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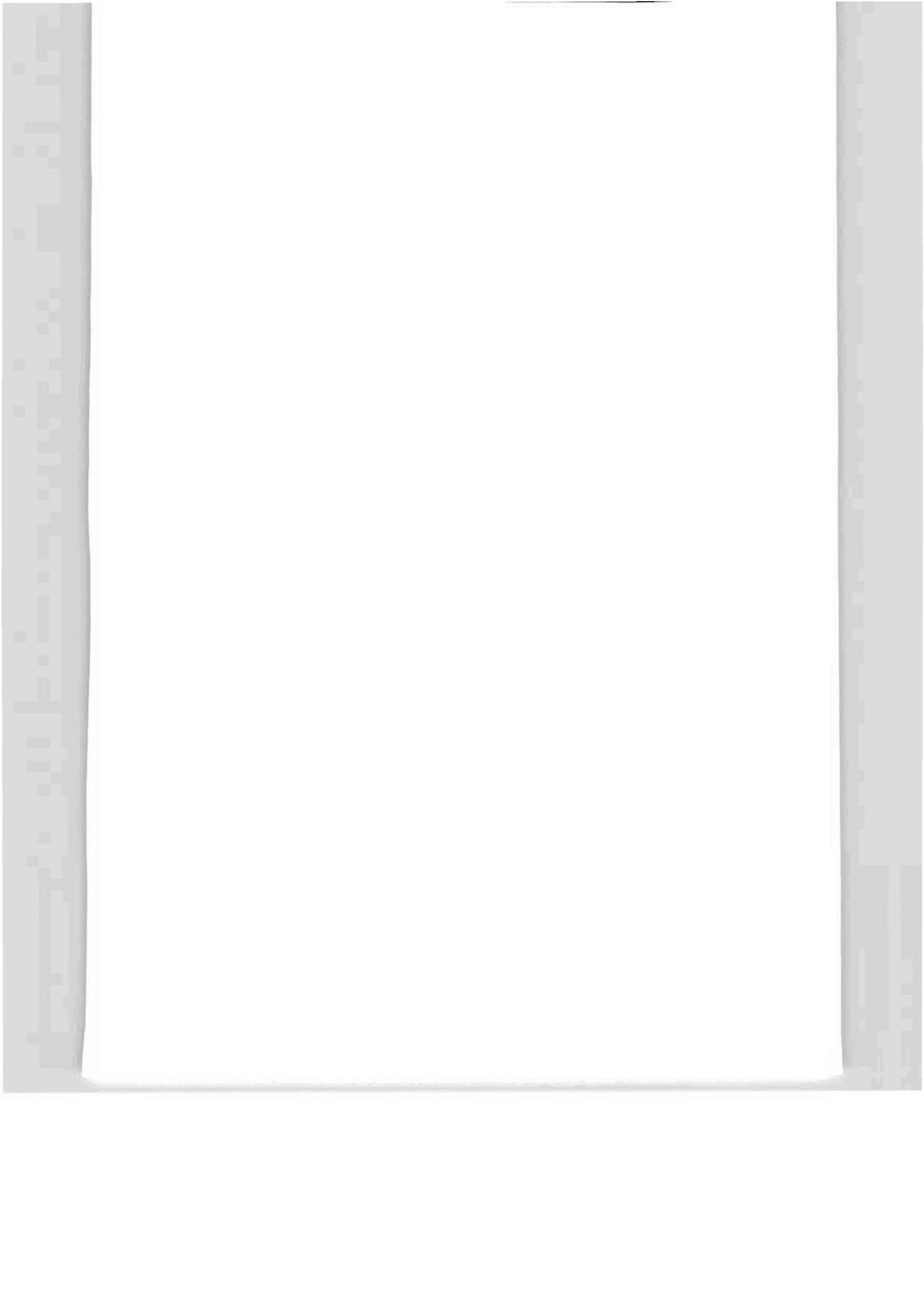
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Dag Dolmen

DIEL RHYTHMS OF *TRITURUS VULGARIS* (L.)
AND *T. CRISTATUS* (LAURENTI) (AMPHIBIA)
IN CENTRAL NORWAY

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by

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ABSTRACT

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Plexiglass fish traps were used to study the diel rhythms of aquatic newts, while terrestrial ones were investigated by making counts.

Adult *Triturus vulgaris* and *T. cristatus* show a crepuscular (or nearly nocturnal) activity pattern, but from early May onwards, the morning activity peak of *T. cristatus* and female *T. vulgaris* disappears. *T. vulgaris* females are more nocturnal than the males; *T. cristatus* is more nocturnal than *T. vulgaris*. The different roles of the sexes during the courtship period may explain the differences in the activity patterns seen in *T. vulgaris*.

At the beginning and end of their aquatic period the activity pattern of adult newts is more arrhythmic; *T. vulgaris*, before going onto dry land, even diurnal. Terrestrial *T. vulgaris* are again crepuscular.

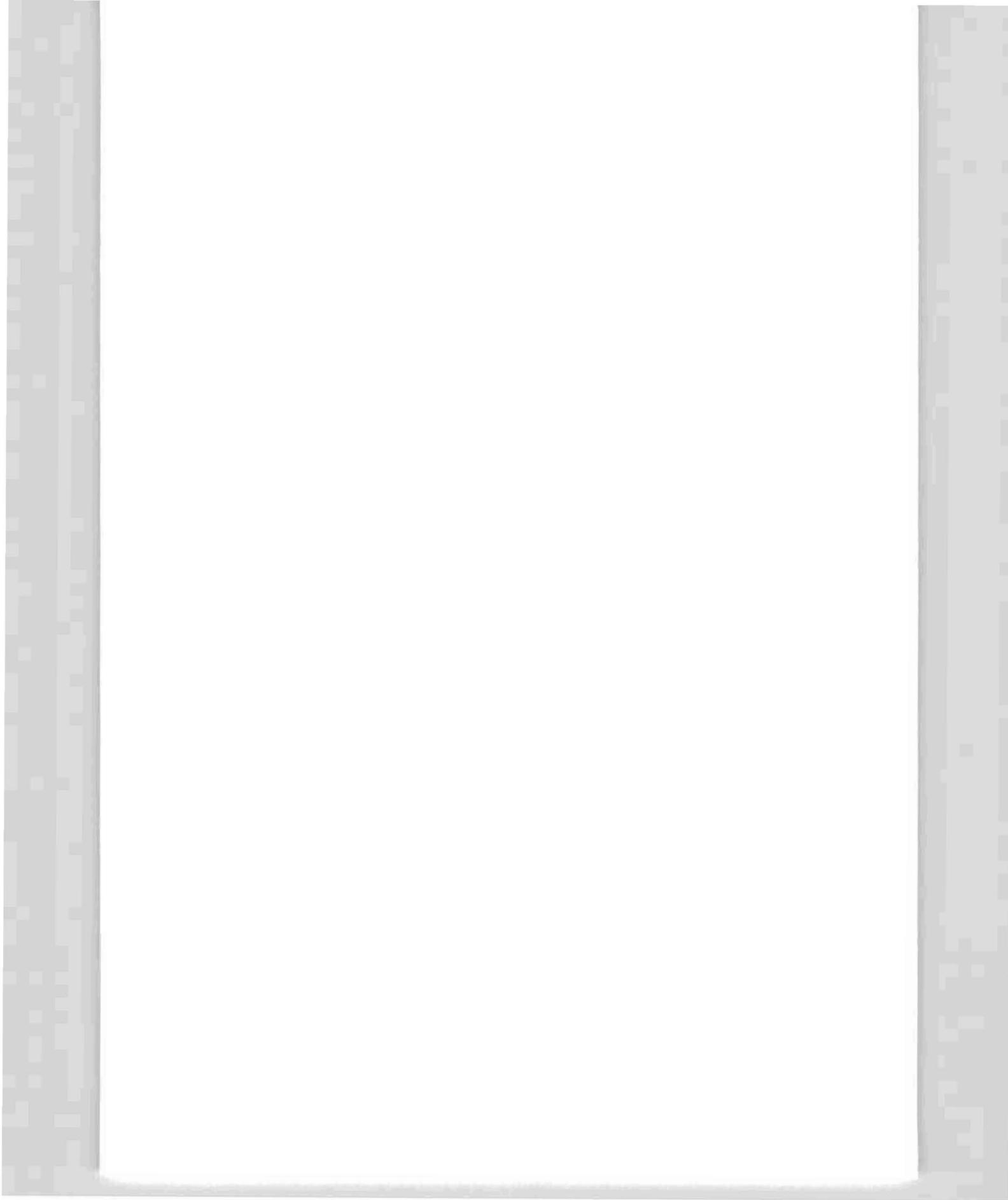
T. vulgaris and *T. cristatus* larvae are clearly diurnal. The different activity patterns of adults and larvae are thought to represent important barriers against cannibalism.

