FOOD PARTICLE RETRIEVAL IN AMPHIBIAN TADPOLES

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Abstract

Amphibian tadpole develops in water, draws nourishment from common pond sources including planktonic suspension, vegetation, detritus and from larvaevory. *Microhyla ornata* is a plankton feeding microphage; *Bufo stomaticus* is vegetation rasper macrophage; while both *Limnonectes* species are macrophagus raspers as well as microphagus plankton feeders. However, *Euphlyctis cyanophlyctis* is detritivorous and *Hoplobatrachus tigerinus* is a larvivore-carnivore. Despite difference in diet, each species employs similar buccopharyngeal technology to glean the particulate food from water current.

Key words

Tadpole, amphibian, buccopharynx, zooplankton

Introduction

The larval period in the life history of tropical amphibians is the least understood, despite strong selection forces. The delicate tadpole is at the mercy of changes in its aquatic environments, like fluctuations in water level, temperature and concentration of water contents which occur from time to time, the tadpole is to cope with all of them within the confines of the pond. Moreover, the tadpole has to protect itself from different predators like fishes, aquatic carnivorous insects, their larvae and sympatric cannibalistic interspecific and intraspecific carnivorous larvae. However, despite fragility in structure, tadpoles tolerate hazards as they are highly plastic in their adaptations, and ability to camouflage against enemies (Inger & Colwell, 1977; Wassersug, 1972, 1974, 1984 & 1989; Wassersug *et al.* 1981; Wassersug & Heyer, 1983; Dodd & Cupp, 1976; Heyer *et al.*, 1975).

Amphibian tadpoles of five species -- *Bufo stomaticus, Microhyla ornata, Euphlyctis cyanophlyctis, Limnonectes limnocharis, L. syhadrensis* and *Hoplobatrachus tigerinus* develop sympatrically in the ponds and puddles of Punjab riparian system, all deriving nourishment from pond resources (Khan, 1991). This paper discusses the bucco-pharyngeal particulate food processing in these species of tadpoles.

Materials and Methods

Tadpoles for the present study were collected by fine meshed hand net from ponds and puddles (Khan & Malik, 1987). *Microhyla* tadpoles were netted at midstream, while those of *Bufo* were scooped from marginal water. However, ranids were difficult to collect, since they retreat to the bottom of the pond when distrubed. They were dredged out with lot of mud, for which the net was kept dipped and the swimming tadpoles were scooped out by a teapot sieve. The collected tadpoles were kept for about half an hour in clear water to wash away the pond debris from the buccopharyngeal region.

Fixation

Tadpoles at Stage 35 (Khan, 1965) were processed. They were fixed in Bouin's fixative following Khan (1965), and were stored in diluted Bouin's with water (1:1), as suggested by Khan (1982). The shape and pigment of tadpole is ideally preserved, although the belly iridiocytes of *Microhyla* are lost. The yellow colour of picric acid accentuates morphological features on oropharyngeal surfaces.

To study the morphology of the cartilaginous support of the ventral velum, the tadpoles were stained by Alcian blue (Henken & Wassersug, 1981). The cartilage was stained deep blue, while the rest of the tissue was light blue.

Surgical Procedure

The tadpole was fixed belly up in a groove, excavated in the center of the dissection dish with wax. Tip of one blade of a pair of fine scissor was gently inserted into a corner of the mouth of the tadpole and the buccal wall cut along the lateral side of the tadpole to its posterior-most end. A similar cut was made on the other side. A third cut was made through the posterior of the pharyngeal region freeing buccopharyngeal floor from its roof

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(Khan, 1991).

For identification of different oropharyngeal features in amphibian tadpoles, text figures showing oropharyngeal features are provided.

