Diel Activity of *Ranodon sibiricus* (Amphibia: Hynobiidae) in Relationship to Environment and Threats

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Abstract.-Field studies on the diel activity of *Ranodon sibiricus* were carried out in Dzhungaria, southeastern Kazakhstan, in August 1994 and June 1995. Counts showed that adults and juveniles were strongly nocturnal, which was also confirmed with the help of IR light/photocell equipment, whereas larvae were active both night and day. The daily activity period of adults and juveniles started near the 5-lux limit and peaked around 23-01 hrs. Its length followed that of the night and was accordingly shorter in June than in August. When the activity of aquatic adults and juveniles started in the early night, about 5% came out of the water and walked on land alongside the brook. Most ranodons, however, were relatively stationary sit-and-wait predators in the water. The nocturnal activity of *R. sibiricus* protects it against dehydration (terrestrial animals), strong UV radiation and diurnal predators. The most important task of the nocturnally and diurnally active larvae is to grow as fast as possible to survive the first, hazardous hibernation. The difference in diel activity between adults/juveniles and larvae reduces intraspecific competition and cannibalism within the population. Because of their secretive life, metamorphosed stages of *R. sibiricus* are not easily accessible to predators or Man. Hence, the most important threat is probably the large herds of cattle grazing in the area. Since adults and juveniles are well hidden by day, when the cattle wade the brooks, they are fairly safe, but cattle may pose a great threat to ranodon eggs and larvae.

Key words.-Ranodon sibiricus, Kazakhstan, diel activity, rare species, environmental adaptation, threats.

Introduction

A threatened, secretive species

The salamander *Ranodon sibiricus* Kessler, 1866 is distributed in the Dzhungarian mountains of southeastern Kazakhstan and the extreme west of Xinjiang province in China. Its range is very small and has undergone many man-made changes during the past. The species is therefore threatened and is on the red list of the former Soviet Union/Kazakhstan (Bannikov et al. 1978; Zhao and Adler 1993). Its habitat is cold, clear mountain brooks. Because of their quite secretive way of life, individuals are not always easy to find even where they may be locally abundant. Although Shnitnikov (1913) found it easily, Brushko and Narbaeva (1988) emphasized the difficulties of finding *R. sibiricus* in the mountain rivers. Its secretive life is also reflected in its nocturnal activity, an aspect briefly touched upon by several authors (Shnitnikov 1913; Paraskiv 1953; Kubykin 1986; Narbaeva and Brushko 1986; Wang 1990).

As part of a wider ecological study of *Ranodon sibiricus* in Dzhungaria, we investigated its activity, partly in 1993, but more thoroughly in 1994 and 1995, to learn the details of its diel activity rhythm and possible adaptations to the environment. Several other questions were also of interest. For instance, do the larvae behave differently from the metamorphosed animals to reduce intraspecific competition and cannibalism (as in *Triturus*; see Dolmen 1988)? Does the nocturnality of the species really make it almost safe from terrestrial predators and Man? To what extent can *R. sibiricus* avoid the heavy impact of some 150 cows which graze along and trample in the brooks when crossing the study area twice a day in summer (Kubykin et al. 1995; Dolmen et al. 1997)?

A preliminary report on these studies was presented by Dolmen et al. (1995). Hereafter, *Ranodon sibiricus* is mostly referred to as ranodon.

Principles of measuring activity

In principle, there are at least three ways of measuring the activity of an animal: 1) with an actograph or other technical device such as light beam/photocell equipment, 2) by interval trapping of active animals, and 3) by counting active animals. All three methods have been successfully used for *Triturus* species (Salamandridae) in Europe (e.g. Himstedt 1971; Dolmen 1983a,b; Griffiths 1985).

Preliminary studies

In June 1993, the trapping technique was tried out for ranodons in a small brook in the Borokhudzir valley in Dzhungaria. On 15 June, 10 simple funnel traps (1 L "Cola traps") and two more complicated traps with eight entrances each (constructed by Arne Haug) were placed in a 15 m long stretch of a small brooklet (Brook 3) in which six ranodons and 50 double clutches of eggs had been registered two days earlier. Alternate traps had their entrances pointing downstream and upstream. The traps were checked/emptied every third hour throughout a day and night, but no ranodons were caught. The water temperature varied between 3.8 °C and 7.6 °C. On 17 June, a similar set-up was tried on a 15 m stretch of another, somewhat larger brook (Brook 1) where, in addition to the ranodons living there naturally, 38 additional ones were released. A few were caught during the next day and night, but never more than two each time.

