INTER- AND INTRA-INDIVIDUAL VARIATION IN LIZARD VOLUNTARY TEMPERATURES

By

IAN F. SPELLERBERG AND NICHOLAS D. SMITH
Biology Department,
Southampton University.

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Lizards have variable body temperatures and they are basically ectothermic (Gordon, 1968). Recent experiments show that lizard voluntary temperatures (i.e., temperatures associated with normal activity) are species specific. The differences in voluntary temperatures in active reptiles and in thermal resistance may be ecologically isolating mechanisms between sympatric species (Licht *et al.* 1966). By far the most common reports on lizard voluntary temperatures are those which deal with body temperatures of animals immediately after capture in the wild (see Brattsrom, 1965); but there are few accounts of laboratory or experimental studies. This could be due to a disparity between laboratory and field values, which suggests a possible lack of ecological relevance and of reliability in the laboratory values obtained for lizard voluntary temperatures.

The present project was designed to investigate inter- and intra-individual variation of voluntary temperatures of *Lacerta sicula* and data were analysed for the presence or absence of regular diurnal (day and night) patterns in the temperature levels.

Previous research into lizard voluntary temperatures using thermal gradient chambers showed that the usual maintenance of high and characteristic body temperature levels of lizards may be abandoned at a time when the animals would normally seek shelter at night (Regal, 1967). Regal (1966) has furthered the work of Cowles and Bogert (1944), and it seems that the concept of the voluntary temperature is complex, because some lizards in captivity seek higher temperatures to assist peristalsis. Some lizard species may suffer marked spermatogenic damage and a decline in appetite and body weight if they are exposed to temperatures 1-2°C above their respective voluntary temperature ranges (Licht, 1965). This work emphasises the importance of voluntary temperatures in relation to ambient temperature ranges where reptiles are maintained for experimental or other reasons. Spellerberg (1974) found that the voluntary temperature levels of some lizards may be altered when they are exposed to different light intensity levels, indicating that a combination of light intensity and ambient temperature levels is important in reptile thermal ecology.

MATERIALS AND METHODS

Specimens of *Lacerta sicula* (average weight 6 grams) were obtained commercially, housed in a large vivarium for several weeks prior to experiments and fed meal-worm larvae, house flies and locusts.

The thermal gradient chamber was a metal box heated and cooled from below, providing substrate temperatures between 45°C and 5°C. Dimensions of the chamber were: Length 200cm; width 18cm; depth 33cm. No food was placed in the chamber, but water was available from each of three dishes, and the bottom surface of the chamber was kept moist. The apparatus was housed in a room exposed to normal day and night light conditions and this gave a light intensity reading at the bottom surface of 250 lux during the day and 0.1 lux during the night. Each lizard was attached to a Yellow Springs Instrument Co., 511 series thermistor probe, inserted through the cloaca into the large intestine. Body temperatures were recorded on a "Servoscribe" recorder. An adjustment period of about 24 hours preceded instrumentation and the experiment continued from 4 to 6 days and nights.

The investigation was divided into three sections:

1. Tests on four different *L. sicula* to investigate inter-individual differences in the voluntary temperatures;
2. Tests repeated four times at about two-week intervals on one individual *L. sicula* (No. 6) to investigate intra-individual differences in the voluntary temperatures;
3. Tests on the effect of providing shelter in the form of a wooden shelf 2cm above the substrate and extending over the whole temperature gradient.

Mean body temperature values for every 20 minutes were transcribed, then converted to percentage frequency polygons showing body temperature levels for the day and night periods.