Observations and Comments

Food acquisition

Orton (1953) classified amphibian tadpoles on the basis of their mode of feeding. *Microhyla ornata* tadpole is placed in type II, which lacks an oral disc and its associated hard parts. While ranoid tadpole of genus *Bufo* and *Rana* are type IV with well developed oral disc and its associated hard parts. Each species of tadpole uses its oral structures in its own way to acquire food. Type II tadpole stays in the plankton-rich layers of pond at midstream gulping in the suspended food particles into its buccal cavity, while type IV tadpoles use their keratinized rows of teeth and sharp, serrated, strong beaks to scrape and glean nutritive material from submerged vegetal surfaces. Bucco-pharyngeal region of both types of tadpoles glean food as it enters suspended in water in the bucco-pharyngeal cavity (Khan, 1991; Khan & Mufti, 1994b).

The "sucking-in" process involves complex buccal mechanism. The bucco-pharyngeal muscular walls help in sucking and pumping the nutritious water current through the oro-bucco-pharyngeal passage. Due to contraction and expansion of the muscles, the Meckel's cartilage is anteriorly displaced and its suspensorium allows forward expansion of the ceratohyal. Thus the articulation of ceratohyal with the platoquadrate causes its up and downward movements, while the floor of the buccal cavity serves as a piston of the buccal pump. One way flow of water is ensured by the valves present in the buccal cavity. As the particulate food passes over glandular surfaces in the buccal cavity, it is gleaned from the water current (Seale & Wassersug, 1979; Khan, 1991).

Food particle processing technology

Khan (1991) recognized three parts of the oropharyngeal passage where food processing takes place:

Oral processing: In ranoid tadpoles, the rasped and cut food particles are made sizable by the action of denticles and beak and are blown in the passing water current into the buccal cavity. While particulate food containing current in *Microhyla* tadpole passes through the "U" shaped mouth of the tadpole, a series of infralabial papillae (8) form a sieve which does not allow large particles to enter the oral cavity.

Buccal processing: Special bilateral strategically arranged buccopharyngeal elements which are disposed on the roof and floor of the buccal cavity and the branchial surfaces of the tadpole, are used in food processing in this part of the oropharyngeal tract. Morphology and arrangement of these elements differ in species of tadpoles, depending on the food particle size and its concentration (Khan, 1991). These bucco-pharyngeal organs are:

Ridges: Special ridge like structures are present along the roof of the buccal cavity, the prenarial ridge (1) and other median ridges (2, 3), which regulate the speed of water current in the buccal cavity. In addition, the prenarial ridge also aids in the cutting of coarse food particles.

Cilia: Microscopical cilia are scattered on the lining of the buccal cavity. Mostly they direct the particulate food to the median ciliary groove leading into the oesophageal cavity.

Papillary organs: In ranoid tadpoles, the buccal lining is thrown in pustules and papillae. Buccal papillae (5, 11) are simple, thin, straight or curved, delicate structures, gradually attenuating into pointed tips, which may be simple or bifurcated. The papillae are arranged in groups. The infralabial (8) and lateral ridge papillae (4) are large and palmate. Pustules and papillae are sensitive to the size of the food particle and its concentration in the current, according to which the tadpole regulates food processing in buccal and branchial cavities. The flat larval tongue (9) is also papillated (10).

In microhylids, the papillae are coalesced at their base to form delicate oblique ridges which guide water current to the glandular strip and pharynx.

Buccal glands: A broad glandular band (6) extends from sides forward all along the outermost border of the roof of the buccal cavity. It is broadest in microhylid tadpole. The strip is covered with fine pores of mucous glands that secret fine sheets of mucous for food entrapment.

Subvelar glands: The buccal floor extends backward over the branchial basket as ventral velum (12). The branchial plates (cb) are attached under it. Part of the branchial cavities (13) under the ventral velum is known as food traps (14). The subvelar morphology (Fig. 1c) and attachment of branchial plates differ in different species of tadpoles, depending on the size and type of the food particle they process (Khan, 1991). In coarse particle feeders it is pitted (16) all over, while in fine particulate feeders it is ridged (17), while in species feeding on hetromorph particles both pitted and ridged pattern is found (Khan, 1991; Khan & Mufti, 1994).