However, a study of a third brook (Brook 5) at night revealed that many ranodons were going onto land and wandering on the dew-wet banks beside the brook. On a 500 m stretch at 23.00-24.00 hrs. (standard time), four men with torches counted 14 ranodons that were active on wet land and 11 hidden under stones alongside the brook. Although aquatic individuals were also active, the main movements up and down the brook seemed to be taking place on land, not in the water. The trapping technique in water was accordingly unsuitable for measuring the activity of ranodons.

For 1994 and 1995, it was therefore decided to use the counting method for measuring the activity of ranodons, and for comparison, data from the use of light beam/photocell equipment could serve as a control.

Description of the area

The study area, on the southern slopes of the River Borokhudzir catchment in Dzhungaria at an altitude of approximately 2200 m, consists of grazing for cattle, bog, and juniper-covered hillsides. Two small tributary brooks to the River Borokhudzir (Brook 1 and Brook 5), approximately 200-300 m apart, were chosen for the study. Both were spring-fed, about 2-50 cm deep and 30-80 cm wide, and had gravelly or stony bottoms. In a few places, turf almost overgrew and covered the water. Boulders, where terrestrial ranodons hid, could also be found on land alongside the brooks. The velocity of the water at different sites along the two brooks varied from 0.0-0.2 and 0.0-1.0 m/s, respectively. Measurements were made in August 1994 when the flow was low.

The weather in both periods was mostly clear. The air temperatures in August 1994 and June 1995 varied between 5.7 °C and 17.1 °C, and 3.5 °C and 21.0 °C, respectively. The air humidity in August 1994 varied from less than 50 to 100% RH, with maximum humidity at night. The water temperature at the site investigated in Brook 1 varied in August 1994 between 5.5 °C in the early morning and 19.3 °C in the afternoon, and in June 1995 between 5.0 °C and 20.0 °C. In Brook 5, the water temperature varied between 6.2 °C and 14.8 °C in August 1994 and 4.8 °C and 15.6 °C in June 1995. A more detailed description of the area is given by Dolmen et al. (1997).

Material and Methods

Field investigations

The study took place in August 1994 and June 1995. Two persons equipped with good torches examined a total of 90 m and 190 m, respectively, along the two brooks (Brook 1 and Brook 5) every second hour for three days and nights. The walking speed was approximately 8 m/min. Deep pools and shallow slowly-flowing water were especially well examined, and also the nearest 2-3 m on land alongside the brooks. No stones were turned, however, and no ranodons were disturbed, except possibly by the torchlight. The two brooks had been divided into sections of 5 or 10 m, respectively, for statistical use, and the number of ranodons in each section were counted separately. The numbers in different main developmental stages were also kept apart: 0+ (young larvae, less than one year old), 1+ (old larvae and metamorphosed individuals from the previous year), larger juveniles, and adults.

Aquarium investigations

In December 1994, additional investigations of the activity of two ranodon individuals, an adult and a large juvenile, were carried out in Almaty. An experimental aquarium was made of transparent plexiglass shaped like a circular channel. The outer diameter was 36.5 cm, the inner diameter 15 cm and the height 10 cm. The aquarium was filled half full of water brought from Dzhungaria and some large stones acted as shelter for the animals and to enable them to climb up into the air. The aquarium was equipped with an infra-red light beam/photocell system (Visolux LS 4-GaAs). The beam was set to a diameter of about 2 mm and focused near the bottom of the aquarium, where the ranodons usually walk around. Interruptions of the beam were recorded by an electric counter (Visolux LU GaAs), which was read every second hour throughout eight days and nights. Food was not provided during the experiment. The aquarium was placed inside a building, close to a north-facing window. The light regime was therefore natural, i.e. approximately like outside. The temperature was constant and slightly lower than the usual room temperature.

The same equipment, connected to a 12 V car battery, was used for an adult and a large juvenile in Dzhungaria in June 1995. The aquarium was protected from disturbance and strong sunshine by being placed halfway under a car and partly covered with a blanket. The water was replenished (in daytime) once during the experiment, which ran for barely three days and nights. On the second evening, the onset of activity was studied in more detail at 5-minute intervals for two hours.

Environmental factors

Light intensities between 0 and 10 lux normally act as Zeitgeber for activity in plants and animals (cf. Dolmen 1983b). The 5-lux value is therefore often used in activity studies as a limit between day and night. In our study it was determined subjectively, evening and morning. The 5-lux value in Dzhungaria occurs roughly 10-15 minutes before (or after) the 0.1-0.5 lux values, which corresponds well with the light intensity required for reading a newspaper, for instance. This was confirmed with a Hartmann and Braun ECLX 4 luxmeter.