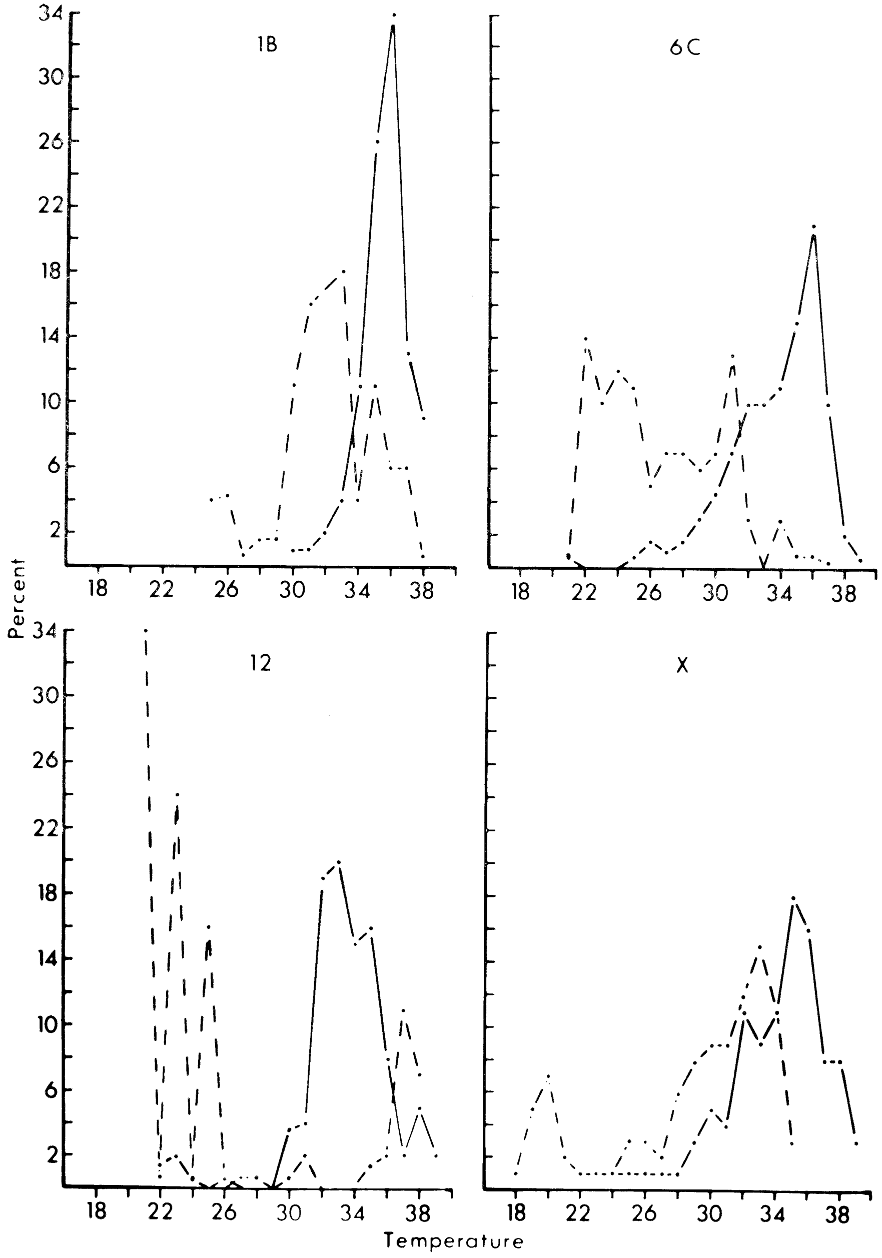
RESULTS

The extent of inter-individual variation is shown for four individuals in Figure 1. During the day (light period) there is a peak in frequency between 34°C and 37°C, a mode usually at 36°C and an abrupt fall in frequency at 38°C. There is little selection of temperatures above 38°C or below 29°C. At night (dark period) there is a consistent fall in temperature of 5°C to 7°C, coupled with a greater range. Mean temperatures during the day range from 33.3°C to 35.5°C (difference of 2.2°C) and at night they range from 25.9°C to 32.1°C (difference of 6.2°C). There is less variation in the upper limits of the temperature range than in the lower limits of both day and night temperatures. All the day frequency polygons are negatively skewed.

Figure 2 shows the results of four tests on one individual (No. 6). It can be seen that intra-individual variation in voluntary temperatures is about the same as the inter-individual variation, although the night temperatures seem to be slightly more consistent. The range of the means for the day temperatures is 3.7°C and the range at night is 3.9°C (Table 1). The negatively skewed pattern is present, as is the greater range of lower limits of the voluntary temperatures.