Food retrieval

The particulate retrieving process takes place in two stages. It starts in the buccal cavity and is completed in the pharyngeal cavities:

Buccal processing: Sheets of mucous secreted from the general buccal lining and particularly from the buccal glandular strip are

blown in the water current; food particles get stuck in it. The food laden mucous is then washed down in the branchial basket, where finer particles which have escaped from buccal entrapment, are entrapped by more sticky mucous secreted from the subvelar glands in the food traps so that the water, which passes through the filter ruffle is free from particulate material.

Pharyngeal processing: The pharyngeal part of the tadpole lies at the postero-lateral sides of the buccal cavity as branchial baskets (Khan, 1991). The cavity of a branchial basket is divided in branchial or filter cavities (13), number of which differ from species to species. The branchial cavities are lined by closely set branchial plates, their lining is thrown into fine intricate folds which is known as filter ruffle; through their fine mesh water passes. The intensity of the mesh of the filter ruffle differs from species to species according to the fineness of its particulate food. The filter ruffle acts as an efficient sieve and retains the food laden mucous in the branchial cavities which is carried through special ciliated grooves into the oesophageal orifice (7), while water passes out of the branchial region through spiracles (Kenny, 1969a,b; Gradwell, 1975; Wassersug, 1980; Sanderson & Wassersug, 1989; Wassersug & Rosenberg, 1979; Khan, 1991).

Conclusions

The five species of riparian tadpole, utilize the common food base available in the pond ecosystem in unique ways avoiding competition. Similar trophic partition has been reported in adults and larvae of southern Indian amphibians (Das, 1991). Though the tadpoles are phytophagus, their diet includes a considerable amount of zooplanktons which they sucks with the water current. The microphagus *Microhyla ornata* takes zooplankton as it filter feeds on ultra microscopical organic planktonic matter that grows in water column and remains suspended (Khan, in press). Though *Bufo* and *Limnonectes* tadpoles are typical raspers on submerged plant surfaces, they ingest large quantities of zooplanktons with particulate food carrying water current (Khan & Mufti, 1994a; Khan, 1996). The large detritus feeder *Euphlyctis cyanophlyctis* tadpole feeds on detritus fauna and rotten vegetation, which thrives at the bottom of the pond (Khan & Mufti, 1995). The larvivorus *Hoplobatrachus tigerinus* tadpole is not an exception, though it feeds mainly on tadpoles of its own kind and other species (Khan, 1997), its feeding current carry zooplanktons also. Larger species like *Daphnia* and *Cyclops* are filtered in its poor filter ruffle, while smaller pass through. Moreover, as pond water becomes older it becomes richer in zooplanktons, enriching diet in protein of *Microhyla* tadpole. In later stages of development, after Stage 35, all ranoid tadpoles seek to supplement their diets with more protein, which they get by occasionally devouring sympatric tadpoles, drowned frogs, earthworms etc., to quicken metamorphic process, which is necessary in unpredictable temperate riparian environs of Punjab.

References

Das, I. (1991). *Trophic ecology of a community of south Indian anuran amphibians*. D. Phil. Thesis, Oxford University.

Dodd, C.K. and P.V. Cupp (1976). The effect of temperature and stage of development on the duration of immobility in selected anurans. *Brit. J. Herpetol.* 5: 783-788.

Gradwell, N. (1975). Experiments on oral suction and gill breathing in five species of Australian tadpoles (Anura:Hylidae and Leptodactylidae). *J. Zool. London.* 177: 81-98.

Henken, J. and R. Wassersug (1981). Double staining technique for skeleton. *Functional Photog.* 16: 22-44.

Heyer, W.R., R.W. McDiarmid and D.L. Weigmann (1975). Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7: 100-111.

