M. Vences, J. Köhler, T. Ziegler, W. Böhme (eds): Herpetologia Bonnensis II.
Proceedings of the 13th Congress of the Societas Europaea Herpetologica. pp. 183-186 (2006)

Motor activity of amphibian larvae - from schools to shoals

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Abstract. The ability of *Bufo bufo* and *Rana temporaria* tadpoles to form aggregations was studied. In natural ponds, we distinguis different kinds of aggregations and discuss causes of their origin. In the lab, series of tests were carried out to estimate differences in motor activity of single individuals as well as groups of 5 and 30 individuals. In *R. temporaria* tadpoles, the social form of aggregations in nature seems to be connected with thermoregulation with individuals moving independently in a vertical mode. In contrast, *B. bufo* tadpole movements are directed and result in polarized shoals. In laboratory tests, larvae of both species differ by the character of motor activity with respect to the presence of conspecific individuals: tadpoles of *B. bufo* reduce and *R. temporaria* tadpoles increase activity. *B. bufo* tadpoles spend more time close to other conspecific larvae than *R. temporaria* tadpoles and show greater disposition to form aggregations.

Introduction

Larvae of a number of anuran species are known to form different kinds of aggregations. In some cases, these look like an irregular distribution of individuals with permanent rotation (schools), whereas others form larger groups with directed moves and one-way orientated polarized shoals (Beiswenger, 1975; Wassersug et al., 1981). The reasons for these aggregations could be different: external factors, e.g., food, temperature, anti predator behaviour, hydrodynamic features, etc. (Wassersug, 1973; Branch, 1983; Spieler and Linsenmair, 1999) or internal factors, like thermoregulation or preference of familiar individuals (O'Hara and Blaustein, 1981; Surova, 1988; Caldwell, 1989). Wassersug (1973) recognized simple and social aggregations. The first one is based on taxis only (biotic and abiotic) and the reason of its formation is obvious. The second one is based on social mutual attraction. The existence of social aggregations implies an importance of the group as an entire system. Any system implies the existence of some features qualitatively different compared to separately taken elements (Prigogine and Stengers, 2000). Maintenance of integrity in particular biological systems requires rather intensive interactions between its members. Such an approach proposes a new interpretation of the importance of groups in tadpoles. Unfortunately, behavioural analyses of tadpoles are sparse (Lehner, 1996). In this study we characterize the behaviour of tadpoles of two anuran species by describing their motor activity. The purpose of the study is to examine the alterations in motor activity of *Bufo bufo* and *Rana temporaria* tadpoles in natural ponds and in the lab with and without the presence of conspecifics and/or predators.

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Material and methods

The study in natural ponds was conducted at the biological station of Moscow State University in Zvenigorod. The pond with *B. bufo* is located in the forest and had a total surface area of 800 m^2. The pond with *R. temporaria* is located in flood-land and its size was 1500 m^2. Abundance was estimated using mesh traps (0.2 m^2), fixed with fishing-line to floats. In random samples we recorded the daily motor activity of tadpole aggregations in the ponds and estimated the density of tadpoles in aggregations. Temperature inside and outside aggregations were measured at 2-3 points 10-15 cm apart from each other. Laboratory experiments were done in aquariums (40 x 20 x 30 cm) with 5 cm water level. The bottom was lined with a 36 square grid, each four centimeters wide. After 5 min of adaptation, the squares crossed by tadpoles and the time of stops were registered during a 5 min period. Using these parameters, we recorded the tracks of larvae, the total distance of movement, and the total time spend with movement. We compared motor activity manifested by single tadpoles which were put in aquariums either in groups of 5 or 30 conspecific individuals or alone. Predator experiments were done using large larvae of *Dytiscus marginalis* which were exposed in a small sack to groups of 30 tadpoles. In experiments on vertical activity water level was increased to 20 cm. The observer searched for individuals in a group of 10 and recorded the number, duration and depth of diving incidents. Water temperature in aquariums was 18-20°C. Five replications were carried out for each series of experiment. Significance was estimated by a Mann-Whitney U-Test.

Results

Field study

Aggregations of both species started to form at about 9:00-10:00 h near the first light spot where the water temperature seems to be a little higher compared

Table 1. Motor activity of tadpoles in vertical water column (** = P < 0.01).

