BRITISH JOURNAL OF HERPETOLOGY

Vol. 5 No. 5 December 1975

Published by
THE BRITISH HERPETOLOGICAL SOCIETY

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CHANGES IN STATUS OF THE GREAT CRESTED NEWT *TRITURUS CRISTATUS* IN THE BRITISH ISLES

By

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(*Received* 5/7/74)

INTRODUCTION

The Great Crested or Warty newt, *Triturus cristatus,* occurs throughout Europe except in the south west, where it is replaced by *Triturus marmoratus,* and north of latitude 67° in Scandinavia. Of the four recognised subspecies, the typical or northern form *T. cristatus cristatus* is found in Britain (Steward, 1969).

The distribution of the Great Crested newt in Britain has been investigated previously (Taylor, 1948, 1963; Arnold, 1973). In general, the species is well recorded in England; much less often from Wales and Scotland; it is apparently absent from most of the Hebrides, all Ireland, the Isle of Man, Orkney and Shetland.

Due to the decreasing frequency of observations of *T. cristatus* by field workers, an investigation of the situation is warranted (Beebee, 1973). For this reason a study was undertaken to determine whether significant changes in status of the Great Crested newt have indeed occurred.

METHODS

The survey was conducted by the distribution of questionnaires, which were sent to as many field observers or other persons considered likely to have relevant information. Those who received questionnaires were: (1) People contributing regularly to the Biological Records Centre; (2) All members of the British Herpetological Society resident in Britain; (3) Miscellaneous other sources. Two or three forms, each designed to secure information from a single geographical area, were supplied to each recipient. No size limits were imposed on the area. 605 people received 1,390 forms and 207 recipients (34%) made some attempt at reply; of these replies, 142 forms contained sufficient data for worthwhile analysis. In addition, requests for information were circulated by the Scottish Wildlife Trust, by publication in the North Wales Naturalists' newsletter, and to Nature Conservancy Wardens.

The questionnaire was designed to determine: (1) The current abundance of *T. cristatus* relative to other newt species; (2) Whether the population size has changed; (3) Fluctuation and types of breeding sites; (4) Whether changes are confined to *T. cristatus*; (5) Reasons for any changes.

RESULTS

1. Relative abundance of *Triturus cristatus.*

Britain was arbitrarily divided into 9 areas (*Figure 1*). The numbers of usable forms returned are also shown (in brackets). Wales was particularly poorly represented, and the meagre data in most cases were of little use.

Paucity of herpetological records in remote areas probably correlate with the small number of observers rather than the abundance of the species. Therefore the questionnaire asked for the abundance of Great Crested newts relative to the smaller species, in order to gain a more accurate impression from the few available records. Very few areas of Britain do not contain sizeable populations of either *Triturus vulgaris* or *T. helveticus*, and this comparison should allow some estimation of the absolute numbers of *T. cristatus*. The results obtained were compared with the proportion of total records at the Biological Records Centre which were for crested newts in each of the regions since 1960 (Arnold, 1973).

From *Table 1* it is apparent that by the first criterion *T. cristatus* occurs with the frequency: East Anglia > Central and S.E. England > London and N.E. England > N.W. and S.W. England > Wales and Scotland. The general preference of the species for southern and eastern regions was confirmed by the B.R.C. data, though details differed and in particular East Anglia was relatively less important.

These results were not unexpected since *T. cristatus* throughout its range is a lowland species (Steward, 1969).

2. Changes in status.

Changes of status were examined pre-1960, 1961-1970 and post-1970, and quantified by the use of an Index of Change (See Cooke, 1972, for common frog and toad) defined as:

$$\frac{\text{Number of increases recorded} \quad - \quad \text{Number of decreases}}{\text{Total Number of records (Including those for no change)}}$$

This ratio was determined for each area and time period (*Table 2*).

The general trend clearly shows an accelerating decrease in all areas except East Anglia and possibly the north east. The decline apparently began prior to 1960 in East Anglia, Central and south western regions, elsewhere in the 1960s except possibly for Scotland where little change was recorded. East Anglia is unique in running against the general trend, the decline easing off since the 1950s.

The information, however, provides only a broad indication of the relative severity of declines between areas and cannot distinguish between recordings of slight and major changes of status. To overcome this problem information was obtained on changes in absolute numbers of breeding sites.

3. Breeding sites.

The sites considered were: Those on agricultural land, garden ponds and assorted other areas (See Cooke, 1972a). The numbers of sites were compared pre-1965 and 1966 onwards (*Table 3*). Only data which covered both time periods were used in this assessment.

The results indicate that in the past, ponds on agricultural land provided the largest numbers of breeding sites for *Triturus cristatus*; these have declined by over 75% in recent times. Other miscellaneous sites have also declined but garden ponds have remained fairly stable. Throughout the country there is an overall decrease in crested newt breeding sites of the order of 50% during the time examined. On a regional basis, several areas have suffered in a generally similar fashion; Scotland and London experienced lower than average declines, whereas that in central England was much higher. The relative importance of garden ponds has risen from 10% to 20% of the total national sample.

4. Changes relative to other species.

The question whether changes in status of the Great Crested newt were confined to that species alone or were a general feature of British newt populations was investigated. (*Table 4*). Whereas in Scotland, Wales and north east England the situation has apparently been coincidental for all species, elsewhere the crested newt has declined preferentially especially in the south east. There was no indication from the data of any selective decline of *Triturus helveticus*, a possibility suggested elsewhere (Prestt, Cooke and Corbett, 1974).

5. Causes of changes.

The frequency with which reasons for status changes were proposed by informants is shown in *Table 5*. Destruction of breeding habitat was clearly considered most important, but many of the activities shown would also interfere with terrestrial habitat. Suburban development included road and house building; agricultural changes mainly related to the trend from dairy to arable farming and consequent drainage alterations but also included increased water abstraction and creation of trout lakes. Rubbish dumping during the creation of tips was a surprisingly frequent reason; pollution was mainly from oil, rubbish dumping and pesticide and fertiliser run-off.

DISCUSSION

Fundamental to any consideration of these data is the validity of extrapolation to national levels. It is difficult to conceive an alternative method for collecting the types of data required, and this is the major justification of the approach. The potential sample size was limited by the ease with which inexperienced observers mistake the male *Triturus vulgaris* in breeding attire for *T. cristatus*. School sources (see Cooke, 1972a) were therefore precluded. The reports by the experienced field workers and recorders should however result in greater accuracy of information when reasonable sample sizes can be achieved. Data were obtained from a number of breeding sites comparable with that used by Cooke (1972a) with common species, though he made more detailed studies on individual sites. Many of the problems inherent in this kind of survey are discussed by Cooke.

It may be possible to project sample size to absolute numbers of crested newt breeding sites. Cooke (*Pers. comm.*) estimates approximately 100 sites in Huntingdonshire, i.e. about 0.3 per square mile. This county, in eastern central England near East Anglia, is an area where *T. cristatus* is relatively abundant. An area of similar extent in N.W. Surrey/N.E. Hampshire has a far lower ratio, around 0.015. Although *T. cristatus* is fairly common in the S.E. region generally (Table 1), it is scarce in this particular zone. If the national average lies somewhere between these figures, calculation reveals that the survey may reveal up to 3% of the total English breeding sites, which would certainly be a reasonable sample on which to ascertain status changes.

Most areas have suffered declines in their crested newt populations which have accelerated to alarming proportions. Lowland areas of England, where the species is most abundant, have suffered more than remote highland districts. East Anglia is an apparent exception to this trend, which may be correlated with the large number of garden breeding ponds in that area. However, the extent of breeding habitat loss is apparently similar in many English regions when total numbers of sites are considered. The greatest reduction was of ponds on agricultural land, though other miscellaneous sites also were considerably reduced in the time examined.

Relative to other newt species, it is apparent that crested newts have suffered preferentially. This difference was particularly marked in the south east.

The data on breeding sites, if truly random, indicate that in absolute terms the number of crested newt sites in England has diminished by at least 50% since 1966. It may well be argued that sites more conveniently situated, close to habitation, would be better known and perhaps more likely to be destroyed. This could indeed influence the decline to some extent, but examination of the data suggests such effects may be minimal. The greatest declines were noted on agricultural land, which in most areas of England includes the most remote ponds. Lack of knowledge of such ponds may tend to underestimate the decline since these sites are affected by overall farming policy irrespective of proximity to urbanisation.

Human interference of some sort was considered the most important cause of decline; suburban development the most popular. A large number of sites have been lost due to the creation of refuse tips. Agricultural changes are also clearly significant, the trend towards arable farming being accompanied by drainage alterations, increased use of chemicals and destruction of suitable terrestrial habitat. Such changes are particularly marked in the Fens and river valley marshes in East Anglia, Lincoln, Kent and Sussex. Adverse effects on amphibian populations have been documented (Menzies, 1962; Cooke & Ferguson, 1974). Newt populations in the interconnecting network of drainage dykes are almost impossible to estimate and it is this habitat as well as the more familiar farm ponds which is in danger of disappearing.