Inger, R.F. and R.K. Colwell (1977). Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecol. Monog.* 47: 229-235.

Kenny, J.S. (1969a). Feeding mechanism in anuran larvae. *J. Zool. London* 157: 225-246.

Kenny, J.S. (1969b). Pharyngeal mucous secreting epithelia of anuran larvae. *Acta Zool.* 50: 143-153.

Khan, M.S. (1965). A normal table of *Bufo stomaticus*. *Biologia* (Lahore) 11: 1-39.

Khan, M.S. (1982). Key for the identification of amphibian tadpoles from the plains of Pakistan. *Pakistan J. Zool.* 14: 133-145.

Khan, M.S. (1991). *Morphoanatomical specialization of the buccopharyngeal region of the anuran larvae and its bearing on the mode of larval feeding*. Ph.D. Dissertation. University of Punjab, Lahore

Khan, M.S. (1996). Oropharyngeal morphology of tadpole of southern cricket frog *Rana syhadrensis* Annandale, 1919, and its ecological correlates. *Pakistan J. Zool.* 28: 133-138.

Khan, M.S. (1997). The oropharngeal morphology and feeding habits of tadpole of tiger frog *Rana tigerina* Daudin. *Russian J. Herpetol.* 2: 163-171.

Khan, M.S.(in press). Buccopharyngeal morphology of *Microhyla ornata* tadpole and its bearing tadpole's feeding ecology. *Asiat. Herp. Res.*

Khan, M.S. and S.A. Malik (1987). Reproductive strategies in a subtropical anuran population in arid Punjab, Pakistan. *Biologia* 33: 279-303.

Khan, M.S. and S.A. Mufti (1994a). Oral disc morphology of amphibian tadpole and its functional correlates. *Pakistan J. Zool.* 26: 25-30.

Khan, M.S. and S.A. Mufti (1994b). Buccopharyngeal specializations of tadpole of *Bufo stomaticus* and its ecological correlates. *Pakistan J. Zool.* 26: 285-292.

Khan, M.S. and S.A. Mufti (1995). Oropharyngeal morphology of detritivorous tadpole of *Rana cyanophlyctis* Schneider, and its ecological correlates. *Pakistan J. Zool.* 27: 43-49.

Orton, G.L. (1953). The systematics of vertebrate larvae. *Syst. Zool.* 2: 63-75.

Sanderson, S.L. and R. Wassersug (1989). Convergent and alternative designs for vertebrate suspension feeding. *In*: *The vertebrate skull*. B. Hall and J. Hanken (ed.) University Chicago Press.

Seale, D.B. and R. Wassersug (1979). Suspension feeding dynamics of anuran larvae related to their functional morphology. *Oecologia* 39: 259-272.

Wassersug, R. (1972). The mechanism of ultraplanktonic entrapment in anuran larvae. *J. Morph.* 137: 79-288.