The times for reading the Visolux counter were set approximately symmetrically around the darkest time of night (ca. 24.00-00.30). All hours mentioned hereafter refer to standard time, not summer time. An important difference in the understanding of diagrams based on the two methods used for measuring activity here is that a) the counting method measures the activity at the time of counting, whereas b) the IR beam/photocell method measures the activity during the two hours preceding the time when the counter is read.

Statistics

Wilcoxon's matched-pairs signed-ranks test (two-tailed) was used to test any significance levels in the activity measured in the field, the number of ranodons within the different brook sections being counted for an hour and comparison being made with the situation two hours later.

The same test was used for the aquarium study, but it was based on the ranodon counts for all the days within a certain time interval combined, and these were compared with the corresponding counts in the next time interval.

The chi-square test was used to find out whether or not the activity patterns had a significant diurnal (06-18 hrs.) or nocturnal (18-06 hrs.) predominance, and the chi-square test with two variables without expected values was used to test any differences in activity pattern between, for example, adults and larvae.

Results

The field activity studies

The activity of *Ranodon sibiricus* was definitely nocturnal, but with some modifications with respect to the developmental stage and the month of the year. The animals in all stages were amazingly clever at hiding during parts of the day and night. Several were seen at night on a gravelly bottom along stretches of the brook which we had searched very thoroughly in daytime without finding any.

In August 1994, the diel activity showed basically the same patterns in both brooks, although the peak apparently varied slightly from day to day between 21 and 01 hrs. (Fig. 1).

Adults and juveniles had similar patterns, and seen together the rise in activity level from 19 to 21 hrs. was always statistically significant ($P<0.002$; Wilcoxon's signed-ranks test, see Fig. 1). Likewise, the decrease in activity from 03 to 05 hrs. was always significant in Brook 5, where most animals were registered ($P<0.002$). The variation in the time of peak activity from day to day was usually not significant.

In Brook 1, the larvae showed a similar rise in activity from 19 to 21 hrs. When 0+ and 1+ larvae are counted together, the increase is significant ($P<0.002$ or $P<0.02$) on two of three dates. The activity of 0+ larvae in Brook 5 was not as well defined as in Brook 1, being much more diurnal. In contrast to adults and juveniles, and also to the larvae of the other brook, which were all mainly nocturnal ($P<<0.001$; chi-square test), the larvae of Brook 5 showed a much higher degree of diurnality (nocturnality tested: $0.20<P<0.30$). Indeed, traces of diurnal activity can also be seen in the 0+ larvae of Brook 1.

The period of activity of this species fitted very well with the light and dark periods, i.e. activity was connected with the part of the 24-hour period when the light intensity was below 5 lux. This was approximately 20.00-05.30 hrs. at that time of year. Except for young larvae, any activity outside that period was negligible.

A pattern similar to that of August 1994 was revealed in June 1995. The period of darkness (<5

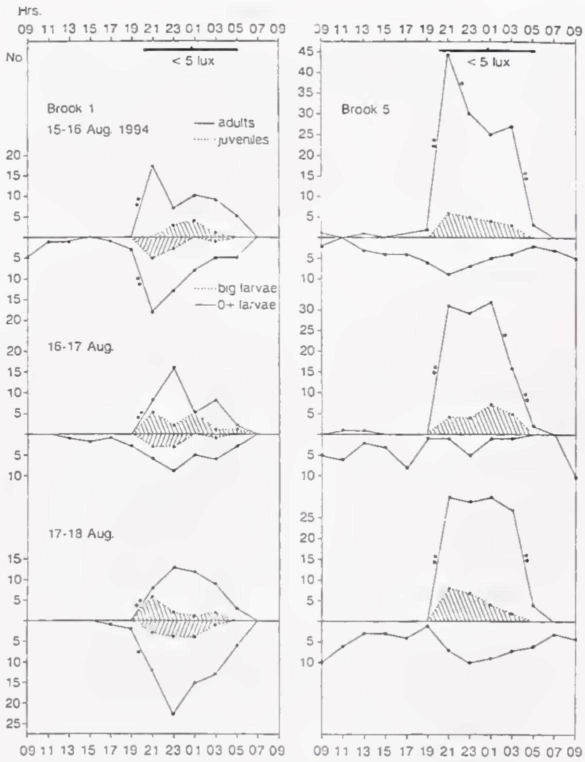

Figure 1. Diel activity of *Ranodon sibiricus*, based on counts in Brooks 1 and 5 in August 1994. Levels of statistical significance: * P<0.05 or P<0.02; ** P<0.01 or P<0.002.