Pollution included suspected effects of fertiliser eutrophication and pesticides and may have been significant with some amphibian populations (see Hazelwood, 1970; Cooke, 1972a, 1972b). Indirect effects, by reducing available food or cover, could be more important (Cooke, 1974). Other pollution factors were those from oil and refuse.

Some sites have been lost by the infilling processes of natural plant succession. All may not be permanent since low rainfall for several successive years has, presumably temporarily, reduced the level of water tables throughout the country.

Collection by both professionals and amateurs was also considered an important factor in the declines.

One possible reason not emphasised in the survey is road mortality, particularly during spring migrations. That it can occur to a considerable extent is documented by Smith (1954).

In the very few instances where increases of *T. cristatus* were reported, these were almost invariably attributed to garden ponds, though the lack of predators in such environs may also contribute. In one instance only, flooding of an old gravel working was observed to provide new habitat; this was temporary, and when the water depth increased beyond a certain point the newts deserted it. The often stated preference of *T. cristatus* for deeper water may thus be an exaggeration; in some cases it is clearly not operative, and the species is able to breed in garden ponds.

The evidence therefore suggests that the Great Crested newt has declined dramatically in recent years, particularly in lowland England. Its status may have changed much less in Wales and Scotland, where it has always been rare. That it has declined relative to the other newt species suggests that it is more fastidious in its habitat requirements, probably less able to adapt to the very small areas of water which the smooth and palmate newts can tolerate. An additional factor, perhaps explaining the large relative difference in the south east, could be selective collection. Extinction on a local scale is already occuring and it is hoped that action taken now to stabilise crested newt populations may avert a repeat of the dramatic decline of the natterjack toad *Bufo calamita* in England in recent years.

CONSERVATION

In the light of the information presented, it is relevant to suggest ways in which the decline of crested newt populations might be arrested.

1. A continuation of data collection, surveying and ecological research relating to this species should be carried out to form a sound basis for further action.

2. Habitat destruction, especially from suburban development, rubbish dumping and some pollution, could be reduced if there was liaison between herpetologists and local authorities, perhaps through the regional officers of the Conservation Committee. To be effective, information on the localities of breeding sites should be compiled by the Conservation Committee and distributed to the regional officers. Ideally, liaison should ensure that planning departments are made aware of site importance as early as possible in any proposed developments. Such activities should be co-ordinated with the Nature Conservancy Council and Local Naturalists' Trusts, with a view to the creation of " Sites of Special Scientific Interest " and local nature reserves. While it would be idle to suppose that local authorities will attach high priority to newt sites, conservation might be achieved where ready alternatives for development can be demonstrated. The Committee would therefore welcome the receipt of such site information.

3. It is difficult to propose any meaningful conservation measures regarding farming policy. Where sites are identified on farming land it would seem valuable to point out their herpetological value to farmers; at least the non-essential infilling of ponds could thus be discouraged. The pest-controlling potential of amphibians can be emphasised.

4. With regard to natural succession, restoration can often be achieved by Conservation Corps or other voluntary bodies.

5. The sale of *Triturus cristatus* should cease to be legal. It may be unrealistic to urge that all amateur collecting should stop, but some recommendations should be stressed: anyone keeping crested newts should make do with the minimum number, normally one pair kept under conditions where breeding is possible, and the adults should be released after spawning. Larvae could be reared to metamorphosis and then released. This combines the most interesting way of keeping amphibians, i.e. permitting observation of the breeding cycle, with a worthwhile conservation effort. However, keeping crested newts under non-breeding conditions should cease and all forms of captivity should normally be avoided. The Countryside Code, approved by the Nature Conservancy and County Naturalists' Trusts, specifically condemns the abstraction of wild specimens of any species for captivity (see Code reference).

ACKNOWLEDGEMENTS

Thanks are due to: those people who contributed to the survey; Dr. Henry Arnold for access to B.R.C. informants; Mrs. Monica Green; Mr. Mike Penn; Mr. David Harvey; Mr. P. Hope Jones; Dr. Alastair Sommerville;

members of the Conservation Committee for their support, especially Keith Corbett and Dr. Arnold Cooke who read the manuscript and offered advice. I am grateful to the World Wildlife Fund (Grant No. 15/73 (P)) for financial support.

REFERENCES

ARNOLD, H. Ed. (1973). Provisional Atlas of the Amphibians and Reptiles of the British Isles. Biological Records Centre, Abbots Ripton.

BEEBEE, T. J. C. (1973). Observations concerning the decline of the British Amphibia *Biological Conservation*. **5**, 20-4.

CODE TO PROTECT WILDLIFE. *Conservation Review* (1974). **8**, 8.

COOKE, A. S. (1972a). Indications of recent changes in status in the British Isles of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *J. Zool. Lond.* **167**, 161-178.

COOKE, A. S. (1972b). The effects of DDT, dieldrin and 2, 4-D on amphibian spawn and tadpoles. *Environ. Pollut.* **3**, 51-66.

COOKE, A.S. (1974). Misfortunes of the British frog. *Field* **244**, (6314), 170-1.

COOKE, A. S. & FERGUSON, P. F. (1974). The past and present status of the frog *Rana temporaria* and the toad *Bufo bufo* in Huntingdonshire. *Rep. Hunt. Fauna Flora Soc.* **26**, 53-63.

HAZELWOOD, E. (1970). Frog pond contaminated. *Br. J. Herpet.* **4**, 177-84.

MENZIES, J. I. (1962) The marsh frog (*Rana ridibunda* Pallas) in England. *Br. J. Herpet* **3**, 43-54.

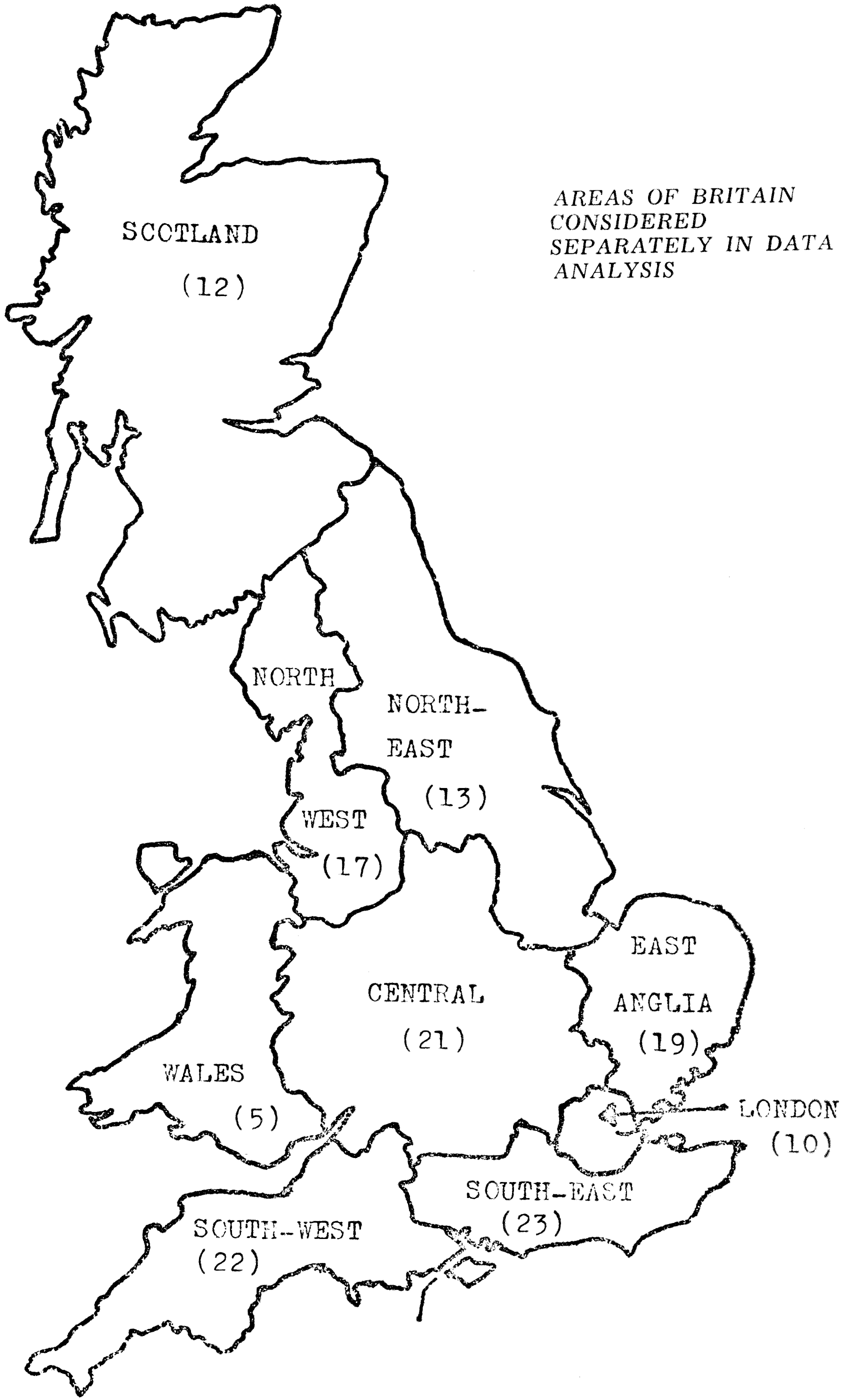
PRESTT, I., COOKE, A. S. & CORBETT, K. F. (1974). British Amphibians and Reptiles (Ed. D. L. Hawksworth). *Systematics Association Special Volume*. **6**, 229-54.

