density bodies along the shoulders of the graben, is in agreement with the present study. This confirms the appropriateness of the model used and the inversion technique employed in our work.


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**Pattern of growth and utilization of abdominal fat bodies during larval development and metamorphosis in five South Indian anurans**

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The tadpoles of *Rana tigrina*, *Rana cyanophlyctis*, *Rana curtipes*, *Polyedatus maculatus* and *Bufo melanostictus* grew in size (mass and snout vent length or SVL) progressively until metamorphic climax. The abdominal fat bodies first appeared in stages 25–30; and accumulation/utilization of fat during larval development and metamorphosis varied with the species. In *B. melanostictus*, fat bodies were barely seen. In laboratory-reared *R. curtipes*, body weight and fat body mass were better developed than in the wild caught. The amount of fat deposition was related to the duration of metamorphosis in the various species studied. The findings thus show that the size of fat bodies in the larval anurans is correlated with the body mass, SVL as well as duration of metamorphosis.

The conspicuous nature of abdominal fat bodies and seasonal and/or annual changes in their mass in adult anurans are well documented1–3. Such changes in the fat body mass in amphibians indicate changes in the nutritional status of a given individual4. The abdominal

*For correspondence.
fat bodies, like the gonads, arise from the mesoderm during embryonic development in amphibians. That the fat bodies have a supportive role in reproduction was recently shown by Saidapur and Prasadmurthy. While the gonadal development and differentiation are studied in a few anurans, there are no reports on the pattern of growth and utilization of the fat bodies during their larval development. The present study deals with the changes in fat body mass, and its possible relationship with body weight and snout vent length (SVL) during the various stages of larval development and metamorphosis in five anuran species, Rana tigrina, R. cyanophlyctis, R. curtipes, Polypedatus maculatus, and Bufo melanostictus. Since R. curtipes exhibits a prolonged larval life, the changes in the fat body mass in the laboratory-reared and wild-caught tadpoles of R. curtipes was also studied.

The tadpoles of different species were collected from ponds around Dharwad and from streams in the western ghats. Each collection included tadpoles in various stages of development. The developmental stages of tadpoles were identified according to Gosner. The tadpoles were autopsied within a few hours of collection. The SVL (mm), body weight (g), and fat body mass (g) were recorded. The fat bodies in B. melanostictus were so minute that they could not be weighed.

The data were analysed using Pearson correlation coefficient analysis to determine the relationship between body fat, body weight, and SVL (SPSS for Windows Release 6.13). The changes, if any, in the body weight and fat body mass after metamorphosis were compared with those of the tadpoles at stage 41 (a stage designated as premetamorphic climax), using Mann–Whitney U test, in case of R. cyanophlyctis, R. curtipes and P. maculatus. Since data on newly-metamorphosed R. tigrina were insufficient, they were not statistically analysed.

For carrying out comparative studies on R. curtipes tadpoles (stage 25–30) from nature as well as laboratory-reared individuals, a group of R. curtipes tadpoles (stage 25–30) was maintained in cement cisterns (7.8’ x 6.8’) with 1.5’ water. The tadpoles were fed boiled spinach ad libitum on alternate days and reared for 2 months. At weekly intervals they were autopsied. SVL, body weight, and fat body mass of corresponding stages of tadpoles from nature-, and laboratory-reared individuals were compared, using Hotelling’s $T^2$ analysis.

The fat bodies were first observed at stage 25–26 in R. curtipes, stage 28–29 in R. tigrina, stage 27–28 in R. cyanophlyctis, and at stage 29–30 in P. maculatus and B. melanostictus. The ranges in SVL, body weight and fat body mass of tadpoles of comparable stages in the five species studied are shown in Table 1. All the species showed a high positive correlation between increase in the body weight and SVL (Figure 1). Figure 2 shows that the fat bodies increased progressively in size as the tadpoles grew to their metamorphic climax except in B. melanostictus. Further, a positive correlation was observed between SVL and fat body mass (Figure 2) as well as between body weight and fat body mass in the tadpoles of all the species of frogs (Figure 3), however, in B. melanostictus fat bodies were barely visible throughout the larval development starting from their appearance at stage 29–30 to the end of metamorphosis.