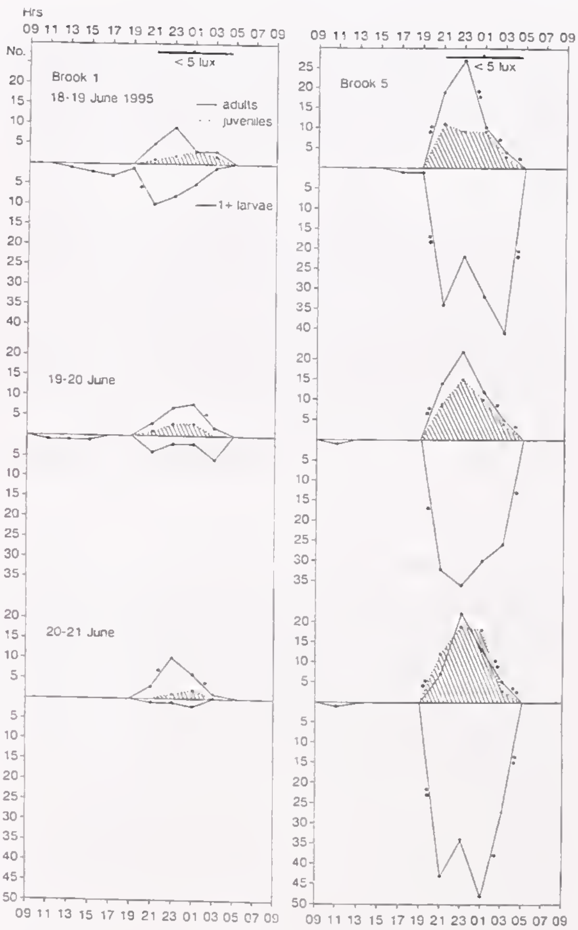

Figure 2. Diel activity of *Ranodon sibiricus* in Brooks 1 and 5 in June 1995. For explanation, see Fig. 1.

lux) in June was shorter than in August, i.e. about 21.00-04.30 hrs., and the activity peaks of adults and large juveniles were narrower, at 23 (21) or 01 hrs. (Fig. 2).

The youngest stage (1+) showed activity peaks varying from 21 to 03 hrs. and also some diurnal activity. At least three times, larvae (one each time) were even registered directly exposed to sunshine, at 11, 13 and 17 hrs. Nevertheless, on the whole, the larvae definitely had a nocturnal pattern.

The activity period of the species again fitted very well with the (shorter) dark period. The rise in activity from 19 to 21 hrs. was always significant (P<0.002 or 0.02) in Brook 5, both for adults/juveniles and 1+ larvae, as was the decline from 03 to 05 hrs (P<0.002, 0.01, 0.02 or 0.05), and usually even 01-03 hrs. for adults and juveniles in both brooks (P<0.002, 0.02 or 0.05). The day-to-day variation in peak activity seen at midnight was not significant.

The aquarium studies

In the aquarium investigations in December 1994, the ranodons also showed a definite nocturnal activity, with peak activity at 20-22, 22-00 and/or 00-02 hrs. A cumulative curve for the whole period of investigation had a main peak at 02 hrs. (i.e. peak activity at 00-02 hrs.) and a minor peak at 22 hrs. (i.e. 20-22 hrs.), with little or no activity during the light hours. The rise in activity from 16-18 to 18-20 hrs. and from 22-00 to 00-02 hrs. was significant (P<0.05), as was the decrease from 00-02 to 04-06 hrs. (two time intervals seen together) (Fig. 3).

The activity period of the animals at this time of year was clearly longer than the activity measured in summer, as was the period of darkness (<5 lux), which lasted from approximately 17.30 to 08.00 hrs.

The aquarium study in June 1995 confirmed the results of the field investigations, although there were minor deviations, probably for methodological reasons. Activity was negligible until 21 hrs. when a rise in activity occurred resulting in a peak at 21-23, 23-01 or 01-03 hrs. (Fig. 4).

In the more detailed aquarium investigations on 20 June, the activity started about 15 minutes before the 5-lux limit was reached in the open. However, since the aquarium was partially covered (see Methods), the

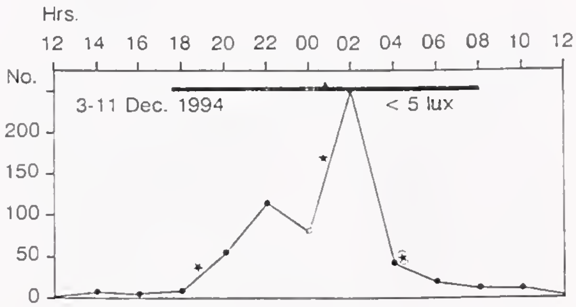

Figure 3. Diel activity of two *Ranodon sibiricus* specimens kept in an aquarium under natural lighting conditions for eight days and nights in December 1994, based on the IR light/photocell method. Level of statistical significance: * P<0.05.

light intensity there was a bit lower and the activity probably started at a light value very close to 5 lux. It increased gradually over the next hour (Fig. 5).