In two of the experiments, temperatures below 29°C were not recorded, and in several other experiments (for example No. 12 and No. X) there is a sharp fall in frequency at 28°C or 29°C. It was noted that temperatures below 29°C during the day occurred in the morning and evening but rarely, if at all, during the middle of the day. Temperatures at the former time tended to be erratic since the lizards did not begin their day time thermoregulation at the same time each morning, nor finish it at the same time each evening. For this reason, both an overall average day temperature (33.7°C) and the average of temperatures greater than 28.0°C (34.5°C) were calculated. They were also calculated for each individual (Table 1). The former figure is identical to that obtained by Licht *et al* (1969) from the same species. When low day temperatures are excluded the range of means for the inter-individual experiments is 1.7°C, and for the intra-individual experiments is 1.5°C. The overall average night temperature is 28.6°C.

Figure 3 shows the 24-hour cycle of temperatures for *L. sicula* (combined results) giving the average for each hour and one standard deviation of the experiment means. There is a relation between the voluntary temperatures and the photoperiod with a rapid rise in the morning temperatures


1B
6C
12
X
34
30
26
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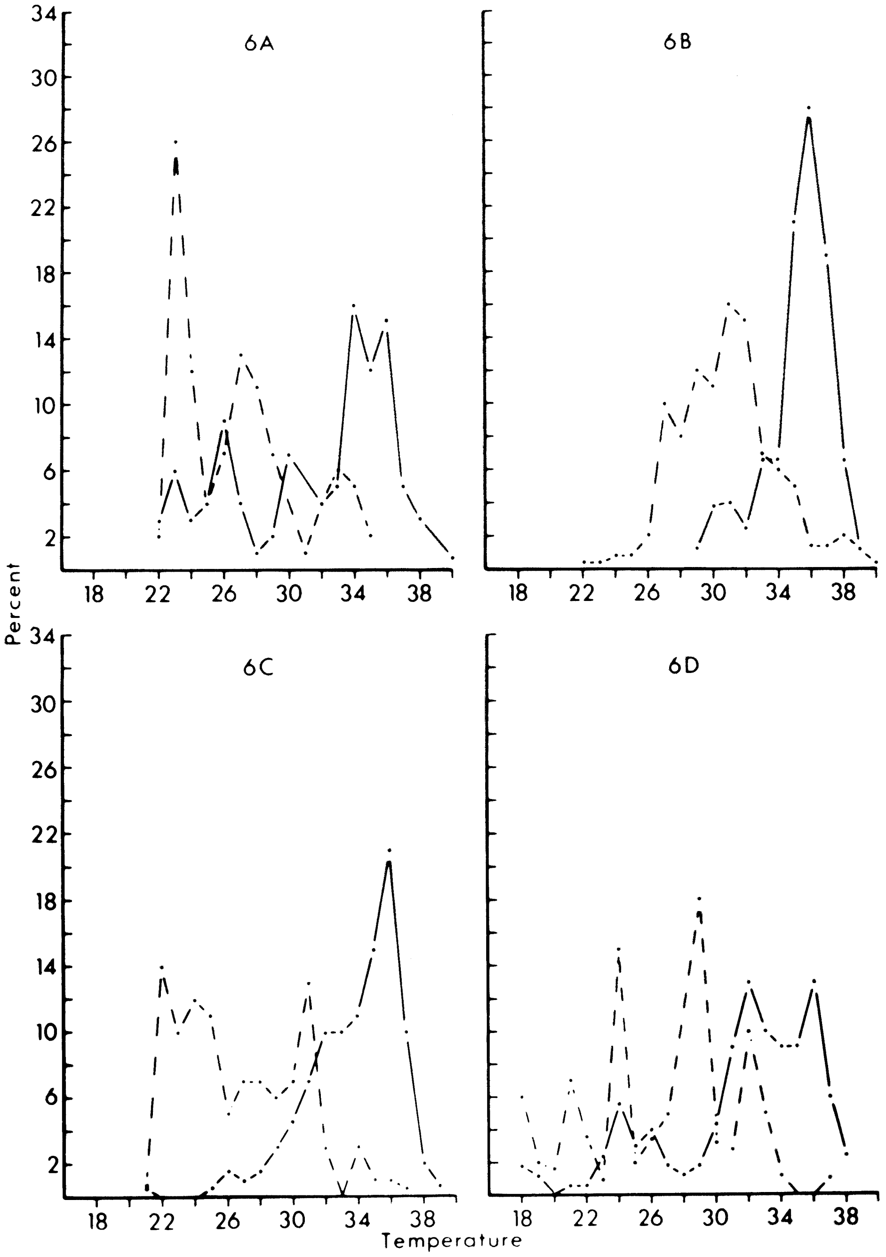
14
10
6
2
18
22
26
30
34
38
Percent
Temperature