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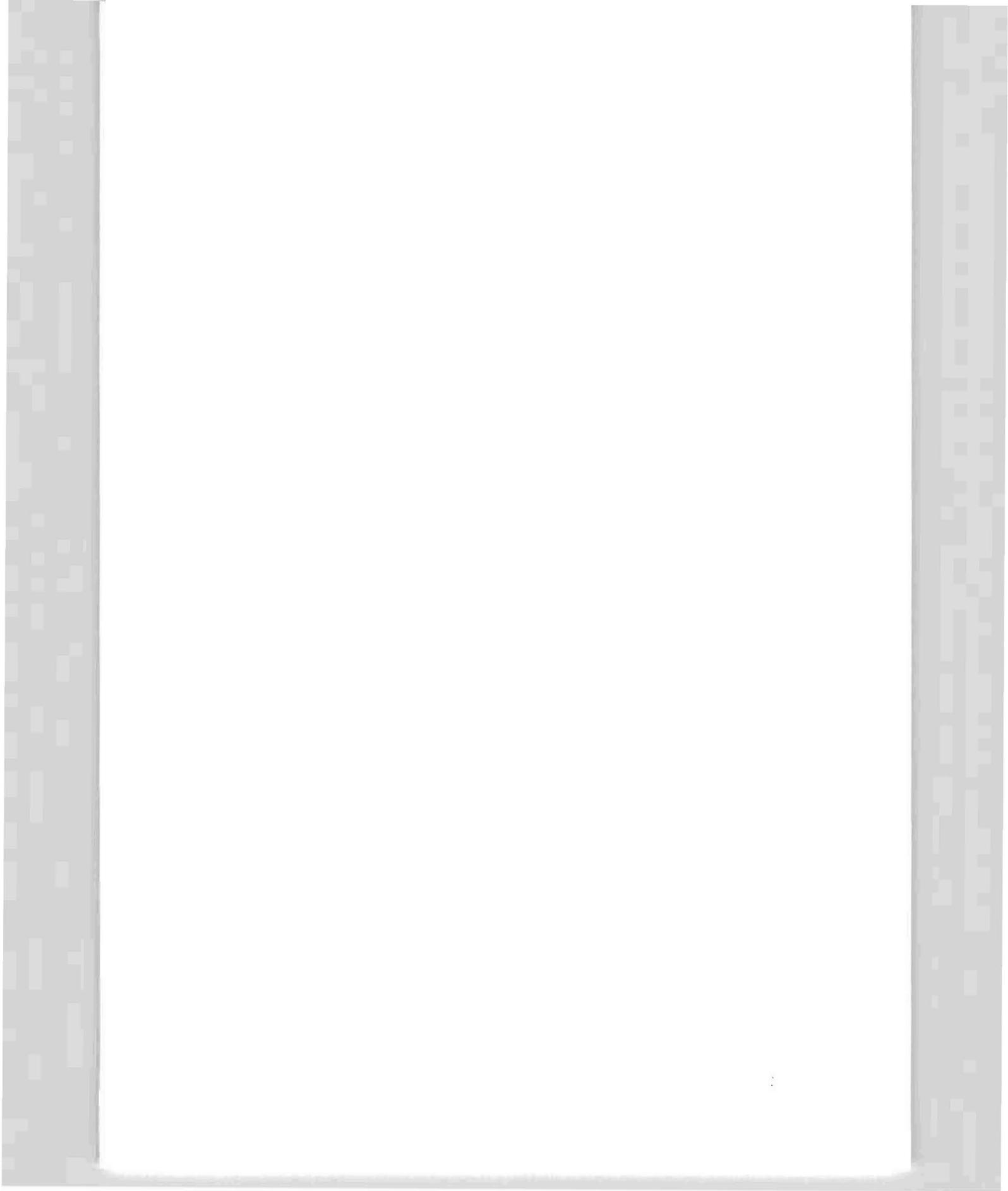
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INTRODUCTION

As regards our native species of newts in Norway, Collett (1918) noted that in its aquatic phase *Triturus vulgaris* hunts especially during the hours of darkness, and by day usually either enjoys the sunshine or is occupied in mating activities. Smith's (1964) experience was that aquatic *T. vulgaris* wander about on the banks, or in the shallow water at the edge of lakes and ponds, particularly at night. By day they hide away either on land or in the water. Høst (1967), however, reported that aquatic newts are active by day, when they enjoy sunning themselves at the surface; terrestrial newts, however, become nocturnal or crepuscular, and hide away during daylight hours.

Some confusion has thus arisen concerning the activity patterns of aquatic newts, but most authors agree that terrestrial newts are nocturnal or crepuscular in their habits (Schreiber 1875, Wolterstorff 1921, Freytag 1954, Knight 1962, Smith 1964). A nocturnal activity would be thought to protect the amphibians from dehydration (cf. Noble 1954).

Himstedt (1971), using a new capacitance actograph (Machan & Himstedt 1970) carried out laboratory experiments on the diel rhythm of *T. vulgaris* and *T. cristatus*, using light intensity as the variable environmental factor. He found that both species, when in the water, exhibited two activity peaks, one maximum in the morning and another in the evening; the activity of *T. cristatus*, however, was more definitely related to the hours of darkness than was *T. vulgaris*. On land the situation was similar to that found in water. Their larvae showed more arrhythmic activity pattern, with those of *T. vulgaris* being slightly more active by day, and those of *T. cristatus* a little more active at night.

The aim of the present investigations has been to try to clarify the activity patterns of both newt species under natural conditions near the northern limits of their distributional areas. The effect of the light conditions at midsummer on the activity pattern of both species was paid particular attention. A new technique for measuring the activity of newts was introduced. It was hoped that more information about the behaviour pattern of newt larvae, in nature, would be gained, to find out whether or not their

activity pattern should be regarded as an arrhythmic one. Some preliminary results have been presented by Dolmen (1976 a,b).