Observations of aquatic and terrestrial ranodons

By far the majority of active ranodons were found in the water, not on land. The frequencies of finds made on land relative to the total number of ranodon counts were only 6.1% (N=425) and 3.6% (N=279) for August 1994 and June 1995, respectively. The number of ranodons counted on land alongside the brooks was thus relatively low, but sometimes increased when the number counted in the water increased. Animals walking on the moist grassy ground beside the brooks had a wet skin and were considered not to be really terrestrial, but aquatic animals which had only left the water temporarily for some reason.

Not all ranodons were active to the same degree at the same time, not even near midnight. In June 1993, when we counted ranodons on land at 23.00-24.00 hrs., i.e. when the activity was at its highest, 14 were seen walking along the bank, but another 11 really terrestrial specimens (with a dry skin) were still passive and very sluggish, hiding under stones.

Discussion

The activity pattern

Ranodon sibiricus proved to be highly nocturnal, with very little, if any, activity during the day. An exception was the young larvae (0+) in August, in part also the one-year old larvae (1+) in June, which showed a certain amount of diurnal as well as nocturnal activity. The 5-min. reading in the aquarium study showed in detail that the ranodons gradually started their activity near the 5-lux limit in the evening. When that limit

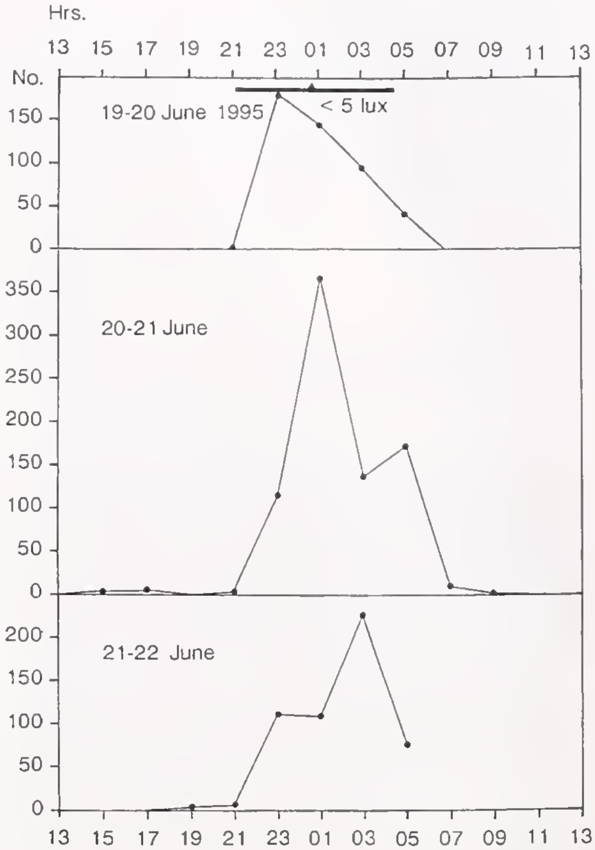

Figure 4. Diel activity of two *Ranodon sibiricus* specimens kept in an aquarium under natural lighting conditions for nearly three days and nights in June 1995, based on the IR light/photocell method.

was again reached in the morning, the activity had decreased to approximately zero. This means that even though the species is clearly nocturnal, it uses all the time it can get for activity, i.e. mainly hunting.

Most earlier authors have noted the extreme nocturnal habits of the ranodons and the more diurnal habits of the larvae (Shnitnikov 1913; Kubykin 1986; Narbaeva and Brushko 1986). Metamorphosed specimens, both in water and on land, hide under stones during the day, but come out at night and often move upstream or downstream for some distance. Wang (1990) stated that in western Xinjiang, China, ranodons also hides among plants and under stones during the day and is active between 24 and 06 hrs. The Xinjiang province, like the rest of China, follows Beijing time, which is three hours earlier than sun time in western Xinjiang. The true activity time of ranodons in western Xinjiang should therefore be around 21-03 hrs., i.e. similar to that found in our investigations in eastern Kazakhstan.