FIG 1


6A
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34
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34
38
Percent
Temperature

FIG 2

to a peak just after midday. There is a rapid fall again just before the onset of the dark period, then a slow fall throughout the night to a minimum just before the onset of the light period. Between 09.00 hours and 16.00 hours the average temperature does not fall below 34°C.

Correlation coefficients of average day and night temperatures, against the average night (r_1) and day (r_2) temperatures were calculated for all specimens. It was found that: r_1 was 0.620, and was highly significant ($p<0.0005$); r_2 was 0.413 and highly significant ($p<0.005$); r_1 and r_2 were not significantly different ($p>0.10$). Day and night temperatures thus show a tendency to rise and fall together, but it seems that day temperatures do not influence night temperatures any more than night temperatures influence the level of the day temperatures. These results show a tendency for the lizards to eventually prefer more equable body temperatures, which is supported by the work of Licht (1968), using *Anolis carolinensis.*

The two tests with *L. sicula* No. 6 (incorporating a shelter) gave conflicting results. In the first test the lizard showed a slightly less obvious reaction to photoperiod, in comparison with the experiments where a shelter was not provided (Figure 4). During the day there is a much greater range of temperatures (12°C–41°C) than in all previous tests, with a very low average temperature (30.5°C). At night the body temperatures ranged up to 39°C but the average of 29.7°C is within the range of means previously obtained. In the second experiment the pattern reverted to that of the "no-shelter" tests with the day and night average temperatures being very similar to the overall averages for previous tests. The average temperature for each hour of the day tended to be low during the day but near the average at night, in the first test. In the second test they were in agreement with the temperature obtained in the absence of a shelter.

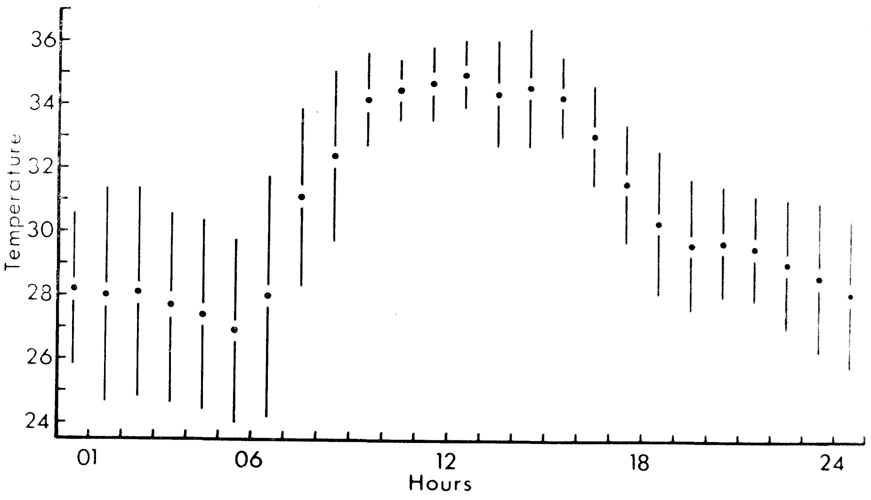

FIG 3

DISCUSSION

The results in Figure 3 support those data reported by Hoffmann (1955, 1957a, 1957b, 1959, 1960) who showed the activity in *L. sicula* and *L. agilis* is determined by photoperiod. Marx and Kayser (1949) also demonstrated the