The observations on the body weight and fat body mass of tadpoles at premetamorphic climax and at metamorphosis (Table 2) showed a significant increase in the fat body mass in P. maculatus following metamorphosis, but not in R. cyanophlyctis and R. curtipes. Also a significant decrease in body weight was observed in R. cyanophlyctis and P. maculatus following metamorphosis but not in R. curtipes. The amount of fat deposition found around premetamorphic climax (stages 39–41 when larval growth is complete) varied within the species (Figure 4). A study comparing the body weight and fat body mass of the laboratory-reared and wild-caught tadpoles of R. curtipes (Table 3) showed that in the laboratory-reared tadpoles the body weight and fat body mass were significantly greater ($F = 3.7485$, $P < 0.05$) than in the wild-caught tadpoles at the corresponding stages.

A discussion of our observations is given below.
adult anurans it is well known that the fat bodies reserve excess energy during the period of food abundance\textsuperscript{1,2}. The increase in size of fat bodies with larval growth in \textit{R. curtipes}, \textit{R. cyanophlyctis}, \textit{R. tigrina} and \textit{P. maculatus} suggests that these tadpoles forage well, and store surplus food energy in the form of abdominal fat bodies. However, \textit{B. melanostictus} is an exception. The amount of fat deposition in the anurans during larval development seems to have some bearing on the duration of metamorphic stage, followed eventually by metamorphosis, in addition to their body size. For instance, in \textit{R. curtipes}, the larval duration is about 6 months, the tadpoles have larger bodies compared to the tadpoles of other four anuran species. Hence, their energy needs are also high. Apparently, these tadpoles feed well and reserve a large amount of energy in fat bodies to overcome unforeseen food droughts, if any, as do the adult amphibians during the periods of food abundance\textsuperscript{1,2}. Likewise, a relationship between fat body mass and body weight/duration of larval period in \textit{R. cyanophlyctis}, \textit{R. tigrina}, and \textit{P. maculatus} is apparent. The larval duration for \textit{R. cyanophlyctis} is about 60–70 days while for \textit{P. maculatus}, and \textit{R. tigrina} it is approximately 45–60 days. The size hierarchy of tadpoles is as follows:

Figure 2. Correlation between SVL and fat body mass in \textit{R. cyanophlyctis}, \textit{R. tigrina}, \textit{R. curtipes} and \textit{P. maculatus}.

Figure 1. Correlation between SVL and body weight in the tadpoles of \textit{R. cyanophlyctis}, \textit{R. tigrina}, \textit{R. curtipes}, \textit{P. maculatus} and \textit{B. melanostictus}.

Figure 3. Correlation between body weight and fat body mass in \textit{R. cyanophlyctis}, \textit{R. tigrina}, \textit{R. curtipes} and \textit{P. maculatus}.
Table 2. Body weight and fat body mass in tadpoles at premetamorphic climax and at
metamorphosis