SMITH, M. A. (1954). *The British Amphibians and Reptiles*, 2nd Edn. Collins, London.

STEWARD, J. W. (1969). *The tailed amphibians of Europe*. David & Charles Ltd., Newton Abbot.

TAYLOR, R. H. R. (1948). The distribution of reptiles and amphibia in the British Isles, with notes on species recently introduced. Br. J. Herpet. **1**, 1-38.

TAYLOR, R. H. R. (1963). The distribution of amphibians and reptiles in England and Wales, Scotland and Ireland and the Channel Islands: a revised survey. *Br. J Herpet.* **3**, 95-115.



AREAS OF BRITAIN CONSIDERED SEPARATELY IN DATA ANALYSIS

FIGURE 1

TABLE 1
REGIONAL ABUNDANCE OF *TRITURUS CRISTATUS*

District	RELATIVE TO OTHER SPECIES Number of recordings showing *T.C.* to be: Less	Equally Abundant	More	Ratio Equ + More Less	% OCCURRENCE IN BRC RECORDS
SCOTLAND	11	1	0	0.09	3
N.W.	15	0	2	0.13	18
N.E.	8	2	0	0.25	15
WALES	2	0	0	0.00	2
CENTRAL	16	4	1	0.31	27
E. ANGLIA	10	6	2	0.80	22
LONDON	8	1	1	0.25	27
S.E.	18	4	1	0.28	22
S.W.	19	1	2	0.15	12

TABLE 2
CHANGES IN STATUS OF *TRITURUS CRISTATUS*

Figures in brackets illustrate the percentage of informants with data for each area and time period

District	Pre 1960	Index of change 1961–1970	Post 1970
SCOTLAND	0 (33)	0 (78)	—0.20 (100)
N.W.	0 (55)	—0.30 (85)	—0.36 (95)
N.E.	0 (67)	—0.67 (100)	—0.57 (74)
CENTRAL	—0.10 (50)	—0.44 (80)	—0.58 (95)
E. ANGLIA	—0.25 (28)	—0.18 (77)	—0.15 (93)
LONDON	0 (10)	—0.33 (90)	—0.37 (80)
S.E.	0 (33)	—0.49 (98)	—0.56 (95)
S.W.	—0.08 (52)	—0.37 (92)	—0.48 (98)

TABLE 3
BREEDING SITES OF *TRITURUS CRISTATUS*

District	Numbers of breeding sites post 1966. Bracketed figures are up to 1965. Agricultural ponds	Garden ponds	Other sites	% drop in No. of total sites
SCOTLAND	1 (1)	2 (2)	2 (2)	0
N.W.	5 (14)	2 (4)	12 (13)	40
N.E.	12 (20)	0 (0)	12 (20)	40
CENTRAL	13 (123)	4 (6)	21 (26)	76
E. ANGLIA	8 (14)	20 (19)	8 (27)	40
LONDON	8 (10)	5 (5)	9 (13)	22
S.E.	11 (31)	9 (6)	28 (41)	40
S.W.	9 (14)	4 (4)	20 (29)	30
TOTALS	67 (227)	46 (46)	112 (171)	

TABLE 4
RELATIVE CHANGES OF NEWT POPULATIONS

District	Number of recordings of: Coincidental status change	Selective decline of *T. cristatus*	Selective increase	Index of change
SCOTLAND	11	0	0	0
N.W.	12	4	1	—0.18
N.E.	10	0	0	0
WALES	2	0	0	0
CENTRAL	15	6	0	—0.29
E. ANGLIA	16	2	1	—0.05
LONDON	8	2	0	—0.20
S.E.	11	11	0	—0.50
S.W.	16	6	0	—0.28

CAUSES OF STATUS CHANGES

TABLE 5

Habitat Destruction directly due to Human Activity

District	Surburban development	Agricultural changes	Rubbish dumping	Pollution	Total	Natural Succession & Climate	Collection
SCOTLAND			No data				
N.W.	5	0	2	2	9	2	5
N.E.	4	2	1	2	9	0	1
WALES			No data				
CENTRAL	6	4	5	8	23	3	6
E. ANGLIA	3	2	3	3	11	2	2
LONDON	6	3	1	1	11	0	0
S.E.	6	3	2	2	13	3	3
S.W.	7	3	3	2	15	3	3
TOTALS	37	17	17	20	91	13	20

THERMAL RELATED ACTIVITY IN THE MESOAMERICAN LIZARD *GERRHONOTUS MONTICOLUS*

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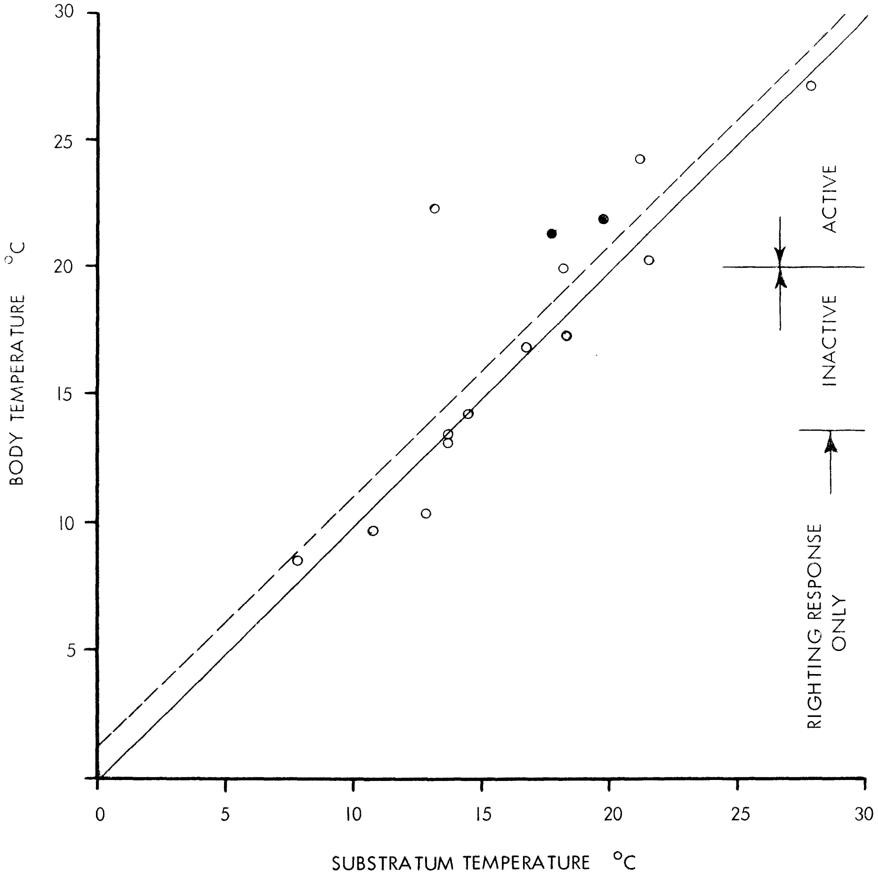
INTRODUCTION

The gerrhonotine lizards comprise an assemblage of over forty species and subspecies ranging from British Columbia to Panama. In the considerable literature relating to temperature requirements or thermoregulation among lizards there are few references to members of this group (see Brattstrom, 1965, and Cloudsley-Thompson, 1971, for compilations and reviews). No previous studies have reported on any aspect of the thermal ecology of tropical species.

FIGURE 1



Gerrhonotus (Barisia) monticolus is restricted to the montane regions of Costa Rica and Panama. In Costa Rica this lizard occupies the higher elevations (above 1,800m) of the Cordillera Central and Cordillera de Talamanca characterised by the Tropical Moist Lower Montane Forest, Tropical Wet Lower Montane Forest and Tropical Montane Rain Forest life zones of Holdridge (1967). Observations treated in this paper were obtained from a population inhabiting the Cerro de la Muerte, Cordillera de Talamanca between September 1961 and July 1963. Details of the climatic regimen and dominant vegetational components of this area have been previously reported (Vial, 1968).