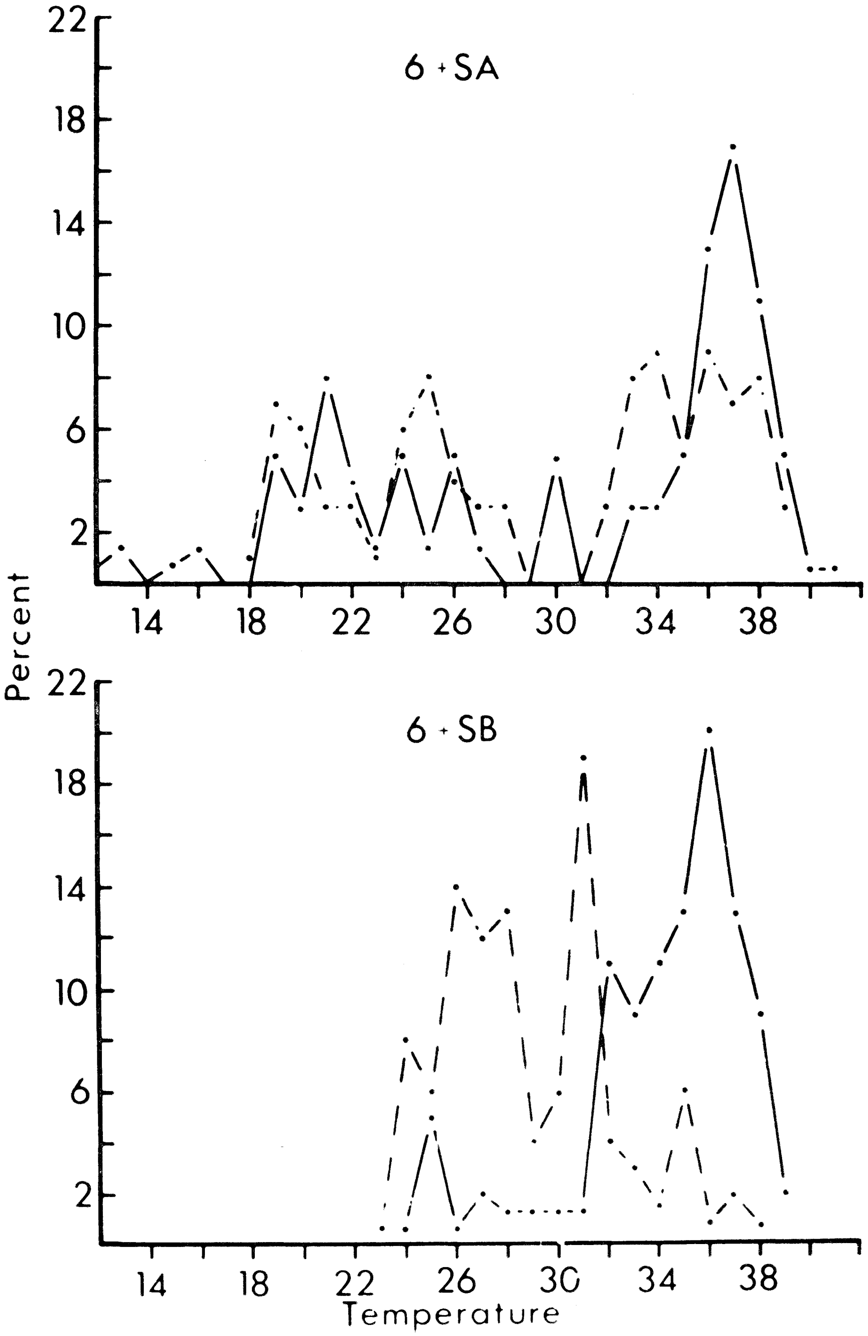

FIG 4

temperature independence of both *Lacerta muralis* and *L. agilis.* However Evans (1966) and Regal (1967) have shown that for some lizards the activity cycle is temperature dependent. Further work is required on this important aspect, but it is likely that evolutionary and ecological trends determine the differences in the thermal behaviour of lizards.