<table>
<thead>
<tr>
<th>Species</th>
<th>Stage 41</th>
<th></th>
<th>Stage 46</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Body wt (g)</td>
<td>Fat wt(g)/100 g body wt</td>
<td>Body wt (g)</td>
<td>Fat wt(g)/100 g body wt</td>
</tr>
<tr>
<td>R. cyanophlyctis</td>
<td>2.97 ± 0.12</td>
<td>1.50 ± 0.07</td>
<td>0.95 ± 0.06*</td>
<td>0.95 ± 0.26</td>
</tr>
<tr>
<td>(4)</td>
<td>(4)</td>
<td>(4)</td>
<td>(4)</td>
<td>(4)</td>
</tr>
<tr>
<td>R. curtipes</td>
<td>3.08 ± 0.81</td>
<td>1.49 ± 0.49</td>
<td>2.97 ± 0.31</td>
<td>1.21 ± 0.45</td>
</tr>
<tr>
<td>(5)</td>
<td>(5)</td>
<td>(6)</td>
<td>(6)</td>
<td>(6)</td>
</tr>
<tr>
<td>P. maculatus</td>
<td>1.23 ± 0.08</td>
<td>0.40 ± 0.06</td>
<td>0.72 ± 0.07*</td>
<td>1.21 ± 0.39**</td>
</tr>
<tr>
<td>(4)</td>
<td>(4)</td>
<td>(5)</td>
<td>(5)</td>
<td>(5)</td>
</tr>
</tbody>
</table>

Figures in parentheses indicate the number of tadpoles; Data is given as mean ± SE; *P < 0.05 **P < 0.001; comparison is made for weight and fat body mass between stage 41 and 46 of development of the same species.

Table 3. Comparison between the body weight and fat body mass of laboratory-reared and wild-caught tadpoles of R. curtipes

<table>
<thead>
<tr>
<th></th>
<th>Wild-caught</th>
<th>Laboratory-reared</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage</td>
<td>Body wt (g)</td>
<td>Fat wt(g)/100 g body wt</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27-34</td>
<td>1.31 ± 0.18</td>
<td>0.09 ± 0.05 (18)</td>
</tr>
<tr>
<td>35-42</td>
<td>2.38 ± 0.32</td>
<td>0.34 ± 0.11 (9)</td>
</tr>
<tr>
<td>43-46</td>
<td>2.05 ± 0.23</td>
<td>0.66 ± 0.18 (18)</td>
</tr>
</tbody>
</table>

*P < 0.05 (Hotteling's T² analysis).

An increase in body size during terminal phase/premetamorphic climax is reported in R. tigrina14. This rise in body weight prior to metamorphic climax is attributed to the accumulation of energy needed for enhancing metamorphism in R. tigrina14. Our present findings on R. cyanophlyctis, and P. maculatus which show an increase in body weight as well as fat body mass at metamorphic climax support the above view. Interestingly, there was no significant change in the body weight of tadpoles between premetamorphic and metamorphosed R. curtipes in both wild-caught and laboratory-reared individuals. This may be because the duration of metamorphic changes is longer in R. curtipes and hence, energy utilization from body source would be at lower pace than in the other two species in which metamorphic duration is very short. The explanation for this observation seems to be that the tadpoles need energy for their growth and metabolism, as well as spend some energy in search of food and predator avoidance. Since the tadpoles reared in the laboratory are exempted from such expenditure, they apparently divert their energy saved in searching food and escaping from predators towards better body growth and fat bodies for storage.

The present study demonstrates a diversity in the deposition of fat and its utilization in anuran tadpoles which, besides the food abundance, may depend on

Figure 4. Amount of fat body mass during premetamorphic (39-41) stage in five anuran species.

R. curtipes > R. cyanophlyctis > R. tigrina > P. maculatus > B. melanostictus. Virtually no fat storage occurs during larval development in B. melanostictus, possibly because it has a very short larval duration (3-4 weeks) and small larval body weight.

During the metamorphic climax, the oral apparatus undergoes drastic structural changes and, therefore, the tadpoles consume less12 or no food12. In R. curtipes metamorphic changes (stage 42-46) take place between 7-10 days, and in other species studied in 2-3 days. Insignificant change in the fat body mass in recently metamorphosed R. curtipes and R. cyanophlyctis suggests albeit indirectly, that the tadpoles might not utilize energy stored in fat bodies during metamorphosis. Interestingly, the fat bodies in recently metamorphosed P. maculatus weighed heavier than those in premetamorphic climax.

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larval duration, expenditure of energy in search of food, and predator avoidance.


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