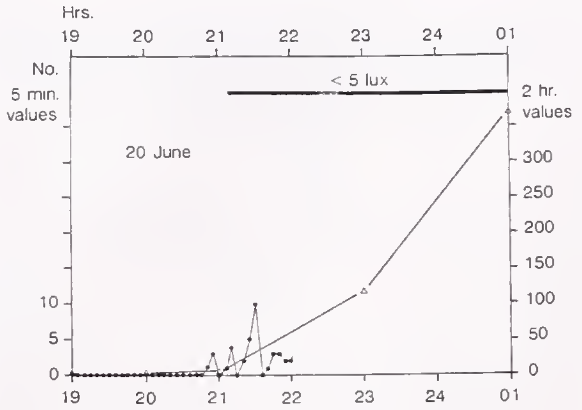

Figure 5. Details of the onset of activity of two *Ranodon sibiricus* specimens kept in an aquarium under natural lighting conditions on 20 June 1995, based on the IR light/photocell method. Activity values are shown as counts per 5 minutes (dots) and per 2 hours (triangles). The activity started near the 5-lux limit of light intensity (see text for further explanation).

We had no opportunity to investigate newly-hatched larvae. In 1995, in the most favourable brook (Brook 1), the first larvae hatched during the second half of June. According to Paraskiv (1953), newly-hatched larvae remain in calm, shallow water well illuminated by the sun, where they hide among stones on the bottom. However, they often come out and lie on the stones, and are active by day, not avoiding the sunshine (cf. Kubykin 1986). We found that at least part of this diurnal activity lasted throughout the summer - although the main activity was nocturnal in August - and even to some extent in the next year (June). A well-defined phase shift from diurnal to nocturnal activity, as described, for example, for *Triturus cristatus* larvae (see Dolmen 1983a,b), probably does not take place. Paraskiv (1953) mentions that older larvae, at the time of their metamorphosis when their gills are becoming resorbed and they are going onto land, avoid the sunshine and keep to shady places.

Water phase and land life

The metamorphosed ranodons stay in water or on land, or alternate more or less regularly between these two media. In daytime, but also sometimes at night, we found terrestrial individuals in damp hollows under stones and the like within a few metres of the water. We made no attempt to specifically measure the activity of such animals. The activity of ranodons in the brooks increased at night, however, and some also went up on to land. We are therefore dealing with two categories of ranodons on land: true terrestrial animals, which have a dry skin and which stay on land for a day or more, and aquatic ranodons, which have a wet skin and which only temporarily come out of the water (Dolmen et al. 1997).

Shnitnikov (1913) and Paraskiv (1953) also noted that juvenile and adult ranodons leave the water or their terrestrial hiding places at twilight and in darkness, and are then active and are found on the banks of brooks, where they often move long distances (cf. Kubykin 1986; Narbaeva and Brushko 1986).

However, as these authors pointed out, not all ranodons leave the water at night, at least not at the same time. The majority, in fact, stay in the water and may only occasionally come up. We found that when the weather had been dry for many days (August 1994 and June 1995), relatively fewer ranodons were found on land, walking around at night or hiding under stones, than when the weather was wet (June 1993).

Environmental adaptations

The nocturnal/crepuscular activity pattern in amphibians is probably ultimately an adaptation to the night and day temperature and air humidity cycles. The vulnerability of the animals to dry conditions makes it necessary for them to hide during the driest and hottest hours, and even when, like the ranodons, they stay in water, this pattern is maintained. Most urodeles are thus primarily nocturnal, although their activity pattern may vary ontogenetically (e.g. Noble 1954; McDiarmid 1994). The activity is proximately controlled by the light/dark cycle. Different temperature regimes, even a rise in temperature of as much as 10-15 °C, seemed to have little, if any, influence on the activity pattern of *Ranodon sibiricus*. Relative humidity, or at least the moisture on the ground, could be important for whether or not amphibians will walk on land, however. All records of ranodons walking on land were made when the air humidity was above 80% RH, always between 21.00 and 03.00 hrs.

Another factor which could represent a threat to *Ranodon sibiricus*, living at high elevations (ca. 1700-2700 m), is the strong UV radiation. Except for a very few larvae of the youngest stages (0+ in August and 1+ in June), no animals were seen voluntarily exposing themselves directly to the sun. For cold-stenothermic animals like *R. sibiricus*, it is probably even more important to be nocturnally active than it is for most other amphibians. High temperatures, i.e. more than 22 °C, are reported to be lethal, at least to ranodon larvae (Brushko and Narbaeva 1988). Temperatures were as low as 6.0-11.5 °C in the air and 4.8-11.0 °C in the water during the peak aquatic and land-walking activity of ranodons at night. Maximum air temperatures during the day were 17.1-21 °C, and water tempera-