DESCRIPTIONS OF THE INVESTIGATED LOCALITIES

The chosen investigation areas for studying newt activity were a system of draining ditches at Vasseljemoen, near the lake Jonsvatnet at Malvik, E of Trondheim in Central Norway (UTM grid reference: 32V NR 815293; at an altitude of 170m) and a pond in a former slate quarry at Hastad, at Skjeldstadmarka in Stjørdal (32V PR 044466; alt.: 230m). Both these localities have relatively dense populations of *T. vulgaris*, and at Vasseljemoen *T. cristatus* is also present. Both areas are surrounded by mixed forest with *Picea abies*, *Alnus incana*, *Betula verrucosa* and *Salix caprea*. A third locality used for a two-day additional investigation of *T. cristatus* larvae, consisted of four bog pools in Blanktjørndalen, NE of the lake Nordre Høgsetvatnet in Bjugn on the Fosen Peninsula, N of the Trondheimsfjord (32V NR 580768; alt.: 130m). The only newt found here is *T. cristatus*. A fourth locality, much further south in the country, was a little pond at Tverrvæd, in Sem municipality NW of Tønsberg (32V NL 854757; alt.: less than 20m), which contains both *T. vulgaris* and *T. cristatus*. Figure 1 shows the positions of the four localities.

METHODS

The traps

A special type of fish-trap made of plexiglass, first constructed and described by Breder (1960) and later recommended by Braum (1971), were used in the investigations. Some slight modifications were made, viz. holes covered over with brass wire-mesh, to prevent the water in the traps stagnating (Solem 1973a). The traps (Fig. 2) measured 15.5 x 15.5 x 29 cm. Two lateral "wings" interrupt any moving animals and guide them towards a narrow slit, which leads into the trap box. A slit about 1 cm in width is suitable for allowing newts to pass through.

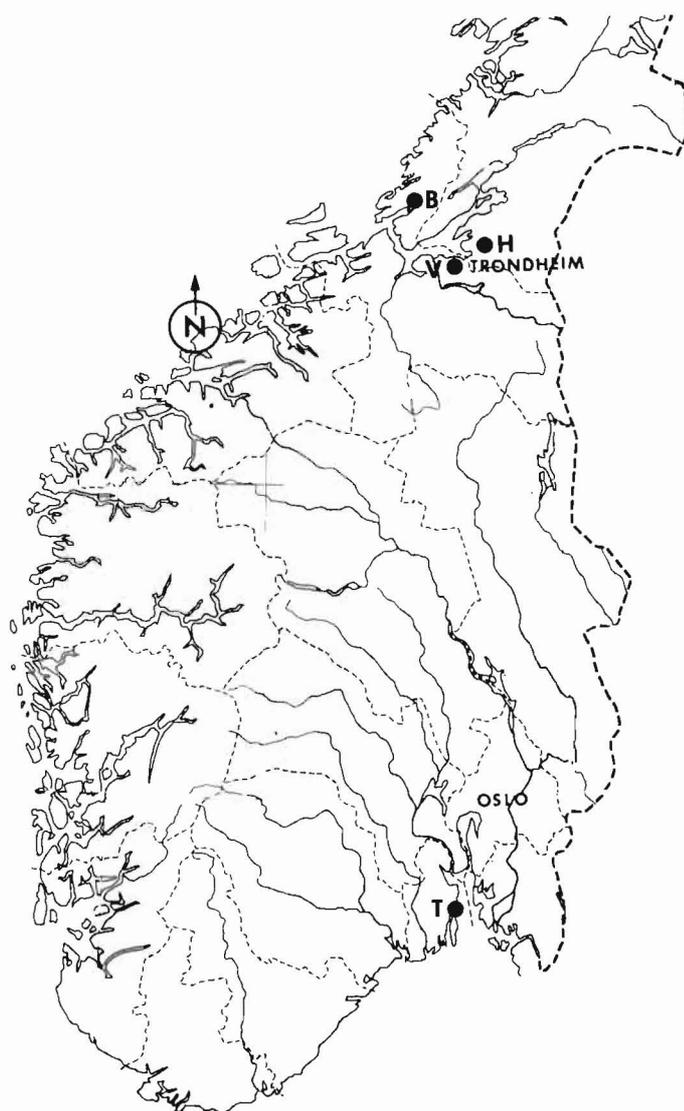


Fig. 1. The geographical situation of the four investigated localities: Vasseljemoen (V), Hastad (H), Blanktjørndalen (B) and Tverrvæd (T).

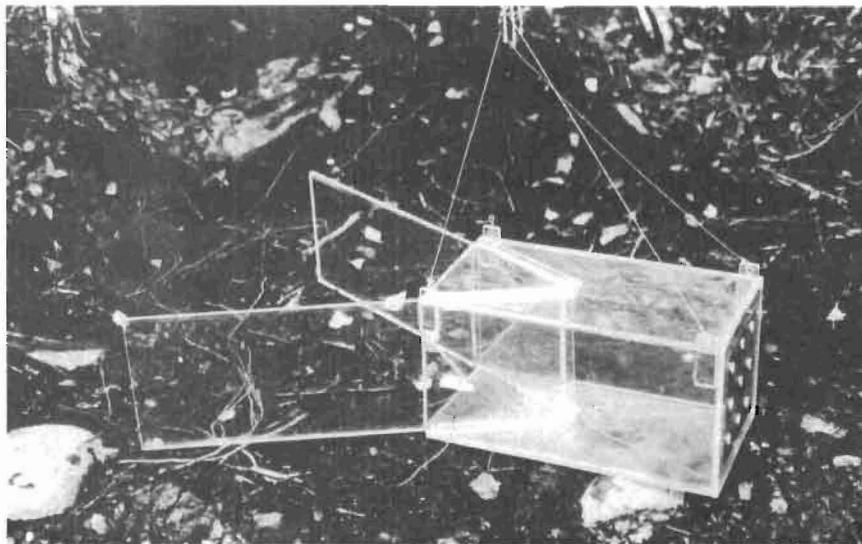


Fig. 2. The trap (photo: P.E. Fredriksen).

The field work

The activity of the aquatic newts was usually investigated with six traps, at both Vasseljemoen, Hastad and Blanktjørndalen. At Tverrvæd four traps were used. (In 1976, however, 14 and 8 traps were used at Vasseljemoen and Hastad, respectively). At Vasseljemoen the traps were placed at a depth of 20-30 cm, at Hastad at 20-50 cm, in Blanktjørndalen at about 20 cm, and at Tverrvæd at 15 cm depth. To prevent the possible influence of phototaxis, the traps were always sited with their openings pointing in different directions, e.g. at Vasseljemoen three faced east and three faced west.

15 days were used for the study of adult *T. vulgaris*, 14 days for adult *T. cristatus*, 7 days for *T. vulgaris* larvae and 4 days for *T. cristatus* larvae.

The traps were emptied at 3-hourly intervals throughout each 24-hr. period. The animals caught were counted and then released. The differences in the total numbers of the newts trapped during each 3-hr. interval throughout a 24-hr. cycle are considered to reflect the differences in activity of the population during the same periods of time. By "activity" is meant all types of locomotor activity, including wandering about, hunting, courtship etc, and it

is here defined as the time when a higher number of newts than the average for the day and night goes into the traps.

Water temperature was measured with an ethanol thermometer, with a centigrade scale, marked off at $\frac{1}{2}^{\circ}$ intervals. Light intensity was measured with a lux meter (Gossen, Panlux) held at the water surface.