The significance of the negatively skewed temperature frequency polygons has been noted by De Witt (1967) for *Dipsosaurus dorsalis.* Since physiological activity has a direct exponential relationship to temperature in reptiles, a temperature frequency distribution must be negatively skewed. DeWitt used the median temperature and 68 percent of the range to describe this distribution. The median day temperature of *L. sicula* (all results) was 34.1°C; the central 68 percent limits were 30.4°C and 36.0°C (difference of 5.6°C). When temperatures less than 29.0°C were excluded, the median became 34.5°C (i.e. equal to the mean) and the 68 percent limits were 31.5°C and 36.1°C (difference of 4.6°C). These latter figures compare favourably with DeWitt's (1967) range of 4.0°C for *D. dorsalis* (median 38.5°C, 68 percent limits 36.1°C to 40.1°C). Unfortunately, unless temperatures less than 29.0°C are excluded, this method does not give a true representation of the thermoregulatory behaviour of *L. sicula* because of the considerable time spent in transition from night to day and day to night temperature levels. The consistently high temperatures between 09.00 hours and 16.00 hours, which do not rise above 35.0°C probably represent the normal activity of the lizard on a day with optimum weather conditions. Since so few temperatures below 29.0°C were recorded during this period it is not surprising that the average temperature is 34.5°C, equal to the mean and median of all temperatures above 28°C during the day.

The median night temperature was 28.6°C (again equal to the mean) with the central 68 percent limits at 22.8°C and 32.5°C (difference of 9.7°C). This again shows that there is a greater variability in the night temperature.

Of the two experiments where a shelter was provided the results from the first deviate from all other results. The reasons for this are not apparent; hopefully it is a reflection of abnormal behaviour. In the second test the results agree well with the previous results and it is suggested that the provision of a shelter has little effect on the lizard voluntary temperatures. If this is correct then lower voluntary temperatures at night are independent of available shelter, and, in laboratory temperature gradients, are dependent on the photoperiod.

The phenomenon whereby lizards select lower body temperatures at night has been discussed by Regal (1967) and Spellerberg (1974). With reference to *L. agilis* and *L. viridis,* Spellerberg (1974) concluded that the onset of the dark period acts as a signal for the lizard to submerge, and this act is coupled with a voluntary decrease in body temperature. It has been shown here that the provision of a shelter is unlikely to have any additional effect. In natural conditions, shelter is of great importance to the animal during the night period, as protection against predation and critical minimum or sub-lethal temperatures. Retreating to a shelter and the lowering of the lizard's body temperature at night (or during the inactive period) would seem to be separate activities, but are a common consequence of the dependence of the animal on photoperiod for its diurnal cycle.

The mean intra-individual difference for the critical minimum temperature of *L. sicula* is 0.5°C with a range of 0.0°C to 1.3°C for 85 tests (Spellerberg, 1973). The variation of the mean voluntary temperature is large when compared to the variation in the critical minimum temperature. This situation presents a problem when attempts are made to compare the voluntary temperatures of different lizard species, and it would seem that the mean preferred

temperature (MPT) has little value as a comparative index in reptile thermal ecology because the MPT presumes a normal distribution if it is presented as the MPT ± one standard deviation.

Further research is needed in order to assess the reliability and use of the voluntary temperature as determined in the laboratory. Preliminary investigations into one European snake species (*Coronella austriaca*) indicate that laboratory determined voluntary temperatures can be very similar to the voluntary temperatures taken from many different specimens in the field (Spellerberg & Phelps, 1975).

The voluntary temperatures selected by *L. sicula* are shown to be characteristic of a small lizard with a shuttling heliothermic method of behavioural thermoregulation. Comparable results have been obtained for other small heliothermic lizards, such as *Eumeces fasciatus* (Fitch, 1954, 1956). The thermoregulatory activities described above are of great importance in the lizard's ecology and further work could relate voluntary temperatures in the laboratory with the lizard's normal activity in the wild.

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TABLE 1

Lacerta sicula voluntary temperatures °C.