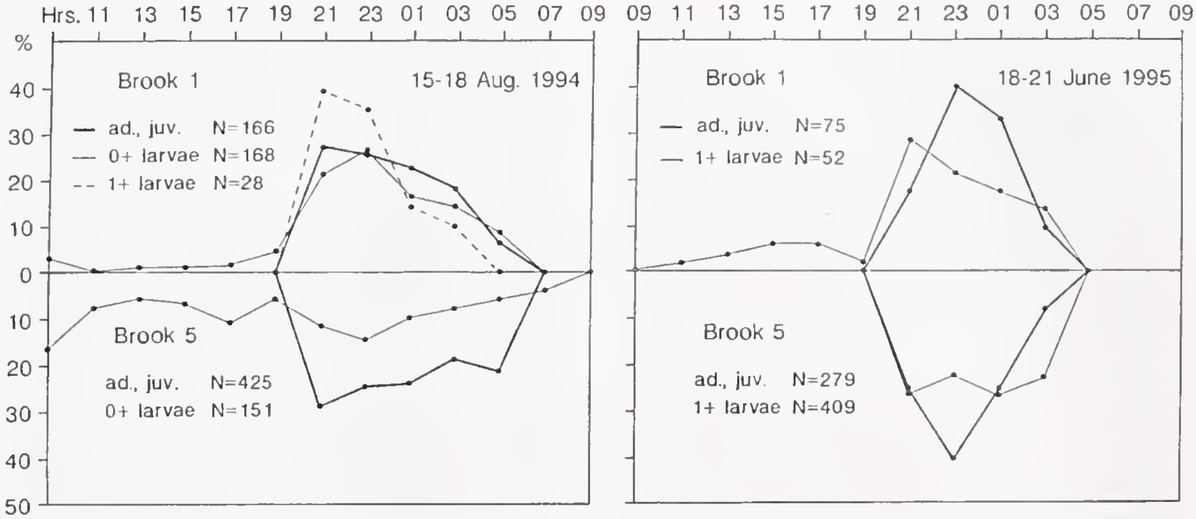

Figure 6. Relative degree of activity (%) of *Ranodon sibiricus* adults/juveniles and larvae in Brooks 1 and 5 (cf. Figs. 1-2). Young larvae (0+, and in part 1+) exhibit a markedly greater degree of diurnality than older life stages.

tures reached 19.3-20.0 °C. A few larvae were counted during the warmest periods, too.

We made no specific study of the possible influence of moonlight on the activity of ranodons. However, when we compared our data on activity with notes on the weather, etc, we found no trend of, for instance, decreasing activity when the half moon (at the most) was sometimes shining. The light regime under such circumstances was also always well below the 5-lux limit.

Ranodon sibiricus is clearly more nocturnal than, for instance, the *Triturus* species studied by Dolmen (1983a,b). It can also be seen that the activity period of *R. sibiricus* in June was shorter than in August, which is in conformity with the length of the night. A similar phenomenon was shown for the more crepuscular *Triturus vulgaris* and *T. cristatus* in Norway (Dolmen 1983a,b). Moreover, although normally two-peaked, in northern latitudes at midsummer the crepuscular peaks of the *Triturus* species fused, and the activity curve thus revealed only one, long midnight peak when real nights (<5 lux) disappeared. Especially *T. vulgaris*, being the more crepuscular species, takes advantage of these long periods of twilight in northern latitudes in that its hunting day thereby becomes longer and its growth better.

The activity period of the strictly nocturnal *Ranodon sibiricus*, however, becomes shorter at midsummer. It is advantageous for an animal to have the opportunity to seek food for as many hours as possible; the ranodons in fact spends the whole night. Its activity is limited, however, by the varying light regime through the season, i.e. the period per day and night when light intensity is below 5 lux, which again is relatively short at midsummer. The need for protection against climatic factors, as described above, and possibly from (diurnal) predators thus seems to be greater than the need for extra growth in metamorphosed ranodons.

However, a marked difference could be seen in the diel activity of metamorphosed ranodons and larvae, especially 0+ larvae aged 1-2 months (Fig. 6). The youngest stages seem to be more or less active both day and night. Still younger larvae than those we have studied are possibly even more diurnally active (cf. Paraskiv 1953). A probable explanation of the prolonged activity of the larvae, compared to older stages, is their need to eat and grow as much as possible during the short frost-free season in the mountains. Being large may perhaps increase their chances of surviving their first, most hazardous, winter. Growing is therefore probably their most important task. A larger size also makes their migration up or down the brook to hibernation sites in late autumn easier and protects them from predatory fish (see below).

By staying during the summer in the lower, warmer part of small brooks, in shallow water, and alternating between shade and sunshine (Paraskiv 1953; Dolmen et al. 1997), the metabolism of the larvae is raised and kept at a near optimal level. There are, however, certain limits for a cold-stenothermic animal like *Ranodon sibiricus*. Small larvae are sensitive to warm weather, and 22 °C is said to be lethal (Brushko and Narbaeva 1988).