(mean ± SE)			
Species	Swimming on the surface (sec)	Duration of diving (sec)	Number of diving
Bufo	166.7 ± 5.16**	13.0 ± 227**	5.7 ± 0.93**
Rana	20.0 ± 5.91	6.2 ± 0.30	17.3 ± 0.26

to other parts of the pond. Later during the day a correlation between tadpole aggregations and sun light was not observed. As the water in the pond was warming up aggregations formed along the shore line and subsequently in the water column. At any time, aggregations included groups from few dozens to several thousand individuals which aggregated around food sources (e.g., water plants, surface of snags where tadpoles eat epibioses, remains of invertebrates, detritus). This kind of aggregation is easy to identify by gnawing moves of tadpoles mouthparts. Aggregations with similar density formed in the warmest parts of the ponds. Here tadpoles did not move at all or they did it slowly in an irregularly shift from the periphery to center. Typical aggregations included those along the shore line before metamorphosis. Tadpoles stayed there the whole day but at night moved to deeper water. The reasons for these three different types of aggregations are almost obvious.

Besides that, both species formed large aggregations in the water column without obvious reasons. These aggregations had an irregular globe shape, sometimes a diffuse shape. They suspended for 10 to 60 min, sometimes longer. Then aggregations completely split or spilled over different parts of the pond. Individuals moved inside aggregations and others out. As a result, we observed that the composition of this aggregation was not constant over time. In *R. temporaria* 30% substitutions happened during 10-20 minutes. The number of aggregations per pond varied from two up to dozens. Sometimes, app. 80% of the population was located in aggregations that occupied about 1.5% of the total pond area, with the density of individuals inside aggregation being several times higher than the average density in the pond (10 and 0.09 individuals/l, respectively). Temperature data show that aggregations may have a pronounced thermoregulatory function (Fig. 1). During cloudy days the temperature inside aggregations is higher compared to ambient ones, but in sunny days vice versa. We suppose that permanent moves of tadpoles up and down create convective streams. It may optimize the temperature regime and improve aeration. It becomes especially important in ditch-water with high probability of over heating and suffocation. This phenomenon has already been described for fish shoals in ditch-water (Gerasimov, 1983).

Bufo bufo had a constant aggregation structure and tadpoles moved in polarized shoals as a whole group. There were several or just one shoal of toad tadpoles in the pond. Shoals may form globes or spirals to form bands again. Such a band might be up to 12 m long and 0.5 m in diameter. It included practically the whole population of the pond (about 96,000 individuals). Some tadpoles left the shoal and came back but rotation was not active as in thermoregulatory aggregation. Average speed of single tadpoles was 2.4 cm/sec while in shoals it was 3.4 cm/sec ($n = 10$, $P = 0.005$). Shoals obviously increased the capacity of tadpole movements.

Laboratory tests

Figure 2 shows changes in registered parameters of motor activity (distance, time of active moves). Toad tadpoles demonstrate maximum values for single maintenance. After five individuals had been added the activity decreased and after adding 30 animals it sharply goes down. The exposition of a predator did suppress the activity even more and the tadpoles looked congealed. On the contrary, tadpoles of *R. temporaria* were more active in groups of 30 individuals, whereas the activity got lower when only five animals were present in the aquarium and reached its minimum when one tadpole stayed alone. The exposition of the predator suppressed tadpole activity in the group. Thus, both species react completely different on the presence of conspecific neighbours. After each test with the 30 tadpoles groups, we calculated the number of tadpoles located in each grid cell at the bottom and estimated the portion of grouped tadpoles compared to their total number. The portion of crowding tadpoles of *Bufo* was 57%, that of *Rana* was 24% ($P = 0.0007$). One hour subsequent to the tests, we documented the distribution of tadpoles within the aquarium. *Rana* tadpoles were evenly distributed at the bottom of the aquarium while *Bufo* tadpoles were crowded in the corner.

Table 1 shows the results of vertical activity tests. *B. bufo* tadpoles spent more time than *R. temporaria* close to the water surface - they rarely dive but stay longer under water. Visual observations indicate that *Bufo* tadpoles prefer upper levels and swim in groups along the aquarium walls. In contrast, frog tadpoles were mostly ungrouped in all water columns.

Discussion

Our study in natural ponds shows that for *R. temporaria* tadpoles the most effective form of integration is thermoregulatory aggregations (schools) with permanent vertical activity and non-stable composition. In *B. bufo* more organized and long-living units (shoals) with directed movements of the entire group and distinct polarized orientation of individuals prevail. In conclusion, *Bufo* tadpoles obviously interacted. The same shoal type with directed orientation was documented for *Xenopus, Scaphiopus, Rhinophrynus* and *Phyllomedusa* (Stuart, 1961; Wassersug, 1973; Beiswenger, 1977; Katz et al., 1981; Branch, 1983). In species of *Hyla, Rana, Pseudacris* and some others very large aggregations (up to several thousand individuals) were reported, but these did not show directed movements (Bragg, 1968; Wassersug, 1973; Caldwell, 1989).

