INTRODUCTION

There has been an increasing realisation over the past 20 years or so that tadpoles are more complicated in their behaviour patterns than was once supposed. For example, anyone with more than a passing acquaintance with common frog and toad tadpoles can scarcely fail to have noticed how secretive the former become as they grow up, while in comparison common toad tadpoles are often to be swimming conspicuously in open water. In fact tadpoles of the Bufo-type toads sometimes demonstrate a dramatic shoaling behaviour that has been witnessed in both North American and European species. It has been much argued as to whether this shoaling serves to stir up food particles from the pond bottom, constitutes a defence against predators or is for some as yet unknown purpose. Natterjack tadpoles are usually easy to see, though unlike those of the common toad they have not been reported to form proper shoals. Searching for natterjack tadpoles and trying to assess their numbers in a pond has become a widely applied practice among conservationists monitoring the various colonies in Britain, since it is one way of assessing breeding success over a period of years. However, this approach does presuppose that the tadpoles always behave in much the same way (i.e. are equally “seeable”) whatever the weather or their stage of development, and some observations in the field have indicated that this assumption might be wrong. In particular there have been cases where whole cohorts have apparently disappeared within a week or so of expected metamorphosis, to be followed a while later by reports of toadlets around the ponds. To try and clarify what might be going on in the breeding ponds, I set up a simple observation tank to record how natterjack tadpoles behave under conditions intended to simulate the edge of a breeding pool.

METHODS

Natterjack spawn was obtained (under licence) for captive rearing as part of a general research and conservation programme. Soon after hatch, 16 tadpoles were transferred to a container with about 5 litres of water arranged as shown in figure 1. A fibre mat was used to support a layer of sand the full length of the angled slope and thus prevent it accumulating at the deepest point. This sand and suitably arranged flat stones provided potential refugia for the tadpoles, which also had available to them water varying from 0 to 12 cm in depth. The tank was set up in a position receiving direct sunshine from at least 0700 to 1900 hours, and the water kept clear of algae etc. for easy observation by gentle periodic flushing with a hosepipe. Food, in the form of rabbit pellets, was added periodically as required and always after the final observations of the day.

Figure 1. The observation tank.
Observations were made up to 3 times each day, at 0800, 1300 and 1900 hours. Record was made of: (a) the number of tadpoles visible (i.e. not concealed in sand or under stones); (b) the number actively swimming, as opposed to resting on the bottom. Occasional tail-wiggling was not recorded as active swimming, the whole tadpole had to be moving through the water. (c) numbers of tadpoles visible in the top (shallow) and bottom (deep) halves of the tank; (d) % cloud cover; (e) water temperatures at the shallow and deep ends (1cm and 12cm depths), using a thermoprobe digital thermometer.

After metamorphosis, the toadlets were released at the site from which the spawn was taken.

RESULTS

For most of their lives in the tank, the natterjack tadpoles were easily visible and did not hide in silt, under stones or in the small pieces of weed also available to them. From the start of the observations (shortly after hatch) until full grown at 25mm or so some 3 weeks later it was unusual to see less than 70% of them at some time each day; on average more than 80% were visible (figure 2a). However, during the final stages of development there was a dramatic decrease in observability coinciding with elongation of the back legs until, during forelimb emergence, all the animals remained hidden (mainly under the submerged stones) at all times of day irrespective of weather.

Figure 2. Tadpole behaviour during development.

Figure 2. •, Numbers of tadpoles visible (average, with range of values for 1-3 records of each day); □, average size of tadpoles; , water temperature (average of 1300 and 1900 hour measurements in shallow end); in figure (a), tadpole numbers represent total visible; in figure (b) they represent the numbers actively swimming (in this case the average and range of just 1300 and 1900 hour records). A = Hind limb buds appear; B = Elongation of hind limbs; C = Forelimbs appear; D = Metamorphic climax.
Although readily visible, natterjack tadpoles were singularly inactive for most of the time. As shown in figure 2b, apart from a brief burst of activity early in life (at 12-14mm long) where up to 50% of them could be seen actively swimming at any one time for just 2-3 days, more than 90% were usually resting virtually motionless on the sandy tank bottom. Although the early peak of activity coincided with warming weather conditions, equally high temperatures later on did not have this activating effect. It appeared that natterjack tadpoles became more sedentary as they grew larger.