On 10-11 July 1975 investigations on the activity of terrestrial newts were carried out at Vasseljemoen. Within each of the above-mentioned 3-hourly intervals newts were looked for under logs and stones on the ground. These are the favourite hide-outs (dwelling-sites) for terrestrial newts, and movements usually take place within easy reach of these sites, and only for short periods of time. The newts were marked individually by toe-clipping codes. *Newly arrived animals at new places or positions within their home range must have been active shortly before, and the numbers of such new newts encountered each time were used as a measure of newt activity during the preceding period.* A continuous-recording thermo-hygrograph (Thies) was used to obtain data on air temperature and relative humidity within the investigated area.

Data for each day were subjected to the chi-square test, to see whether or not the activity pattern differed significantly from a constant, average, level. Wilcoxon's signed-ranks test for two groups (one-tailed, with basis in Himstedt's 1971 results, and common theory of circadian rhythms) has been used to test the differences in the level of activity from one 3-hr.-interval to the next.

RESULTS

The physical factors

The nights became progressively shorter during May, and throughout June and most of July the light intensity never fell below 5 lux, i.e. there was never any real night. (In biochronology the threshold value of 5 lux has very often been used to distinguish between "light" and "dark": Bünning 1969, 1972, cf. e.g. Müller 1965). On two nights in May, the air temperature fell below

0°C in 1974. The diel variation in temperature was often as much as 24°C. Relative humidity near the ground level always rose to 100% about or just before midnight, - or during rainy weather.

In the middle- or end of May the water temperature exceeded 10°C by day, but fell below this value at night. From the beginning of June the water temperature generally remained about 10°C by night as well as by day. Water temperatures below 10°C were once again recorded in September.

Aquatic *T. vulgaris*

At Vasseljemoen the first newts to arrive were seen at the end of April, though the majority came later. The first eggs were found in the first half of May. A distinct pattern of activity in the newts was not always seen until the second or third week of May. From that time, however, and onwards, both males and females showed distinct activity patterns (Vasseljemoen and Hastad, Fig. 3). The males had two peaks of activity, one in the evening and one in the morning, the first lasting longer than the second. This pattern was repeated, with only minor deviations, in May and during the first half of June. The females had one peak in the late evening (sometimes also a minor peak in the morning had been seen at the beginning of May).

In June, when the light intensity never fell below 5 lux, the interval of maximum activity by the females shifted to midnight. In May 2. half and June 1. half, six of seven days these patterns were significant for both males and females (Chi-square test: $P < 0.05-0.001$). Courtship was last observed to occur in the middle of June. At the end of June the activity pattern once again became diffuse, showing both diurnal and nocturnal activity. The two last days of the investigations (26-27 June and 2-3 July) maximum activity both in males and females were around noon or in the early afternoon. This increase recorded in the activity of the males at 11.00-14.00 hrs. was significant (Wilcoxon's signed-ranks test: $P < 0.05$).

In addition to a higher percentage of diurnal activity, another characteristic feature of the behaviour of the *T. vulgaris* population was observed from mid-June and during the rest of the aquatic phase: The animals were frequently seen sunning themselves

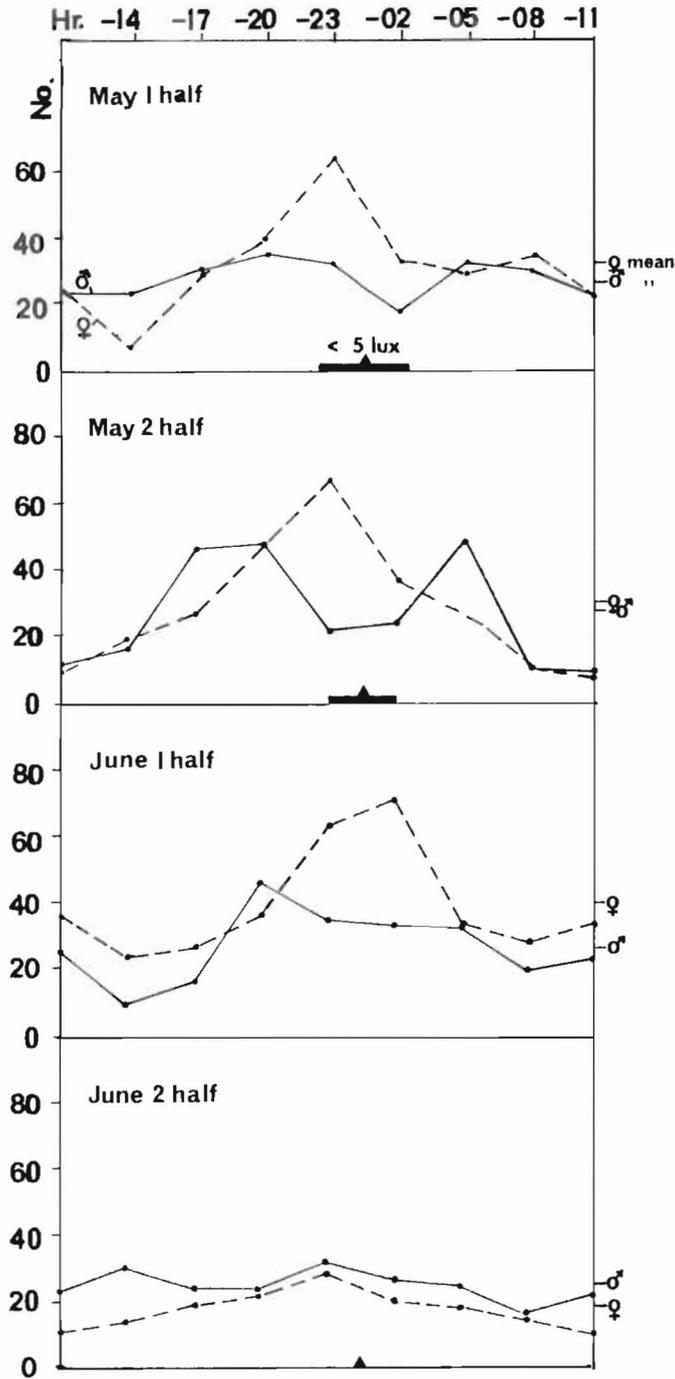


Fig. 3. Seasonal progression of the diel activity of aquatic *T. vulgaris* adults at Vasseljemoen and Hastad. Black triangles show midnight. The diagrams are based on 3, 5, 3 and 4 days, respectively.

in the water surface, or resting on submerged twigs and plants just below. Especially the females were also very often observed swimming lazily, or floating, just below the water surface, or in the middle water layers, hunting for Cladocera and other small, freely-swimming, animals.

In the first half of May the activity pattern of the males was not very distinct (not significant, Chi-square test: $0.2 < P < 0.3$), although in the females it was ($P < 0.001$), and as was also the case for both males and females in the second half of May ($P < 0.001$) and in the first half of June ($P < 0.001$). The main difference between the patterns found in the second half of May and the first half of June, apart from the shift in maximum activity of the females from 20.00-23.00 hrs. to 23.00-02.00 hrs., is the fact that the males showed a relatively higher degree of activity during the period around midnight (23.00-02.00 hrs.). In the second half of June the activity patterns of both males and females did not deviate significantly from a pattern of steady activity throughout the 24-hr. period ($0.5 < P < 0.7$ and $0.1 < P < 0.2$, respectively).

Table 1. Level of activity in aquatic *T. vulgaris* adults compared to that of the foregoing interval. Data taken from the main courtship season (second half of May and first half of June). Wilcoxon's signed-ranks test for two groups (one-tailed), significance levels. (When considering each individual trap, the number is put in brackets.) Arrows indicate increasing or decreasing activity.