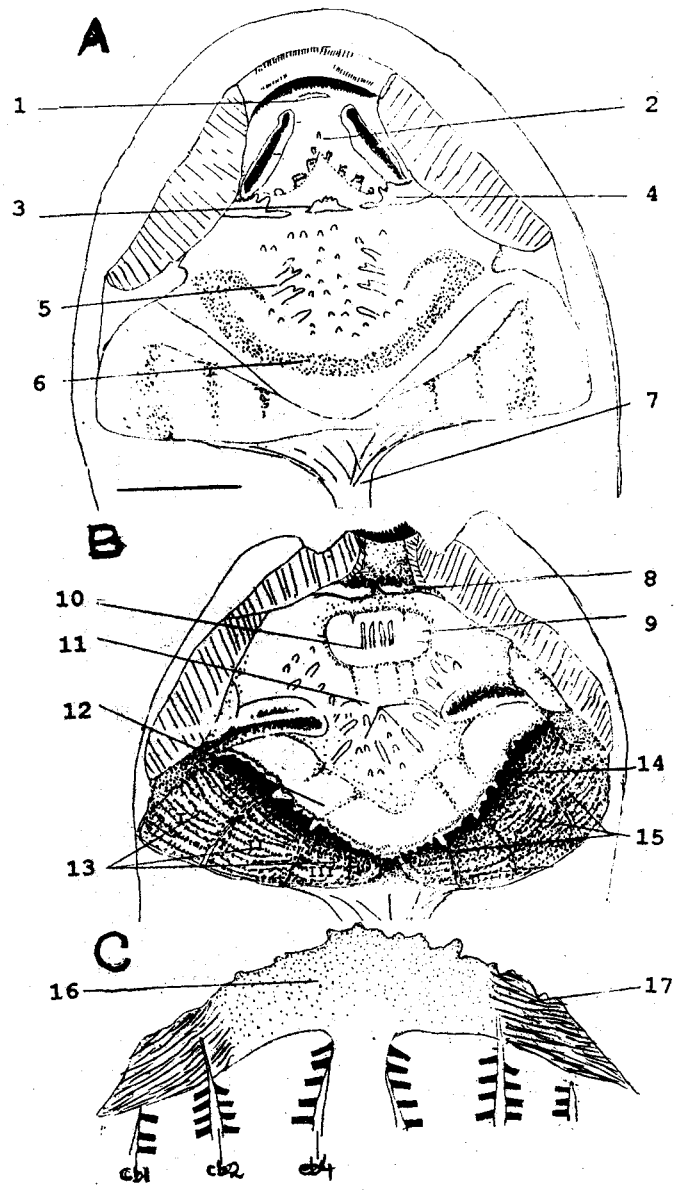

Figure 1. Bufo stomaticus *tadpole at Stage 35 (Khan, 1965)*
[A. Buccopharyngeal roof;
B. Buccopharyngeal floor;
C. Ventral velum, showing subvelar glandular surface]
dissected to show buccopharyngeal structures referred to in the text: 1 = Prenarial ridge; 2 = Narial pustular ridge; 3 = Median ridge; 4 = Lateral ridge papilla; 5 = Buccal roof papillae and pustules; 6 = Glandular pitted band; 7 = Oesophagus; 8 = Infralabial papillae; 9 = Larval tongue; 10 = Tongue papillae; 11 = Buccal floor papillae; 12 = Ventral velum; 13 = Filter cavities; 14 = Food traps; 15 = Filter plates; 16 = Pitted; 17 = Ridged; Cb1-4 = Ceratobranchials.

Wassersug, R. (1974). Evolution of anuran life cycles. *Science* 185: 377-378.

Wassersug, R. (1980). The internal oral features of larvae from eight anuran families: Functional, systematic, evolutionary, and ecological considerations. *Univ. Kansas Mus. nat. Hist. Misc. Publ.* 68: 1-146.

Wassersug, R. (1984). The *Pseudohemisus* tadpole: a morphological link between microhylid (Orton type 2) and ranoid (Orton type 4) larvae. *Herpetologica* 40: 138-149.

Wassersug, R. (1989). Locomotion in amphibian larvae (or "Why aren't tadpoles built like fishes?"). *American Zool.* 29: 65-84.

Wassersug, R., K.J. Frogner and R.F. Inger (1981). Adaptations for life in tree holes by rhacophorid tadpoles from Thailand. *J. Herpetol.* 15: 41-52.

Wassersug, R. and W.R. Heyer (1983). Morphological correlates of subaerial existence in leptodactylid tadpoles associated with flowing water. *Canadian J. Zool.* 61: 761-769.

Wassersug, R. and W.R. Heyer (1988). A survey of internal oral features of leptodactyloid larvae (Amphibia: Anura). *Smithson. Cont. Zool.* 457: 1-99.

Wassersug, R. and K. Rosenberg (1979). Surface anatomy of branchial food traps of tadpoles: a comparative study. *J. Morph.* 159(3): 393-425.