Lizard Number	*Night temperatures* mean	*Night temperatures* range	*Day temperatures* mean 1.	*Day temperatures* mean 2.	*Day temperatures* range
1B	32.1	25-38	35.5	35.5	30-38
12	25.9	21-38	33.3	33.8	22-39
X	29.1	18-35	34.2	34.5	25-39
6C	26.7	21-37	33.7	34.1	21-39
6A	26.7	22-35	31.5	34.4	22-40
6B	30.6	22-38	35.2	35.2	29-40
6D	26.7	18-34	31.5	33.7	18-39
6+SA	29.7	18-39	30.6	36.3	12-41
6+SB	28.9	23-38	34.1	35.0	24-39

Day temperatures: mean 1 = all temperatures included;
mean 2 = temperatures less than 29°C. excluded.
Intra-individual values taken from lizards 1B, 12, X, 6C.
Inter-individual values taken from lizard 6C, 6A, 6B, 6D.
Other values (6+SA and 6+SB) are for conditions with a shelter.

EXPLANATION OF TEXT FIGURES

FIGURE 1.
Inter-individual temperature frequency polygons for different *Lacerta sicula* in thermal gradients. Solid lines represent temperatures during the light period, broken lines represent temperatures during the dark period.

FIGURE 2.
Intra-individual temperature frequency polygons for one *Lacerta sicula* in a thermal gradient. Graphs as in Figure 1.

FIGURE 3.
Daily temperature cycle for *Lacerta sicula*, showing means and one standard deviation of means.

FIGURE 4.
Voluntary temperatures for *Lacerta sicula* where a shelter is provided in the thermal gradient. Graphs as in Figure 1.

SPAWN CLUMPS OF THE COMMON FROG *RANA TEMPORARIA*: NUMBER OF OVA AND HATCHABILITY

By

A. S. Cooke
Monks Wood Experimental Station, Abbots Ripton,
Huntingdon.

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INTRODUCTION

In 1898, Boulenger noted that the number of ova in spawn clumps of the common frog (*Rana temporaria*) had been found to be:

Observer	*Number of clumps counted*	*Number of ova per clump*
Greening	Not stated	Range: 1500-2500
Heron-Royer	Not stated	Range: 2856-4005
Boulenger	5	1155, 1188, 1584, 1744, 2044 Mean ± S.E. = 1540 ± 170

Spawn examined by Heron-Royer was French in origin, while that studied by Boulenger and Greening appears to have been from Britain. Since then no one in Britain seems to have recorded the number of ova in spawn clumps. Neither of the standard works covering the life history of the frog in Britain (Savage, 1961; Smith, 1969) contains additional information. This paper describes the examination in 1973 of seven spawn clumps in order to indicate (1) the number of ova in contemporary clumps, (2) the reliability of a simple technique for estimating the number of ova and (3) percentage hatchability.

METHODS

Six spawn clumps were collected from St Neots Common in Huntingdonshire and one was taken from a stock pond at Monks Wood. Because the sites were visited regularly and because the spawn clumps were judged to have been only partially swollen when collected, the date of lay of each clump was known to within a day. Except when the numbers of ova were being estimated or counted in the laboratory, clumps were kept out of doors in separate tanks containing 4-5 litres of aged tap water. Four or five days after the spawning date, the number of ova in each clump was estimated as follows. The whole clump was placed in a net to remove surplus water and then its volume was determined in a measuring cylinder. A small part, usually consisting of 50-100 eggs, was gently detached from the clump; its volume was measured and the number of ova counted. Thus, by simple proportions the total number of ova in the clump was estimated to be equal to:

$$\frac{\text{The number of ova in the detached part x volume of the total clump}}{\text{volume of the detached part}}$$

For each spawn clump, within two days after the last tadpole hatched, counts were made of the total number of tadpoles and the number of ova that failed to hatch.

RESULTS

Results are given in Table 1. The total number of ova, based on the counts, ranged from 1067 to 1608 (Mean ± S.E. = 1329 ± 68). Estimates of the numbers of ova were within 20% of the counts for each clump, the estimated mean being only 2% lower than the actual mean.