	Hr. 11-14	14-17	17-20	20-23	23-02	02-05	05-08	08-11
Sex								
♂♂	-	0.01 ↗ (0.005)	0.05 ↗ (0.025)	0.025 ↘	-	≈0.05 ↗	0.005 ↘	-
P<								
♀♀	-	0.05 ↗	0.01 ↗	0.025 ↗	-	0.025 ↘	0.05 ↘	-

Considering the second half of May and first half of June, the main courtship and egg-laying season, the activity patterns with a single midnight peak for females and two peaks, evening and morning, for males are statistically significant (Table 1). Activity and

distinct activity patterns could be found at all registered temperatures (down to 5-6°C).

Terrestrial *T. vulgaris*

In the terrestrial investigations only a relatively small number of newts were studied. 10-11 July (1975) normal conditions for the summer period were registered. The minimum air temperature was 6-7°C during the night, and the newts were relatively highly active during this period, though showing little activity during the day. The peak of (total) activity in the late evening recorded (Fig. 4) was significantly greater than the activity before and after this time of day (all values are compared to those of the foregoing interval, Wilcoxon's signed-ranks test: 20.00-23.00 hrs. $P < 0.005$; 23.00-02.00 hrs. $P < 0.05$). As a whole the activity seems two-peaked and probably not much different in the two sexes. Activity was noted when the relative humidity exceeded about 85%.

T. cristatus

At the course of the trapping investigations at Vasseljemoen for aquatic *T. vulgaris*, some specimens of *T. cristatus* also went into the traps. Although relatively few newts were caught, the basic activity pattern of *T. cristatus* is fairly clear and is readily comparable with that obtained by Himstedt (1971).

The maximum activity obtained by the females fell during the interval 20.00-23.00 hrs. early in the season, but shifted to 23.00-02.00 hrs. later on in the year. There may perhaps be a minor peak of activity recognisable in the morning. The activity pattern of the males seemed to be essentially the same as that of the females. At the start and finish of their aquatic phase, the activity pattern of the entire newt population seemed to be more or less steady.

Fig. 5 shows the changes in the pattern of activity of adult *T. cristatus* throughout the trapping season at Vasseljemoen. When both halves of May and the first half of June are taken togeth-

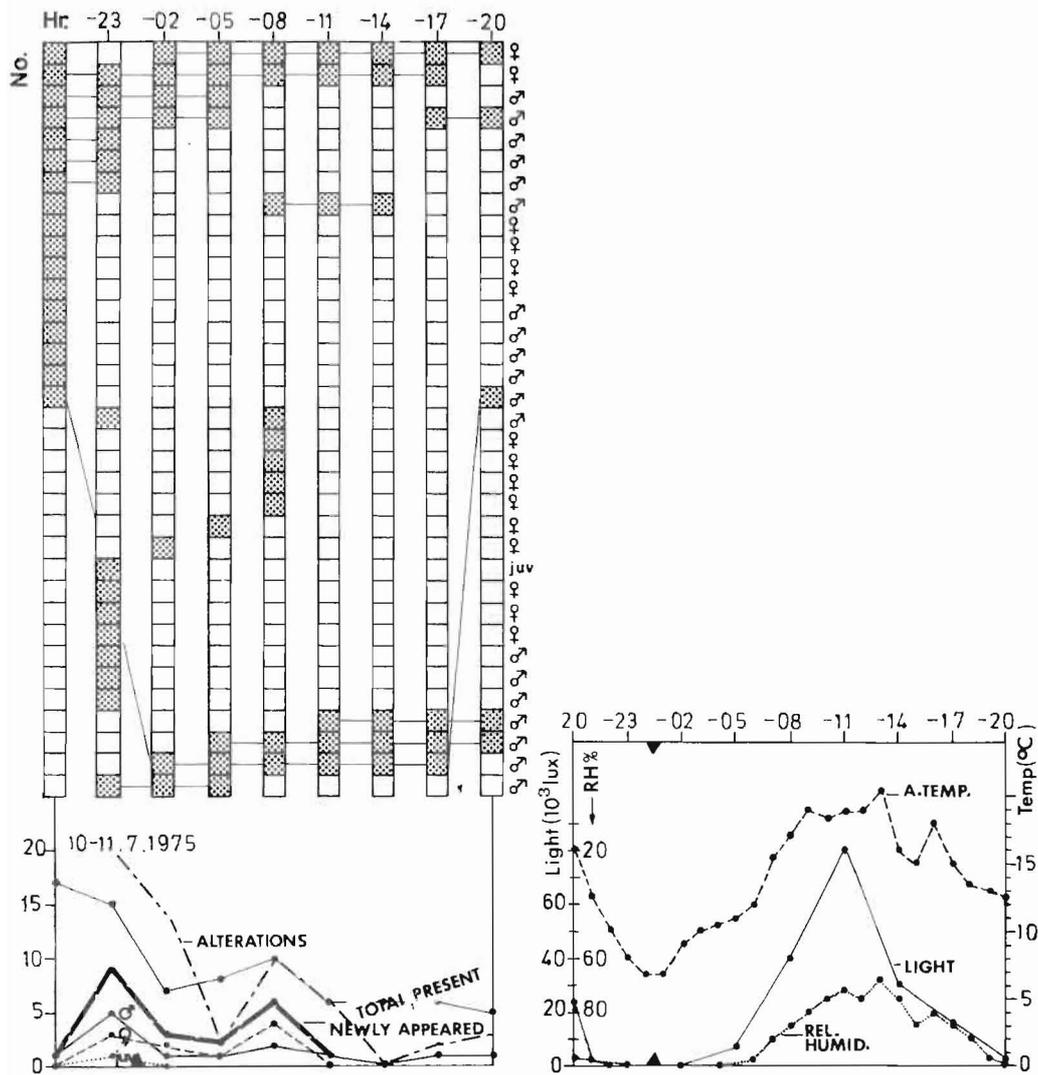


Fig. 4. On left: Diel activity of terrestrial *T. vulgaris* in a day and night at Vasseljemoen. The activity is reflected through the number of newly appeared newts at certain sites (see Methods), to some extent also through the curves for alterations in positions among the animals, and the total number of newts present. Hatched squares show the presence, empty squares the absence, of a newt. Horizontal lines connecting squares indicate the presence of an animal at a site over more than one interval, slanting lines indicate the movement of an animal from one site to another. On right: Light, temperature and relative air humidity values.