### TABLE 1. Daily patterns of tadpole behaviour.

<table>
<thead>
<tr>
<th>Time of day</th>
<th>Average no. tadpoles visible</th>
<th>Average no. tadpoles actively swimming</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Tank top (shallow end)</td>
</tr>
<tr>
<td>0800</td>
<td>9.1(4.0)</td>
<td>3.2(3.5)</td>
</tr>
<tr>
<td>1300</td>
<td>13.2(1.6)</td>
<td>8.7(3.0)</td>
</tr>
<tr>
<td>1900</td>
<td>11.8(3.0)</td>
<td>4.9(4.1)</td>
</tr>
</tbody>
</table>

Standard deviations are given in brackets.

There were tendencies to select different water depths at different times of day (table 1). The usual situation was for the fewest tadpoles to be visible early in the day, and these would generally be inactive in the deeper part of the tank. By mid-day most had moved into the shallows, swimming activity was greater and the highest proportion of animals visible. In the early evening a move back towards deeper water and/or concealment was detectable, though small tadpoles could be very active at this time (1900 hours).

**Figure 3.** Tadpole behaviour and water temperature.

**Figure 3.** •, records taken at 0800 hours; ●, records taken at 1300 hours; ●, 13 hour records in which the deep water was warmer than the shallow end; □, records taken at 1900 hours.
There were clear correlations between water temperature and the part of the tank selected by the tadpoles (figure 3). At 0800 hours, cloud cover was poorly (insignificantly) related to water temperature (data not shown) but the warmer the water, the more tadpoles accumulated in the shallow end ($r=0.857$, $p=0.001$) indicating a response to warmth rather than light intensity. All this despite the fact that the temperature gradient across the tank was never more than 1°C (data not shown). By 1300 hours the water was approaching its daily maximum temperature and up to about 25°C there was still a significant (but different) correlation between numbers of tadpoles in the shallow end and water temperature there ($r=0.735$, $p=0.01$). Above 25°C the situation seemed to change, selection for shallow water dropping off markedly. Observations at 1900 hours indicated yet another significant but different correlation between tadpole positioning and water temperatures ($r=0.680$, $p=0.01$); at this time of day tadpoles accumulated in the deeper water at temperatures which, at 0800 hours, would have enticed them all into the shallows (i.e. 14-17°C). At both 1300 and 1900 hours there were strong inverse correlations between cloud cover and water temperature, making it impossible to distinguish between the effects of temperature and light intensity on the behaviour of the tadpoles.

**DISCUSSION**

These observations were made under conditions which neither completely mimicked a pond (there was a very restricted range of water depths, for example) nor permitted separate control of factors such as light and temperature. It is important to realise these limitations, and what was seen cannot be taken to reflect the full repertoire of natterjack tadpole behaviour by any means. Nevertheless I think the results are of some interest and seem to relate to aspects of behaviour noticed in the field. The relative inactivity of natterjack tadpoles, and their tendency to live on the pond bottom, contrast with the more active and mid-water existence of common toad tadpoles to the extent that behaviour might even assist with identification in the field. Telling common and natterjack toad tadpoles apart by appearance alone is notoriously difficult.

It looks as if we should expect natterjack tadpoles to be readily visible (i.e. not hidden in silt, etc., or in deep water) for most of their development, except perhaps on very hot days when water temperature exceeds 30°C in the shallows. This can certainly happen, I once recorded 38°C (warmer than blood heat!) in a shallow natterjack pond on a sunny day in June. Observers should expect to see few, if any tadpoles under such conditions since the lethal limit is 30-33°C and the animals are likely to be seeking cooler surroundings at the pond bottom. The above observations also appear to explain why whole populations of tadpoles sometimes seem to disappear just before metamorphosis. They become very secretive at this time, and not seeing any cannot be taken to mean that they are not there. At earlier stages of development, up to the appearance of distinct hind limb buds, the middle of the day (except when very hot, as above) is probably the best time to look for natterjack tadpoles around the pond margins. It looks as if there may be a basic diurnal rhythm, with tadpoles retreating to deeper water at night but preferring shallow pond edges by day, subject to modification by environmental factors the most important of which is probably water temperature. There is obviously scope here for more systematic study under controlled conditions.

Finally, it is tempting to use these observations to help explain the different responses of common and natterjack tadpoles to food shortage. Food stress causes early mortality of common toad tadpoles leaving the survivors to grow normally (i.e. there is intense competition) whereas natterjack tadpoles respond by a general reduction in growth rates and little or no mortality. The greater activity of common toad tadpoles perhaps leads to a rapid utilisation of metabolic reserves, thus putting weaker animals at high risk of mortality quite quickly if food runs short. The more leisurely natterjack tadpoles should use up their reserves more slowly, and thus be more likely to survive in a situation where encounters with food are infrequent.