 77 21–25

Sahu A. K 1994 Dichotomous key to the tadpoles of twelve anuran species from northeastern India; *J. Bom. Nat. Hist. Soc.* 412-419

Saidapur S K 1989 Reproductive cycles of amphibians; in Reproductive cycles of Indian Vertebrates pp 166-224 ed S K Saidapur (New Delhi: Allied Publishers Limited)

Saidapur S K and Girish S 2000 The ontogeny of kin recognition in tadpoles of the toad *Bufo melanostictus* (Anura; Bufonidae); *J. Biosci.* 25 267-273

Saidapur S K and Girish S 2001 Growth and metamorphosis of *Bufo melanostictus* tadpoles: Effects of kinship and density; *J. Herpetol.* 35 249-254

Sekar A G 1990a Observations of the developmental stages of tadpoles of the malabar gliding frog *Rhacophorus malabaricus* Jerdon, 1870 (Anura: Rhacophoridae); *J. Bom. Nat. Hist. Soc.* 87 223-226

Sekar, A G 1990b Notes on morphometry, ecology, behavior and food of tadpoles of *Rana curtipes* Jerdon, 1853; *J. Bom. Nat. Hist. Soc.* 87 312-313

Sekar A G 1992 A study of the food habits of six anuran tadpoles; *J. Bom. Nat. Hist. Soc.* 89 9-16

Waldman B 1991 Kin recognition in amphibians; in *Kin Recognition* pp. 162–219 ed P G Hepper, (Cambridge: Cambridge University Press)

Wilber H M 1977 Interactions of food level and population density in *Rana sylvatica*; *Ecology* 58 206-209