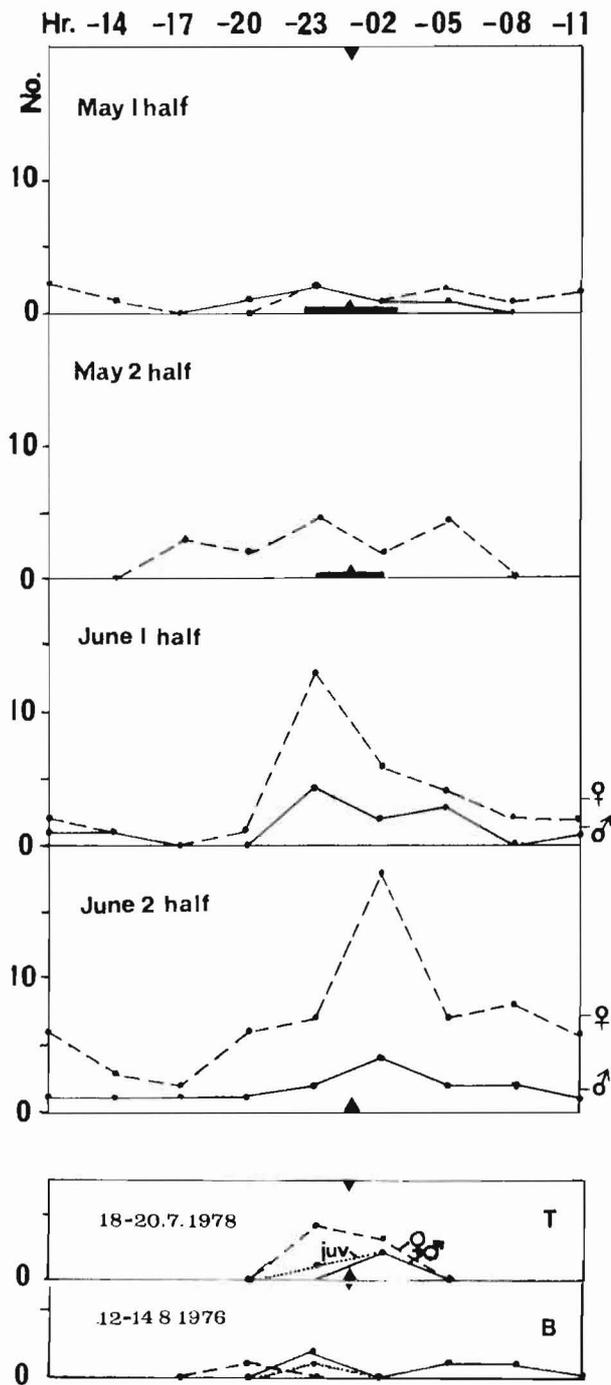


Fig. 5. Seasonal progression of the diel activity of aquatic *T. cristatus* adults at Vasseljemoen, and the activity at Blanktjørndalen (B) and Tverrvæd (T). The upper diagrams are based on 3, 2, 1 and 4 days, respectively.

er (Chi-square test: $P < 0.001$) and in the second half of June ($P < 0.01$), the activity maximum of the females and the late evening increasing activity of the males were statistically significant (Table 2).

Table 2. Level of activity in aquatic *T. cristatus* adults compared to that of the foregoing interval. See legend to Table 1.

Month	Sex.	Hr.	11-14	14-17	17-20	20-23	23-02	02-05	05-08	08-11
	♂♂		-	-	-	≈ 0.05 ↗	-	-	-	-
		P <								
May	♀♀		-	-	-	0.005 ↗	0.025 ↘	-	-	-
June 1										
June 2			-	-	-	-	0.025 ↗	0.005 ↘	-	-

A comparison of the activity patterns of *T. vulgaris* and *T. cristatus* is shown in Fig. 6, in which the data are expressed as percentages of the total numbers caught. At 20.00-23.00 hrs. *T. vulgaris* males start to become less active, while *T. cristatus* males still increasing their activity. *T. cristatus* is, on the whole, a more dark-loving species than is *T. vulgaris*. This tendency is also seen in diagrams from Blanktjørndalen and Tverrvæd (Fig. 5). At Vasseljømoen and at Tverrvæd, *T. cristatus* adults were often observed by night, but very rarely by day. This was also Frazer's (1978) experience from Britain.

T. vulgaris larvae

At Hastad the *T. vulgaris* larvae showed a diurnal activity pattern during each investigation period throughout the season, i.e. from mid-July (mean larval body-length 11 mm; mean total length 21 mm) to the end of September (16 mm/31 mm). Fig. 7 provides a picture of the diel variation in activity. This, practically speaking, is symmetrical around noon or early after noon. The activity patterns for each day at Hastad are significant (Chi-square test: for July 1974: $P < 0.001$, August 1974: $P < 0.05$, September 1974:

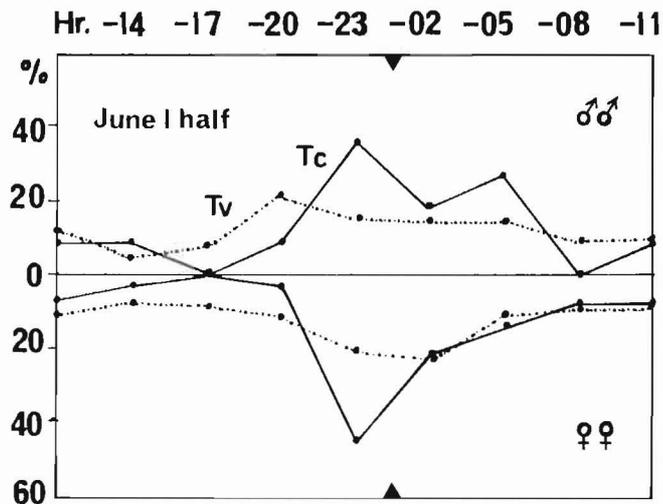


Fig. 6. Relative degree of activity (%) through a day and night of *T. vulgaris* and *T. cristatus* in the first half of June. The percentages are based on the following number of animals: *T. vulgaris*: 215 males, 321 females; *T. cristatus*: 11 males, 29 females.

($P < 0.001$, August 1975: $P < 0.001$ and September 1976: $P < 0.001$). The data for July and September showed a mid-day maximum, while the data for the other times of year showed a somewhat reduced level of activity at mid-day. During the night (cf. the 5-lux limit) only a very few larvae were found moving around. All in all the morning increase in activity was statistically significant (Wilcoxon's signed-ranks test: 05.00-08.00 hrs. $P < 0.025$; 08.00-11.00 hrs. $P < 0.005$), as was the decrease in activity in the evening (17.00-20.00 hrs. $P < 0.005$; 20.00-23.00 hrs. $P < 0.01$; 23.00-02.00 hrs. $P < 0.05$). The investigations made at Tverrvæd, in southern Norway, also showed that *T. vulgaris* larvae exhibited minimum activity during the period around midnight.

T. cristatus larvae

Both the investigation in Blanktjørndalen and that at Tverrvæd (each two days at Tverrvæd, $P < 0.001$) showed that *T. cristatus* larvae have a diurnal activity pattern with a very low level of activity when the light intensity falls below 5 lux (Fig. 8). The increase in their level of activity in the morning is signifi-

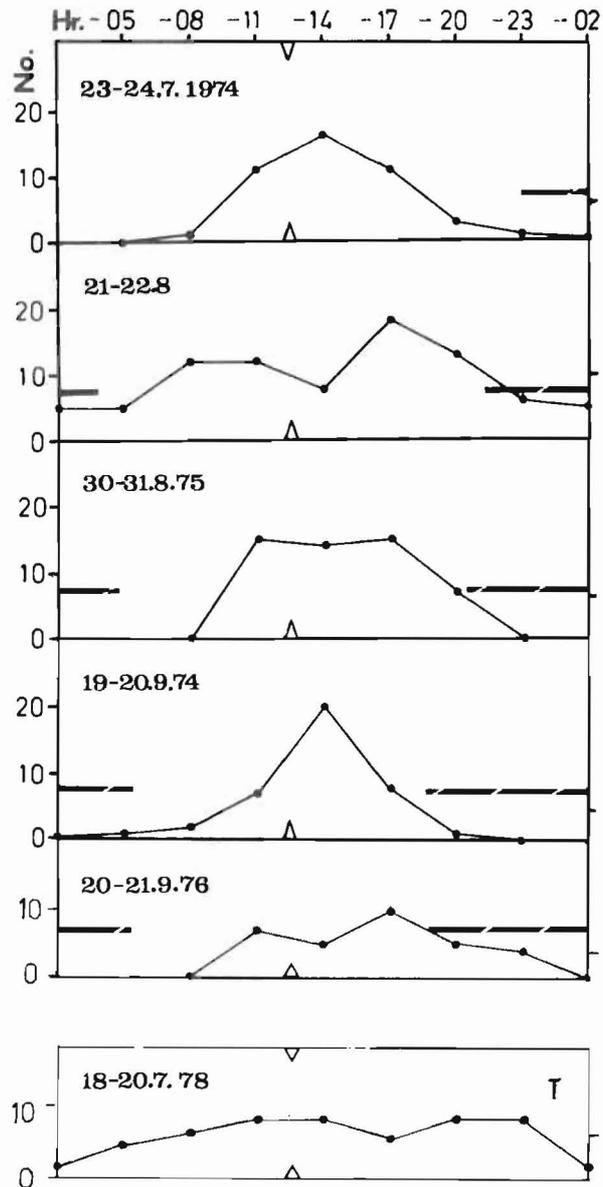


Fig. 7. Diel activity of *T. vulgaris* larvae at Hastad and Tverrvad (T). White triangles show midday.