METHODS

These secretive and relatively slow moving lizards were easily collected by a little cautious stalking and a quick hand grasp. Temperatures were taken with a Schultheis rapid reading small animal thermometer. Body temperatures were obtained at time of capture. While holding a hind foot, the entire thermometer bulb was inserted into the cloaca and read at stabilisation. If the animal had been markedly stimulated by collecting activity or if the thermometer did not stabilise within 15 seconds, the reading was discarded. Surface temperatures at the point of first sighting were recorded mostly during overcast conditions, but otherwise were shaded from direct radiation. The thermometer was held horizontally and pressed into the soil until only the uppermost surface of the bulb was exposed. Air temperatures (at 2cm above ground surface) above the sighting point were read in the observer's shadow.

RESULTS

G. monticolus is common in the area, if not abundant. It retreats beneath moss, rocks and logs during periods of inactivity. Upon emerging it will bask on the surface until becoming active. Active lizards were seen most frequently at the base of shrubby, relatively open vegetation, or in mats of moss, lichens or grass. They were rarely sighted among cleared or rocky areas. Except when basking on a log or rock (at levels never more than about 0.5m) the animals were entirely restricted to the ground surface in their movements.

Reliable temperature records were obtained from lizards captured between elevations of 2,780m and 3,210m. All months were represented in the sampling period. Daytime substratum and air temperatures at 2cm (in parenthesis) ranged from a minimum of 9.2°C (8.2°C) in May to a maximum of 39.0°C (37.2°C) in April. The rate of change could be striking on occasion as, for example, between 0730 and 0930 (GMT—6) hours on January 27, 1962 when temperatures rose from 11.6°C (12.4°C) to 23.2°C (19.2°C). Night-time temperatures were recorded as low as 0.4°C (-0.2°C) and 3.4°C in the microhabitat.

Body temperatures for *G. monticolus* ranged from 8.6°C to 27.2°C (mean 17.5°C, N=15). Below 13.6°C animals were capable of a righting response when placed on their dorsum, but not even a minimum escape effort was shown. Between 13.6°C and 20.1°C no lizards were active. Basking behaviour was noted for two emerging individuals at temperatures of 21.8° and 22.0°C. The lowest temperature observed for an active lizard was 20.2°C and all records above this level (maximum 27.2°C) were from active (or basking) animals (mean 23.0°C, N=6). The maximum substratum—air temperatures at which *G. monticolus* was observed (without a body temperature record) were 28.0°C (24.2°C), whereas the lowest were 7.8°C (7.4°C).

Correspondence of body and substratum temperatures are plotted in Figure 1. The regression coefficient of 0.98 produces an essentially parallel alignment of the body-substratum isothermal and regression lines. Thus, body temperatures correlate significantly (r=0.85) with those of the substratum although, as would be expected because of exposure and behaviour prior to observation, variations are more extreme among the active animals than inactive ones.

Because of the wide range of temperatures occurring within short periods on the Cerro de la Muerte *G. monticolus* does not hibernate, but demonstrates irregular periods of dormancy entirely dependent on the temperature regime. These lizards were inactive between dusk and dawn. Although numerous all night studies were made at regular intervals throughout the year, substratum air temperatures never attained the minimum level at which activity was observed in daylight hours.

No colour changes were ever expressed by any individuals nor were thermal responses different between the reportedly dichromatic sexes (Taylor, 1956; Walters, 1953) throughout the range of observations.

DISCUSSION AND CONCLUSIONS

Although Brattstrom (1965) categorises the species of *Gerrhonotus* as diurnal-nonbaskers, *G. monticolus* does indeed exhibit basking. Basking behaviour has also been reported for the Mexican *G. viridiflora* (Bogert & Porter, 1967), *G. multicarinatus webbi* (Cunningham, 1966) and *G. coeruleus* (Levin, 1967). This habit and the ability to absorb solar radiation enables *G. monticolus* to attain body temperatures considerably in excess of the microclimate; a phenomenon well known for many lizards including other neotropical high altitude occupants such as *Liolaemus multiformis* in the South American Andes (Pearson, 1954) and some montane species of *Sceloporus* (Bogert, 1949).

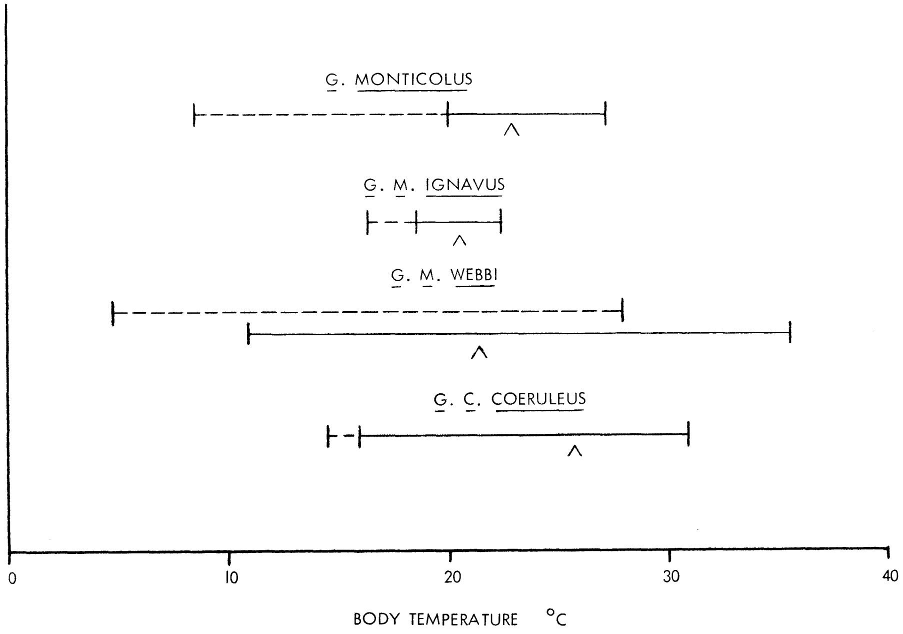
According to Brattstrom (1965) there is little difference between body temperatures of *Gerrhonotus* in the open (active) and those under objects, but he is unclear as to whether the latter represents hypothermic inactivity or retreat from excessive heat loads (or both). In *G. multicarinatus webbi* the body temperature range of inactive animals (9.6°C – 27.9°C) substantially overlaps that of active (11.0°C – 35.7°C) ones (Cunningham, 1966); however, Levin (1967) observed a definite thermal level at which *G. coeruleus* became active (16.0°C). The voluntary minimum temperature of *G. multicarinatus ignavus* obtained by Zweifel (1958) was 18.7°C. These data are graphed in Figure 2, which also shows that *G. monticolus* has a higher minimum voluntary temperature (20.2°C) than any other gerrhonotine for which information is available.

Zweifel (1958) recorded body temperatures of 18.7° – 22.4°C (mean 20.6°C) for active *G. multicarinatus ignavus* on San Martin Island. The activity range of *G. m. webbi* (11.0°C – 35.7°C) was reported by Cunningham (1966) to include the lowest mean (21.4°C) for any North American diurnal lizard. Although he overlooked Zweifel's (1958) paper, the records of active *G. m. ignavus* are based on only three observations and, as such, this lower mean is of limited value. The erroneous mean of 22.4°C for the latter subspecies given in Brattstrom's (1965) review is undoubtedly a typographical mistake. *G. c. coeruleus* is active over a thermal range of 16° – 31°C (mean 25.9°C) (Levin, 1967). As shown in Figure 2 both the thermal range and mean (23.0°C) of active *G. monticolus* are intermediate between those of *G. m. webbi* and *G. c. coeruleus*, which can be interpreted as support for Templeton's (1970) conclusion that tropical reptiles possess activity temperatures similar to temperate forms.

Because of the relatively small sample in an elevational difference of only 430m, a broad diel range and rapid rate of change in temperatures, no evidence can be gleaned that indicates a correspondence of body temperatures to altitude or seasonal changes within the vertical distribution of *G. monticolus*. In comparison to high altitude species of *Sceloporus*, the mean temperature for active *G. monticolus* (23.0°C) at an elevation of 2,500m (the midpoint of its vertical distribution on the Cerro de la Muerte) would be considerably lower than that projected by Brattstrom (1965). Unfortunately there are no equivalent data by which comparisons can be made among the species of *Gerrhonotus*.

Gerrhonotines are generally considered to be cold-tolerant, diurnal thigmotherms (Brattstrom, 1965; Regal, 1967; Templeton, 1970). Cunningham (1966) reported that *G. m. webbi* can survive a minimum temperature of 2.2°C; he also found several active amid snow fields above 1,980m. In view of the otherwise similar thermal parameters of the two species, it seems reasonable to predict that *G. monticolus* can easily survive temperature depressions during nocturnal inactivity at the 3.4°C level measured in the microhabitat. Apparently the restriction to diurnality is temperature regulated in *G. monticolus*. Certain other members of the genus are reported to be crepuscular or even nocturnal (*e.g. G. multicarinatus*, Fitch, 1935; Stebbins, 1954; Van Denburgh, 1922). Further, Stebbins (1954) concluded that gerrhonotine occupants of the more humid and cooler habitats (*e.g. G. coeruleus*) tend to be more diurnal than those inhabiting warmer and drier regions.