Such a difference in diel activity and microhabitat between adult urodeles and their larvae is not uncommon (McDiarmid 1994). Dolmen (1983a,b; 1988) interpreted it as a means to reduce intraspecific competition between different developmental stages and as protection against cannibalism, which may be common in salamanders and which is also known to occur in *Ranodon sibiricus* (Kubykin 1986; Wang 1990; Kuzmin 1991a). In species whose adults and larvae live sympatrically, a behavioural mechanism which favours the avoidance of cannibalism could presumably be of adaptive value.

Hunting strategy

During our preliminary studies in June 1993, the method we used for trapping ranodons in water failed and we concluded that most translocations of *Ranodon sibiricus*, at least at that particular time of year, probably took place on land. However, only a small proportion of our many records of active ranodons in 1994 and 1995 were made on land. We therefore conclude that most of their activity, like hunting (not longer translocations), is nevertheless aquatic. Hence, ranodons are probably largely sit-and-wait hunters, as maintained by Paraskiv (1953), too; they do not move about much in the water. This contrasts with the European *Triturus* species (see Dolmen 1983a,b), which live in the stagnant water of ponds and small lakes. For a running-water species like *R. sibiricus*, it may be more economic to sit and wait for drifting prey than to spend energy looking for them.

Our preliminary results on food items showed that *Ranodon sibiricus* is an opportunist when it comes to choice of prey, and thus supports the results of stomach analyses made by Kuzmin (1991b). There was also a tendency for ranodon stomachs to be at their fullest after midnight. Based on the undigested stomach contents of a few specimens caught in daytime, Shnitnikov (1913) suggested that the ranodons feeds by day. However, apparently no ranodons caught by him at night were examined.

Diel activity and predators

During the day, metamorphosed ranodons cleverly hide under boulders and in earth cavities in the brook bed and are often difficult to catch. Because of their strict nocturnality and their ability to hide in daytime, night searches with good torches are the best way of looking for ranodons in a brook. Searches in daytime may be strenuous, and often negative if the population density is not large. At night, however, the animals are easy to see in small and medium-sized brooks.

It can be expected that the activity cycles of a predator and its prey will coincide. Wild boars *Sus scrofa* and grey herons *Ardea cinerea* are said to be natural predators of ranodons (Brushko and Narbaeva 1988), likewise black storks *Ciconia nigra* (Shnitnikov 1913). We think that some of the many species of birds of prey which occur in great numbers in the mountains (e.g. buzzards *Buteo* spp.) will also occasionally take ranodons if they had the opportunity. However, of these terrestrial predators, only the wild boar is nocturnal. Adults and large juvenile ranodons therefore seem to have few, if any, really important predators. However, two kinds of fish (*Diptychus maculatus* and *D. dybowskii* (Cypriniformes)) are present in the River Borokhudzir, at least in the main river. Fish, which are usually nocturnal or crepuscular, may therefore be potential predators of ranodon larvae. However, since these fish are absent, or extremely rare, in the small, spring-fed brooks in which the ranodons breeds, they are hardly a threat to the ranodons there.

The influence of cattle

The negative influence of cattle on *Ranodon sibiricus* has been mentioned by several authors (Kubykin 1986; Narbaeva and Brushko 1986; Brushko and Narbaeva 1988; Wang 1990; Dolmen et al. 1997). Damage is mechanical when the cattle trample in the brooks, crushing ranodons and destroying eggs. Their excrements may also pose a threat to eggs and small larvae.

In 1993, up to about 150 cows, watched by shepherds on horseback, twice daily crossed the brooks of the study area. There were also flocks of horses, sheep and goats. Corresponding numbers of domestic animals were seen in 1994 and 1995. Most crossing of brooks took place in daylight at about 8 hrs. and 20 hrs., and at that time the adult and juvenile ranodons were still relatively safe in their hiding places. Nevertheless, we twice found dead ranodons which had been crushed under the feet of cows. On other occasions, we came across mechanically damaged eggs, presumably the victims of wading cattle. Larvae, too, may suffer from cattle. However, we believe that the damage to metamorphosed ranodons is not really large (cf. Kubykin 1986).

Conclusions

Ranodon sibiricus is a nocturnal species in the juvenile and adult stages, whereas the activity of young larvae is more evenly distributed through the day and night. The difference in diel activity between larvae and metamorphosed stages probably reduces intraspecific competition and cannibalism. In daytime, the ranodons hide cleverly in the brook bed or on land. This secretive life makes them difficult to find, both for diurnal predators and people. At night, however, the ranodons are easy to see. Their nocturnality also makes adult and juvenile ranodons less vulnerable to mechanical damage from grazing cattle, but eggs and larvae may easily be harmed.

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