cant when the data for all four days and nights are taken together (Wilcoxon's signed-ranks test: 02.00-05.00 hrs. $P < 0.025$), as is the decrease in activity shown in the evening (20.00-23.00 hrs. $P < 0.005$). It would appear that the main period of activity falls in the afternoon/early evening (Tverrvad). A characteristic feature of

the behaviour of the larvae of *T. cristatus* is the way they swim to-and-fro, or hover in the middle water layers, by day.

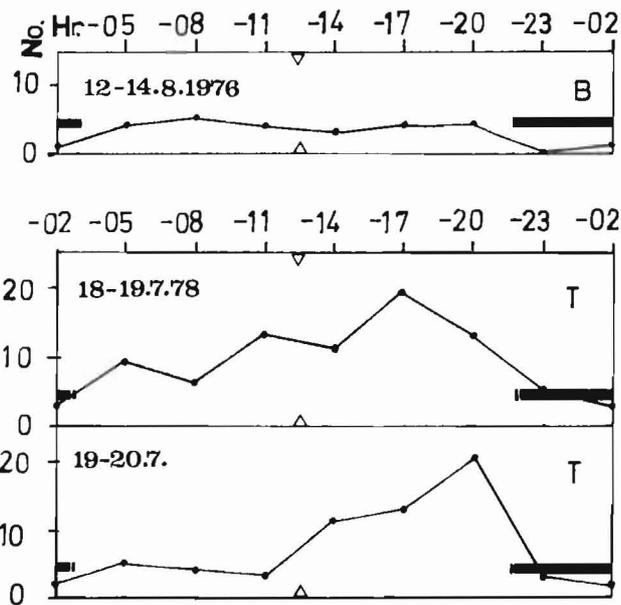


Fig. 8. Diel activity of *T. cristatus* larvae at Blanktjørndalen (B) and Tverrved (T).

DISCUSSION

The effect of light

Both aquatic- and terrestrial adults of *T. vulgaris* and *T. cristatus* are seen, from the results of the trapping investigations, under natural conditions, in Central Norway, to have a two-peaked, or one-peaked, crepuscular, or almost nocturnal, activity pattern. A crepuscular activity pattern in these species was also demonstrated by Himstedt (1971), under laboratory conditions in Vienna, using an actograph, when the illumination was controlled (dark/light periods as under normal conditions, but sometimes out of phase). Wherever the summer nights are extremely short, as in Trøndelag, the twilight, and therefore also the maximum activity, more or less coincides with midnight, and the two activity peaks fuse together.

An arrhythmic activity in the *T. vulgaris* populations was found in the present study, under natural conditions, at the end of their aquatic phase of life, when no real darkness occurs, i.e. in June-July (the activity even tended to be diurnal). When Himstedt's (1971) newts lived under constant light conditions, he too was unable to find any clear-cut rhythm in their pattern of activity. In Adler's (1969) experiments with the salamander *Plethodon glutinosus*, the animals became arrhythmic within a few days after the change-over to constant light conditions (darkness). At high latitudes at midsummer, when the nights become extremely light, the result has very often been that the animals, losing contact with the natural Zeitgeber, follow their own (free) endogenous rhythm, becoming desynchronized in the process; in this way members of such populations have acquired an arrhythmic activity pattern (Swade & Pittendrigh 1967, Müller 1968, 1970a, 1972, 1973, Erkinaro 1969a, Eriksson 1972, Solem 1973a).

Just before the newts (*T. vulgaris*) left the water, even a high degree of diurnal activity was seen. It is also well known that some species of fish and mammals on northern latitudes at certain times of the year change from nocturnal to diurnal activity or the other way (Erkinaro 1969b, 1972a,b, Müller 1970a,b, 1972, Andreasson 1972, Eriksson 1973, Solem 1973a,b, 1974a). Such a change in phase is often correlated with seasonal changes or shifts in habitat (Palmgren 1944, Nyholm 1965, Gwinner 1967, Lofts 1970, Erkinaro 1972b).

The result obtained for *T. cristatus* in Trøndelag is also affirmed by those obtained experimentally by Himstedt (1971). In both cases the activity of this species was more closely linked to the hours of darkness than that of *T. vulgaris*. The activity maximum either thus occur closer to midnight, or the activity around midnight is relatively greater than that of *T. vulgaris*.

Under natural conditions at the three localities in central and southeastern part of Norway, the larvae of both species of newts showed a distinctly diurnal pattern of activity. Himstedt (1971) obtained no unequivocal results about a diel pattern of activity by *T. vulgaris* and *T. cristatus* larvae. However, he found that the larvae were definitely more diurnal (percentually) than the adult newts. In addition, *T. vulgaris* larvae seemed to be more

diurnal than those of *T. cristatus*, which in fact tended to have a predominantly nocturnal pattern of activity. A diurnal activity pattern is to be expected, however, from the fact that *Triturus* larvae first achieve their full colour vision at an illumination intensity of 30 lux, compared to a value of 10 lux for the adults (Himstedt 1967, 1973), as also with positive phototaxis shown in general by Urodela larvae (Noble 1954, Schneider 1968, see also Salthe & Mecham 1974).

Maximum activity by the larvae was recorded before noon and again in the afternoon (or only around noon), the exact time probably depending on the prevailing weather conditions. As in Himstedt's (1971) experiments, all the larvae belonged to Glaesner's (1925) *Triturus* stadium 52-53. When the length of the night period in Himstedt's experiments was similar to that in Trøndelag, i.e. 6 hrs., however, his larvae can be seen to show small activity maxima during the same intervals of time, i.e. at 08.00-11.00 hrs. and 14.00-17.00 hrs., as found by me. This diel rhythm probably continues until the larvae have metamorphosed. According to Himstedt (1971), and also to Kalmus (1940), any previous larval periodism shown by *Triturus*, *Salamandra* and "axolotl" disappeared completely during metamorphosis, but after some weeks of terrestrial life, a diel rhythm reappeared, this time similar to that shown by adult newts.