FIGURE 2



ACKNOWLEDGEMENTS

Field work for this study was accomplished during the tenure of grant support provided by the American Philosophical Society (Penrose Fund 3029) and the National Science Foundation (GE 4705).

REFERENCES

BOGERT, C. M. (1949). Thermoregulation and eccritic body temperatures in Mexican lizards of the genus *Sceloporus*. *An. Inst. Biol. (Univ. Mexico)* **20**, 415-26. Bogert, C. M. and A. P. Porter (1967). A new species of *Abronia* (Sauria, Anguidae) from the Sierra Madre del Sur of Oaxaca, Mexico. *Amer. Mus. Novitates* No. 2779 pp. 1-21.

BRATTSTROM, B. H. (1965). Body temperatures of reptiles. *Amer. Midl. Nat.* **73** (2), 376-422.

CLOUDSLEY-THOMPSON, J. L. (1971). *The Temperature and Water Relations of Reptiles*. Merrow, Watford. pp. 166.

CUNNINGHAM, J. D. (1966). Thermal relations of the alligator lizard, *Gerrhonotus multicarinatus webbi*. *Herpetologica* **22** (1), 1-7.

FITCH, H. S. (1935). Natural history of the alligator lizards. *Trans. St. Louis Acad. Sci.* **29**, 1-38.

HOLDRIDGE, L. R. (1967). *Life Zone Ecology*. 2nd Ed. Tropical Science Center, San Jose, Costa Rica. pp. 1-206.

LEVIN, F. H. (1967). Temperature relations of the northern alligator lizard, *Gerrhonotus coeruleus*, on Ano Nuevo Island. *In: Biological Investigations in Ano Nuevo State Reserve. Annual Report* 1966-1967. (Compiled by Peterson, R. S. and Gentry, R. L.) Appendix B. pp. 1-9.

PEARSON, O. P. (1954). Habits of the lizard *Liolaemus multiformis* at high altitudes in southern Peru. *Copeia* 1954:111-16.

REGAL, P. J. (1967). Voluntary hypothermia in reptiles. *Science* **155**, 1551-53.

STEBBINS, R. C. (1954). *Amphibians and reptiles of western North America*. McGraw-Hill, New York. pp. 528.

TAYLOR, E. H. (1956). A review of the lizards of Costa Rica. *Univ. Kansas Sci. Bull.* **38**, Pt. 1, No. 1:3-322.

TEMPLETON, J. R. (1970). Reptiles. *In: Comparative Physiology of Thermoregulation*. Vol. 1 Invertebrates and nonmammalian vertebrates. Whittow, G. C., ed. Academic Press, New York. pp. 167-221.

VAN DENBURGH, J. (1922). *The reptiles of western North America*. Vol. 1 Lizards. Calif. Acad. Sciences. San Francisco. pp. 611.

VIAL, J. L. (1968). The ecology of the tropical salamander, *Bolitoglossa subpalmata*, in Costa Rica. *Rev. Biol. Trop.* **15**, 13-115.

WALTERS, V. (1953). Notes on reptiles and amphibians from el Volcan de Chiriqui, Panama. *Copeia* 1953:125-7.

ZWEIFEL, R. G. (1958). Notes on the reptiles and amphibians of the Pacific coastal islands of Baja California. *Amer. Mus. Novitates* No. 1895 pp. 17.

EXPLANATION OF TEXT FIGURES

FIGURE 1.

Plot of corresponding body and substratum temperatures taken for *G. monticolus*. Isotherm is shown as solid line, regression line is dashed. Solid circles represent basking animals. Regression equation for $Y' = 1.43 + (0.98)X$, $r = 0.85$, $N = 15$.

FIGURE 2.

Comparative temperature ranges of four alligator lizards. Solid line denotes active range; dashed line, range for inactive animals; inverted "v" indicates mean thermal level of active animals. Sources: *G. c. coeruleus*, Levin (1967); *G. m. webbi*, Cunningham (1966); *G. m. ignavus*, Zweifel (1958).

INTER- AND INTRA-INDIVIDUAL VARIATION IN LIZARD VOLUNTARY TEMPERATURES

By

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(*Received* 18/5/74)

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.