Simple taxis (food, temperature, oxygen) may result in aggregations as a sum of individual responses to an environmental gradient. Movements of animals in such kind of aggregations are not adjusted to each other and do not lead to the appearance of a new function. The types of aggregation in *Rana* and *Bufo* described above differ clearly from this and contain a social component where individuals mutually interact (Wassersug, 1973). As a reason to form non-polarized social aggregations heat accumulation by masses of dark coloured animals and coordination of tail moves during feeding was assumed. This results in directed water flow or stirring silt at the bottom that makes food resources like detritus and plankton available (Beiswenger, 1975). We found another function of non-polarized aggregations, namely active control of the temperature regime. Mutual vertical shifts in aggregations as well as flow of food items require coordination of behaviour and provide an obvious advantage for individuals.

The existence of long-life polarized shoals has to be explained as well. Short distance between animals and a one way direction create very mobile structure, which is able to move quickly. That is why this type of aggregation (especially in *Bufo*) usually is connected with predator escape behaviour (Altig and Christensen, 1981; Spieler and Linsenmair, 1999; Richardson, 2001). Nevertheless, formation of shoals can not impute just utilitarian significance. In our ponds there are not predator fishes and carnivorous insect larvae are rare (we never found them in the center part of the ponds and just occasionally along shore line - note that aggregations mostly are formed at the center). Taking into consideration tadpole and insect distribution, as well as total number of tadpoles (at the moment of the study

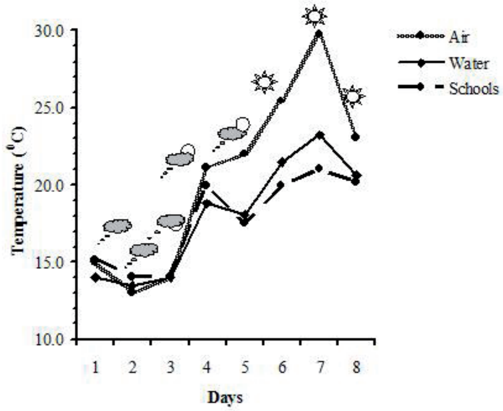

Figure 1. Temperature dynamics in *Rana temporaria* schools and ambient environment.

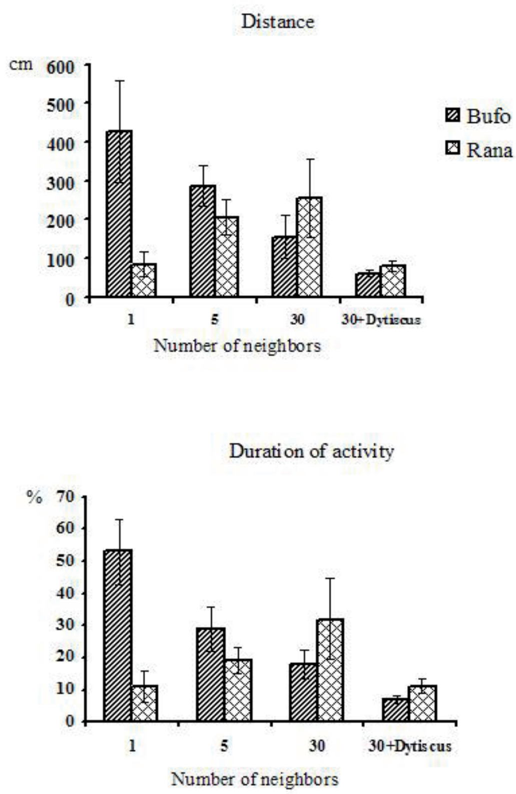

Figure 2. Motor activity of tadpoles in differently sized groups and with the presence of predators (larvae of *Dytiscus marginalis*).

the number of tadpoles was estimated to be 100,000), predator pressure can not be a significant factor for distribution and behavioural changes. Our laboratory tests with predators showed decreases of motor activity but did not increase the rate of aggregation formation.

We suppose that shoals of *Bufo* tadpoles do not have significance to supply particular biological functions but carry important information about population condition in the pond. It was demonstrated for fish shoals (Gerasimov, 1983) that living in group greatly decreases oxygen consumption compared to isolated individuals conduced to quite behavior. We noted this phenomenon in our tests with toad tadpoles. We conclude that different reactions to the group size in *Bufo* and *Rana* tadpoles (declining motor activity in groups of *Bufo* and increasing one in *Rana*) reflect different capabilities of studied species to form intra-population aggregations – schools and shoals.

Acknowledgments. I am grateful to my friends Natalia Lavrova and Ksenia Perfilieva for their help conducting the tests and my husband Alexei Surov for critics and help in preparing this contribution. This study was supported by grants RFBR 05-04-48701a and Leading Research Teams 8045.2006.4.

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