The influence of temperature and humidity

At Vasseljemoen, terrestrial newts have been found to be quite inactive when the air temperature falls below 0°C (see Dolmen 1976b). In water, during the present investigations, distinct activity patterns were found at all registered temperatures (down to 5-6°C). According to Wolterstorff (1921) courtship may take place at temperatures as low as 6-8°C, and Smith (1949, 1964) states that newts, when hibernating under the ice-cover of ponds, still always eat some food during the winter. Probably a definite activity pattern therefore could be found at lower temperatures than observed by me. Although temperature does not usually control the activity pattern (Sollberger 1962), according to van't Hoff's generalization ($Q_{10} = 2-3$) one would expect it to be capable of modifying the magnitude of peak activity (Sweeney & Hastings 1960,

Cloudsley-Thompson 1961, Bünning 1972). In fact, and in agreement with the above postulate, in this study the first (evening) peak is always the most prominent, and the second (morning) peak, especially in the females, often is missing completely (cf. Figs 3 and 5, and Himstedt 1971). This is also the typical situation found in nocturnal animals (Aschoff 1957, see also e.g. Hagerman 1969). The newt larvae, likewise, are most active when the temperature is at its highest, i.e. in the after-noon (cf. Figs 7 and 8).

Quite in agreement with the picture achieved of the activity of terrestrial *T. vulgaris*, Joly (1959) observed that *Salamandra salamandra* never left its hiding-place before the relative humidity of the air had reached 90-100%. These values are normally only attained in the late evening and during the night in Trøndelag, although also during daylight hours after rainfalls, when terrestrial newts may be seen to move out of their hidings (cf. Jungersen 1907, Wolterstorff 1921).

According to Himstedt (1971) and Grüsser-Cornehls & Himstedt (1976) the length of the periods of activity of aquatic newts are much longer than those of terrestrial newts, since sunlight and drying present to threats when the newts are in the water.

Temporary changes in activity patterns

Populations of *T. vulgaris* and *T. cristatus* are quite arrhythmic in their activity and are even active by day at the finish, and to a certain extent probably also at the start of the aquatic season. In spring a diurnal habit, connected with a positive phototaxis, as in the fish *Lota lota* (see Müller's 1970b investigation), may possibly result in the newts staying in the warm, shallow-water, regions of the pond or tarn (see Hvass 1936), whereby they enjoy a maximum of warmth, at the time at which their gonads are starting to function. At the end of their aquatic phase, on the same principle, the newts will tend to move into shallower water and towards the shore. A negative phototaxis would be thought to bring the animals out to deep water. Under normal circumstances adult newts would be expected to be negatively phototactic. This has in fact been demonstrated to be the case for e.g. the adults of *Triturus* species (Czeloth 1931, Himstedt 1967).

Nevertheless, even adult newts exhibit a certain positive phototaxis under special conditions, as was shown by Muntz (1963) for *T. cristatus*. Moreover, Stier (1926) points out the fact that starved newts, *Diemyctylus (Notophtalmus) viridescens*, are negatively phototactic while well-fed ones are either positively phototactic, or indifferent to light. This may be one explanation for the diurnal nature of the activity pattern of newts after the end of the courtship period, as also for the characteristic basking, and also hovering of *T. vulgaris* in nature, when they are hunting small invertebrates in daytime in summer. Harker (1964) also states that an abundance of food, or starvation conditions, may effect the timing of the activity phases. Newts which are about to start their terrestrial phase are usually extremely well-fed. It is in this final stage of their aquatic phase one most often catches sight of *T. vulgaris*, basking below the water surface. This behaviour has previously been reported by Collett (1918), Ruud (1949), Ekman (1956), Kauri (1964), Høst (1967) and Hvass (1971).

Periodicity differences in relation to sex and species

The sex difference in the activity pattern of *T. vulgaris* is presumably a reflection of the difference in type of activity during the 24-hr. cycle.

Both sexes of both newt species have a red/orange belly, which presumably acts as a warning to predatory fish e.g. (*T. cristatus* is well known for secreting distasteful toxins from its skin; *T. vulgaris* is probably an example of mimicry, see Beebee 1980). Nevertheless, the fact that additional colour nuances of red and blue are seen in the courtship dress of *T. vulgaris* males, indicates that courtship behaviour is, at least to a certain degree, adapted to light conditions. Colour vision is well-developed in newts (see e.g. Diebschlag 1935, Freytag 1954, Muntz 1963, Kasperczyk 1971, Himstedt 1972, Himstedt & Fischerleitner 1974, Grüsser-Cornehls & Himstedt 1976). According to Himstedt (1967), the limit for colour discrimination by *Triturus* lies at about 0.001 lux. At 0.06 lux the retinal rods are still dominant in *T. vulgaris*, but at 0.6 lux the cones take over completely. The optimal visual ability of adult *Triturus*, however, occurs at a value of 10 lux and

upwards (Himstedt 1973), with a somewhat higher value for *T. vulgaris* than for *T. cristatus* (Birukow 1950). The courtship should therefore take place when not too dark.

Mertens (1960) also points out that the sexes in *Triturus* are differently coloured, and the courtship activity is thought to take place by day, since it is based on visual, as well as on olfactory, stimuli (see also Noble 1954 and Salthe & Mecham 1974). The present observations, however, more exactly indicate that the evening and morning hours are the preferred times for mating, i.e. the times of the two main activity periods of the males throughout the 24-hr. cycle. The females always are rather passive at the time of day at which the males start their courtship display; they very seldom actively seek out a male partner. Nor during this same period, do they enter the traps as frequently as the males.

The main activity of the females newts in spring is egg-laying, and according to observations by the author, egg-laying behaviour reaches its climax in the evening, or at night (thus agreeing with the findings of Mertens 1947 (for *T. cristatus*) and Freytag 1955).

Hunting for food also influences the activity patterns of both sexes. In aquaria, hunting especially occurs in the dark period. *T. vulgaris*, having the better vision of the two species (Himstedt 1967), to a great extent localizes its prey visually (Steward 1969); naturally, therefore hunting takes place when not too dark, i.e. in the evening and in the early morning. By the two different patterns of activity at this time of year, the males and females of *T. vulgaris* thereby perhaps manage to fill two slightly different niches in their habitat, which is advantageous for any animal living under crowded conditions when food is scarce, as frequently happens in northern latitudes.

In contrast to *T. vulgaris*, the courtship dress of *T. cristatus* males is quite sombre, except for the yellow/red on the belly. However, their tall, saw-toothed, crest gives the animal an impressive silhouette, and the white warts form a contrast superbly against the otherwise almost all-black skin. The retina of the eyes of *T. cristatus* comprises of a much lower percentage of cones and double-cones (60%) than that of *T. vulgaris* (87%). The eyes of *T. cristatus*, therefore, should be relatively more adapted to dark surroundings (Möller 1951). The individual newts ought therefore

to be able to see each other in relative darkness; and under the light conditions which prevail during the mating hours of *T. cristatus*, the body contour and contrasting white warts on the males should be evident to the females.

In the genus *Triturus*, both the visual and olfactory senses are used in courtship. Steward (1969) points out that for *T. vulgaris* the sense of smell is of greater importance than for other species of the genus (see also Himstedt (1967); vision is therefore probably of less importance, and in fact, a blind, aquatic, *T. cristatus* may be as good a hunter as any newt with normal sight (Cooke & Fulford 1971). Himstedt (1971) found that terrestrial *T. cristatus* was also more nocturnal in its habits than *T. vulgaris*.

The larvae of both *T. vulgaris* and *T. cristatus* show a pattern of activity which is basically different from that of the adults. This has a positive value as regards larval survival, because the adults of both species of newts are cannibalistic, and the aquatic phase of the adults lasts for quite a long time. The operation of this survival principle is best seen in the results for *T. cristatus* (compare Figs 5 and 8). During the period in which the adult newts are diurnal in their habits, cannibalism is avoided also to a certain extent by the selection of different microhabitats by adults and larvae.

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