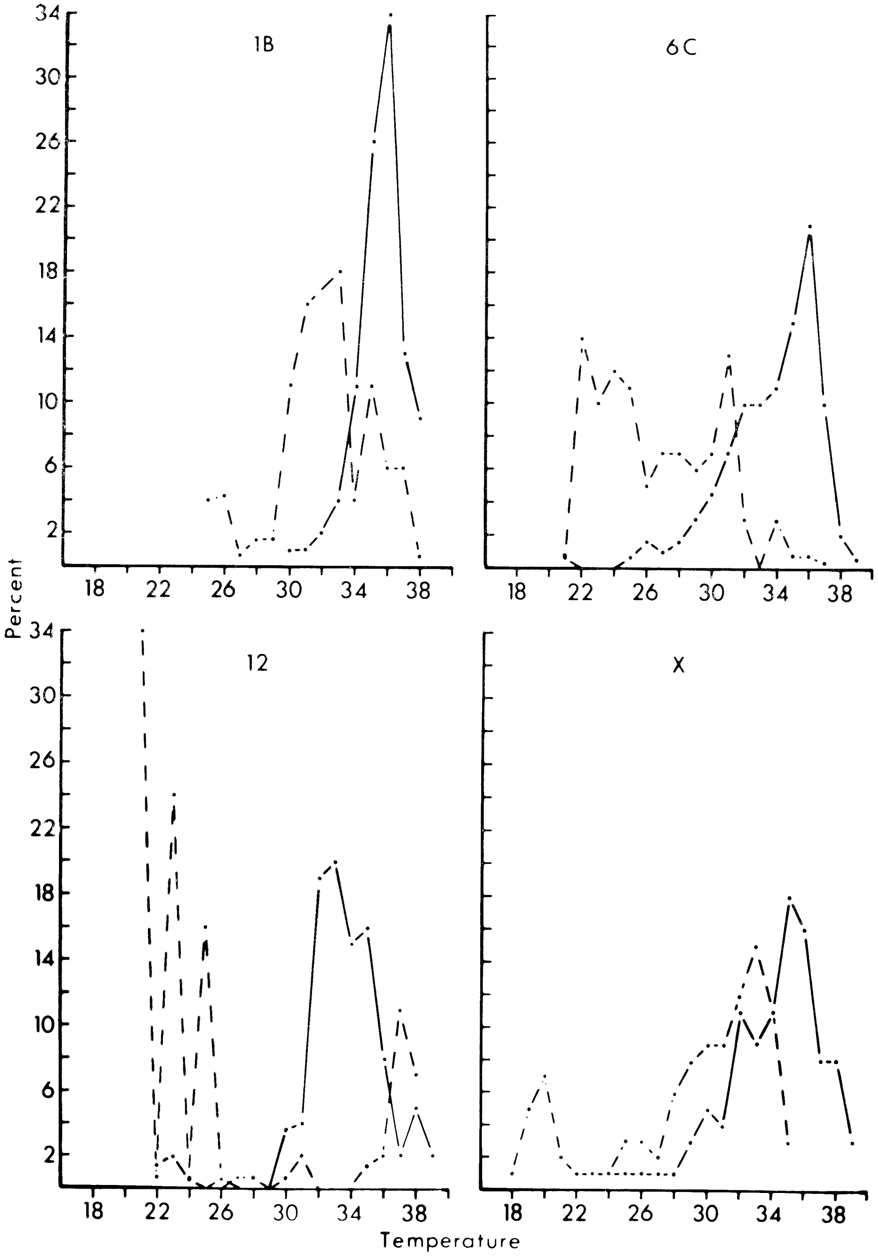
RESULTS

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
Percent
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6
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14
18
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34
18
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26
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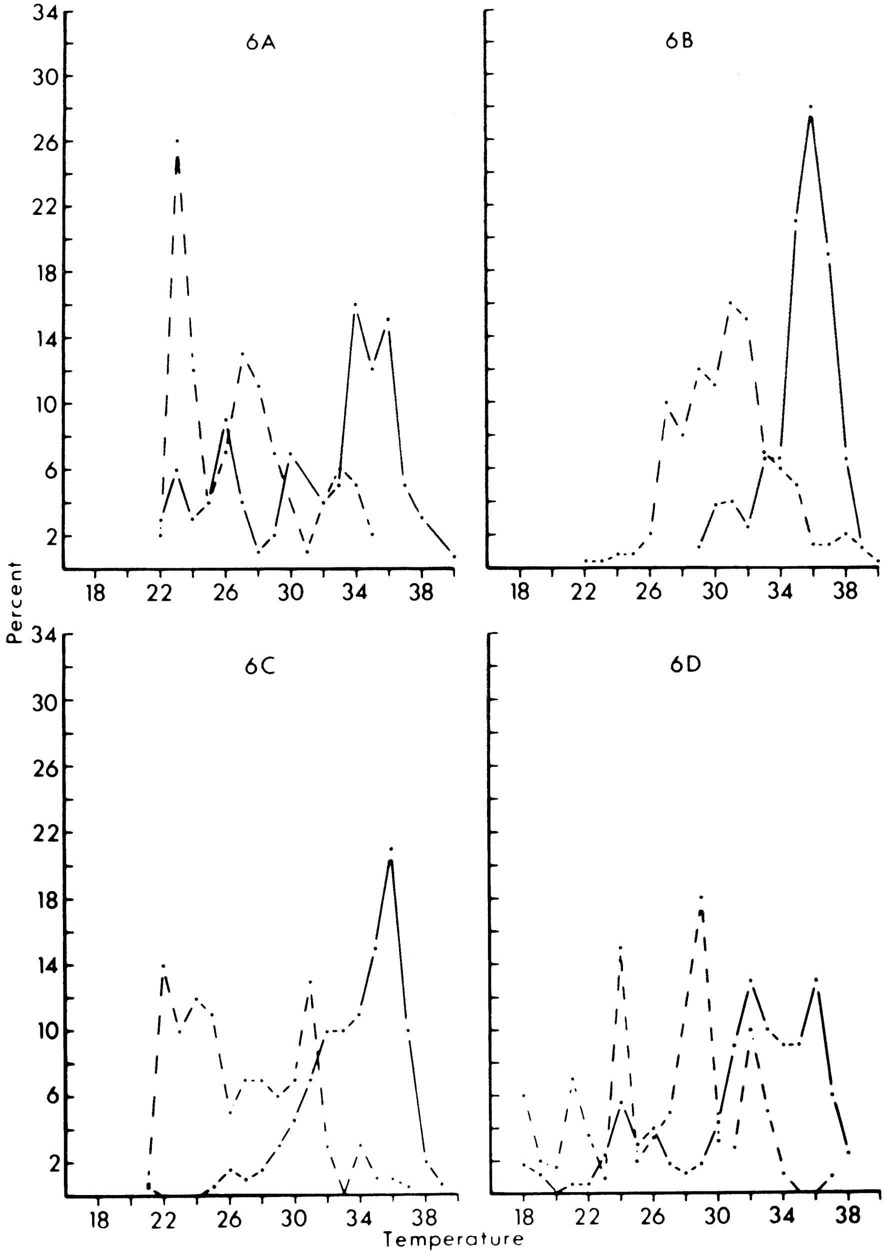
38
Temperature

FIG 1


6A
6B
6C
6D
Percent
2
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34
18
22
26
30
34
38
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.

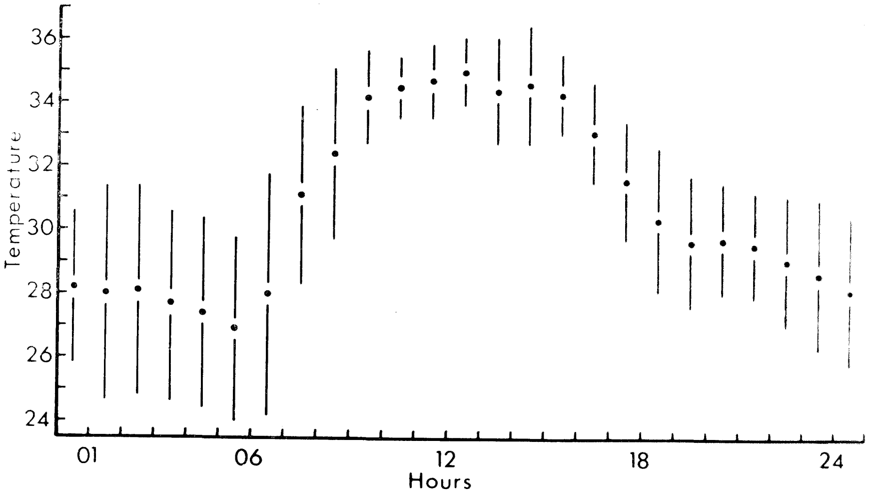

FIG 3

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

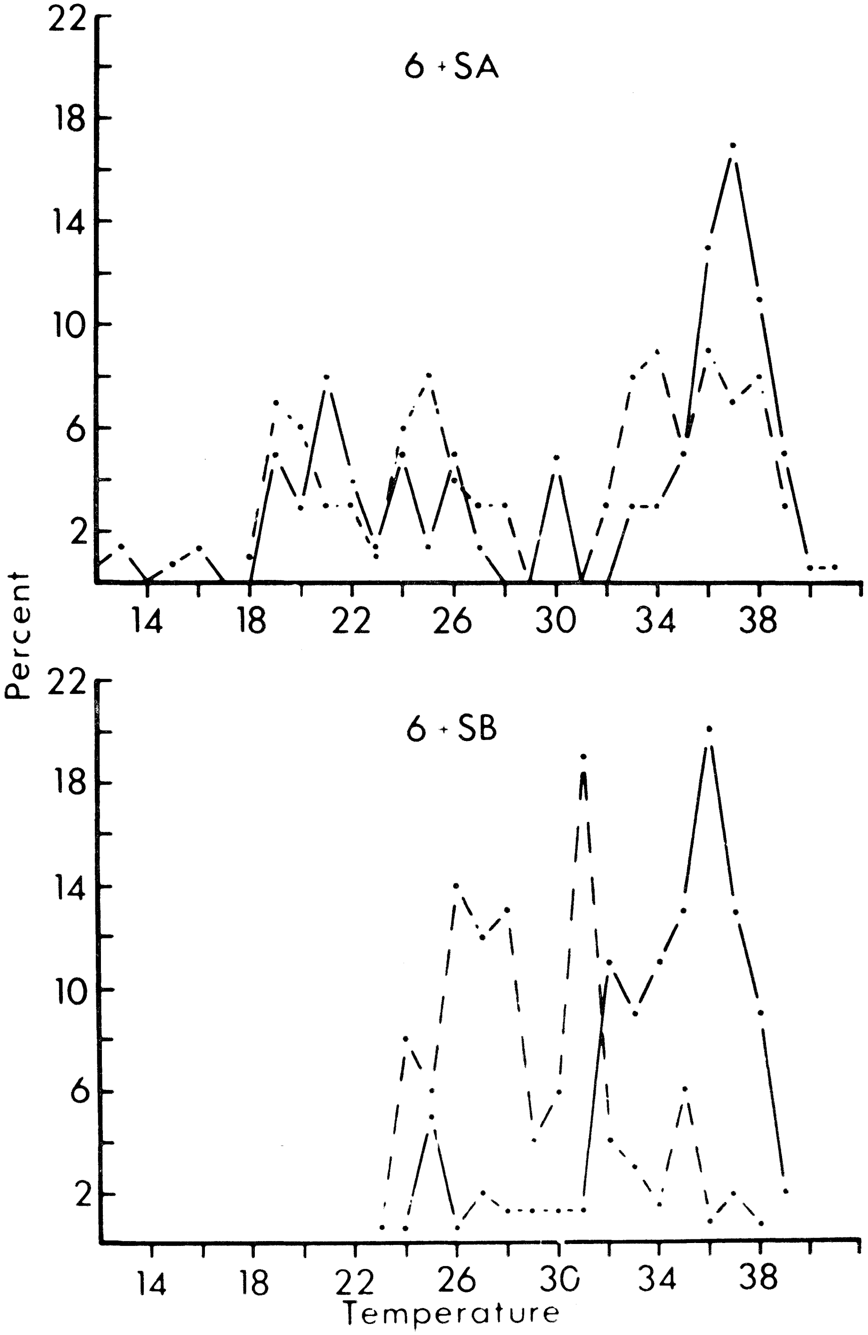

FIG 4

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.

REFERENCES

BRATTSTROM, B. H. (1965). Body temperatures of reptiles. *Amer. Midl. Nat.* **73** (2), 376-422.

COWLES, R. B. & BOGERT, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bull. Amer. Mus. nat. Hist.* **83**, 265-96.

DeWITT, C. B. (1967). Precision of thermoregulation and its relation to environmental factors in the Desert Iguana *Dipsosaurus dorsalis*. *Physiol. Zool.* **40** (1), 49-66.

EVANS, K. J. (1966). Responses of locomotor activity rhythms of lizards to simultaneous light and temperature cycles. *Comp. Biochem. Physiol.* **19**, 91-103.

FITCH, H. S. (1954). Life History and ecology of the Five-Lined Skink *Eumeces fasciatus*. *Univ. Kans. Publ. Mus. nat. Hist.* 8, 1-156.

FITCH, H. S. (1956). Temperature responses in free-living amphibians and reptiles of northeastern Kansas. *Univ. Kans. Publ. Mus. nat. Hist.* **8**, 417-76.

GORDON, M. S. (1968). *Animal function: principles and adaptations*. 560p. London. The MacMillan Co.

HOFFMANN, K. (1955). Aktivitätsregestrierungen bei frisch Geschlüpften Eideschsen. *Z. vergl. Physiol.* **37**, 253-62.

HOFFMAN, K. (1957a). Uber den Einfluss der Temperatur auf die Tagesperiodik bei einem Poikilothermen. *Naturwiss.* **44**, 358.

HOFFMANN, K. (1957b). Angeborene Tagesperiodik bei Eideschsen. Naturwiss. **44**, 359-360.

HOFFMANN, K. (1959). Die Aktivitätsperiodik von im 18- und 36- stunden-tag erbrüteten Eidechsen. *Z. vergl. Physiol.* **42**, 422-32.

HOFFMAN, K. (1960). Versuche zur Analysis der Tagesperiodik. 1. Der Einfluss der Licht. intensität. *Z. vergl. Physiol.* **43**, 544-66.

LICHT, P. (1965). The relation between preferred body temperatures and testicular heat sensitivity in lizards. *Copeia* 1965 (4), 428-36.

LICHT, P. (1968). Response of the thermal preferendum and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. *Amer. Midl. Nat.*, **79**, 149-58.

LICHT, P., DAWSON, W. R., SHOEMAKER, V. H., MAIN, A. R. (1966). Observations on the thermal relations of western Australian lizards. *Copeia* 1966 (1), 97-110.

LICHT, P., HOYER, H. E., Van OORDT, P. G. W. J. (1969). Influence of photoperiod and temperature on testicular recrudescence and body growth in lizards, *Lacerta sicula* and *Lacerta muralis*. *J. Zool., Lond.* **157**, 469-501.

MARX, Ch., et KAYSER Ch. (1949). Le rythme nycthermeral de l'activitie chez le lezard (*Lacerta agilis, Lacerta muralis*) *C. r. Soc. Biol.*, **143**, 1375-77.

REGAL, P. J. (1966). Thermophilic response following feeding in certain reptiles. *Copeia* 1966 (3), 588-90.

REGAL, P. J. (1967). Voluntary hypothermia in reptiles. *Science* **155** (3769), 1551-3.

SPELLERBERG, I. F. (1973). Critical minimum temperatures of reptiles. p 239-247. In Wieser, W. (1973). Effects of temperature on ectothermic organisms. Springer-Verlag, Heidelberg. 298p.

SPELLERBERG, I. F. (1974). Influence of photoperiod and light intensity on lizard voluntary temperatures. *Br. J. Herpet* **5** (2), 412-20.

SPELLERBERG, I. F. & PHELPS, T. (1975). Preliminary investigations into the voluntary temperatures of the Smooth Snake, *Coronella austriaca*. *Copeia* 1975 (1), 183-185.

TABLE 1

Lacerta sicula voluntary temperatures °C.

Lizard Number	*Night temperatures* mean	range	*Day temperatures* mean 1.	mean 2.	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

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(*Received* 7/1/74)

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.

Percentage hatches for six of the seven clumps were >90% (Mean ± S.E. = 96 ± 1%), and it should be pointed out that the process of detaching the small lump of spawn was probably responsible for some ova being damaged and failing to develop. In the remaining clump, 80% of the ova failed to hatch. Dead embryos and ova, covered with fungus, were left after the tadpoles had hatched from the clumps. Ova were not examined to determine whether cleavage had taken place, so it is not known whether infected ova had been fertile.

The lengths of time that the spawn took to hatch are also given in Table 1. Surviving tadpoles from the clump with the abnormally low hatch, emerged over a period of only two days, while the other clumps hatched during periods of from four to seven days. While the spawn was developing, the temperature was about normal for March and April, the mean (± S.E.) of the daily average air temperatures (minimum/2 + maximum/2) being 6.2°C ± 0.4°C (27 days).

DISCUSSION

Spawn selection on St Neots Common, where 134 clumps were laid in 1973, depended on the freshness of the clumps, and there is no reason to suppose that the six clumps chosen were atypical with regard to numbers of ova. The Monks Wood spawn clump was the only one laid in the stock ponds this year. The mean number of ova in these seven clumps was 14% less than the mean number in the clumps examined by Boulenger (1898), but the difference was not statistically significant. The ranges of Greening and Heron-Royer (quoted by Boulenger, 1898) were, however, much higher. The technique described for the rapid estimation of numbers of ova was found to be satisfactory. Although the estimates were sometimes inaccurate by >10%, there was no tendency for them to be either too high or too low.

If spawning is delayed, there can be a marked increase in the incidence of spawn clumps containing abnormally high numbers of infertile eggs (see Savage, 1961), but normally in the field such clumps are relatively rarely encountered. For instance, on St Neots Common in 1972, I found only one clump that had an abnormally low hatch, while the remaining 121 clumps to survive the development period (see below) all had a normal percentage hatch. In 1973, six clumps out of 103 apparently failed to produce a single tadpole. The effect of this hatching failure was quite small compared with the loss of spawn clumps due to the combined effect of collection by humans, trampling by cattle or horses, and desiccation: in 1971 22% of the clumps were lost; 1972, 13%; 1973, 20%.

For spawn of the American toad (*Bufo americanus*), the percentage hatch is usually >95% (Voris and Bacon, 1966), but spawn laid by wood frogs (*Rana sylvatica*), studied in Alaska by Herreid and Kinney (1966), was found to suffer a much higher failure rate. In 50 ova taken from each of 53 spawn clumps, the mean percentage (± S.E.) that failed to pass through early cleavage was 22 ± 4%, while the mean mortality during gastrulation was 4 ± 1%. Fungal infections were frequently noted on dead embryos. The ecology of *Rana aurora* in Marion Lake, British Columbia has been intensively studied by Calef (1973). In 35 spawn clumps, the mean percentage (± S.E.) of eggs with a fungus infection was found to be 2.4 ± 1.0%. Fungus has also been reported on spawn of the spade-foot toad (*Pelobates fuscus*) in Holland (van Gelder and Kalkhoven, 1971) and is quite common on spawn of the common toad (*Bufo bufo*) in Britain. Very many people must have observed fungus on the spawn of *Rana temporaria*, but I have never found a published reference to such an incident. Whether the fungus is saprophytic or parasitic remains to be determined.

TABLE 1

An examination of seven spawn clumps laid by common frogs (*Rana temporaria*): number of ova and hatchability

Place of origin	Estimated no. of ova	Counted			No. of ova: estimated / counted	Percentage of ova that hatched	Hatching period (Approx. no. of days after spawn was laid)
		Live Tadpoles	Dead ova & embryos	Total			
St Neots	1270	987	80	1067	1.19	92.5	18 – 25
	1480	1388	65	1453	1.02	95.5	15 – 20
	1110	1152	57	1209	0.92	95.3	16 – 23
	1190	1196	17	1213	0.98	98.6	17 – 23
	1340	1588	20	1608	0.83	98.6	19 – 23
	1280	284	1114	1398	0.92	20.3	20 – 22
Monks Wood	1380	1312	41	1353	1.02	97.0	18 – 23
Mean	1290	1130	199	1329	0.98	85.4	18 – 23

SUMMARY

A method for giving a rapid and reasonably accurate estimate of the number of ova in a clump of frog spawn was developed. The mean (± S.E.) number of ova in seven clumps was determined, by counting, as being 1329 ± 68 (range, 1067-1608). The average hatching period was 18-23 days after the spawn was laid, mean ambient temperature during this period being 6.2°C. In six of the clumps, >90% of the ova hatched, but in the remaining clump only 20% hatched. A fungus was noted on dead ova, as has been observed on anuran spawn elsewhere in Europe and in North America.

ACKNOWLEDGEMENTS

I thank Dr. N. W. Moore and Dr. F. Moriarty for their comments on the manuscript and P. F. Ferguson for assistance in the field and in the laboratory.

REFERENCES

BOULENGER, G. A. (1898). *The Tailless Batrachians of Europe*. Part II. Ray Society, London.

CALEF, G. W. (1973). Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology* **54**, 741-58.

van GELDER, J. J. and KALKHOVEN, J. T. R. (1971). Eiren van de knoflookpad (*Pelobates fuscus* Laur.) in de Hatertse en Overasseltse Vennen. *Natuurlist. Maandblad* **60**, 39-44.

HERREID, C. F. and KINNEY, S. (1966). Survival of Alaskan wood frog (*Rana sylvatica*) larvae. *Ecology* **47**, 1039-41.

SAVAGE, R. M. (1961). *The Ecology and Life History of the Common Frog*. Pitman, London.

SMITH, M. (1969). *The British Amphibians and Reptiles*. 4th edition. Collins, London.

VORIS, H. K. and BACON, J. P. (1966). Differential predation on tadpoles. *Copeia 1966*, 594-8.

ADDENDUM

Since the final draft of this paper was prepared, several publications have appeared reporting fungus on spawn. In April 1973, at high altitudes in the Lake District, Fryer (1973) and Greenhalgh (1974) independently found spawn with vitelli covered by a white fungus, identified as *Saprolegnia ferax*. Fryer (1973) intimated that pesticides could have been the primary cause of the egg spoilage by affecting the female frog, but Greenhalgh (1974) considered that the hard weather experienced in early April was the probable cause. Greenhalgh's explanation would seem to be more likely since (1) this was the worst weather that he had ever recorded in April and the first time he had noticed spawn spoilage during eight years of observation; (2) the incidence of spawn spoilage was much reduced at low altitudes where one would expect more clement weather, but a greater likelihood of pesticide contamination; and (3) eggs in the centres of the clumps were frequently noted by both authors to be unaffected. Nevertheless, it is worth pointing out that if pesticides contributed to the decline of frog populations in heavily-treated areas such as the Fenland or Huntingdonshire (see Cooke and Ferguson, 1974), then their action probably tended to cause unspectacular and easily-missed effects such as infertility or reduced survival of spawn (Cooke, 1972a).

So what was the sequence of events in the high Lakeland tarns in 1973? In view of what was known about the fungus, Fryer (1973) considered it likely to have been saprophytic, so death of the developing ova because of the cold weather followed by fungal infestation is a plausible suggestion. However, Smith (1974) reported that *Saprolegnia* fungus could kill embryos of *Bufo bufo* and *B. calamita,* particularly during the neurula stages. Thus, it is conceivable that the cold weather for some reason increased the incidence of infestation by the fungus, and the fungus ultimately caused the spoilage.

Smith (1974) also reported that tadpoles badly infested with *Saprolegnia* suffered limb and tail deformities. Exposing tadpoles to insecticides can cause a high incidence of the same or similar deformities (Cooke, 1972b, 1973a, b). One explanation for this is that insecticides lower the resistance of the tadpoles to the fungus; the insecticides, therefore, being only indirectly responsible for the deformities. *Saprolegnia* fungus may also have been involved in the incident studied by Hazelwood (1970), in which much spawn failed to hatch and deformed tadpoles were noted after herbicide was sprayed near a breeding pond.

COOKE, A. S. (1972a). Indications of recent changes in status in the British Isles of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *J. Zool., Lond.* **167**, 161-78.

COOKE, A. S. (1972b). The effects of DDT, dieldrin and 2,4-D on amphibian spawn and tadpoles. *Environ. Pollut.* **3**, 51-68.

COOKE, A. S. (1973a). Response of *Rana temporaria* tadpoles to chronic doses of pp'-DDT. *Copeia* **1973**, 645-52.

COOKE, A. S. (1973b). The effects of DDT, when used as a mosquito larvicide, on tadpoles of the frog *Rana temporaria*. *Environ. Pollut.* **5**, 259-73.

COOKE, A. S. and FERGUSON, P. F. (1974). The past and present status of the frog (*Rana temporaria*) and the toad (*Bufo bufo*) in Huntingdonshire. *Rep. Huntingdon Fauna Flora Soc.* (1973) **26**, 53-63.

FRYER, G. (1973). Unusual egg spoilage in the common frog. *Naturalist, Hull* **926**, 105-6.

GREENHALGH, M. E. (1974). Egg spoilage in the common frog in high-level Pennine tarns. *Naturalist, Hull* **928**, 39.

HAZELWOOD, E. (1970). Frog pond contaminated. *Br. J. Herpet.* **4**, 177-85.

SMITH, S. H. (1974). *Hybridisation in the two species of amphibia (Bufo bufo and Bufo calamita) in controlled conditions and in the wild at Ainsdale, South West Lancashire*. MSc thesis, University of Manchester.

A NEOTONOUS FEMALE OF SMOOTH NEWT, *TRITURUS VULGARIS*

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(*Received* 20/9/74)

Neotony in the smooth newt, *Triturus vulgaris* (Laurenti, 1768), is rarely met with in Scandinavia (Gislén & Kauri, 1959) and the European continent (Steward, 1969). Thus it may be of interest to report a specimen in Denmark, where it has never been reported (Schiötz, 1970).

The specimen (Fig. 1) was seen in central Jutland on 30 March 1974 and its total length was 7.5cm. The newt appeared in typical breeding condition with the sexual coloration of a normally developed female. On 9 April the female was placed with a male in an aquarium. Freshly laid eggs were found on 18 April. Five days later the specimens were observed depositing a spermatophore and eggs. The eggs, however, never developed.

The last sight of the neotonous female was on 31 May. One week later the external gills were completely resorbed and the animal had left the water.

The locality where the neotonous animal occurred was inspected on 25 April. The pond (10 x 15m) had peat bog surroundings and was situated in an open area of a pine-spruce plantation. The water was not particularly cold.

During the spring 28 specimens of *T. vulgaris* were captured in this pond. Only one specimen was neotonous.

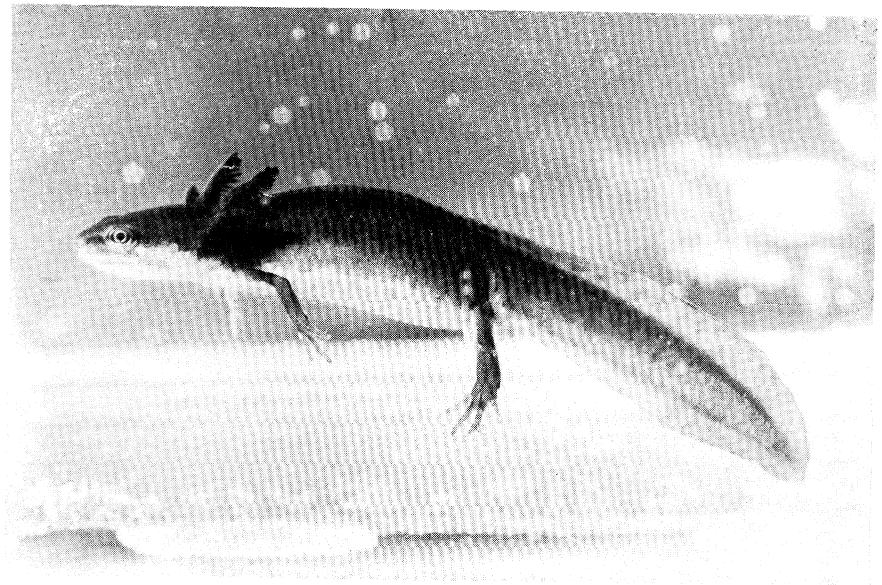

FIG. 1

REFERENCES

GISLEN, T. & KAURI, H. (1959). Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta Vert.* **1** (3), 200-397.

SCHIOTZ, A. (1970). Lille salamander; pp 99-102, in Hvass, H. *Danmarks Dyreverden* **5**, Copenhagen. Rosenkilde og Bagger. 10 vols.

STEWARD, J. W. (1969). *The tailed amphibians of Europe*. Newton Abbot, David & Charles.

LETTER TO THE EDITOR

BROODING PYTHONS

In the interesting account of breeding in *Python molurus bivittatus* by J. Coborn (*Br. J. Herpet.* 5, 471-472, 1975) the author mentions the convulsive twitching of the brooding female and suggests that this activity may serve to promote blood circulation during periods of immobility, to promote air circulation around the eggs, or may be a maternal reaction to the presence of eggs between the coils. In fact the detailed physiological studies of this species by Hutchison, Dowling and Vinegar (*Science, N.Y.* 51, 694-696, 1966) showed conclusively that the spasmodic contraction of the muscles produces metabolic heat, in a manner akin to shivering in mammals. This rise in body temperature above that of the surrounding air assists in the incubation of the eggs and explains why it is only seen at this time.

This interesting phenomenon of endogenous heat production in a reptile was first described in 1832 by Lamarre-Picquot in the same species but a full physiological study was not performed until the early 1960's. Other observations suggest heat production by the same mechanism in brooding females of other species of python.

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(*Received* 12/9/75)

BOOK REVIEWS

Adam, K. M. G., Paul, J. and Zaman, V. (1971). *Medical and Veterinary Protozoology*. Churchill Livingstone, Edinburgh & London. Pp. **199**. Figg 186. Price £6.

Bancroft, J. D. and Stevens, A. (1975). *Histopathological Stains and their Diagnostic Uses*. Churchill Livingstone. Edinburgh & London. Pp. **149**. Figg. 30. Price £4.50.

There must be, among the readers of this journal, some who have access to a laboratory where the investigation of a reptile or an amphibium can be carried a little further than the purely taxonomic stage. Readers who have the interest to carry out simple dissections and who have a small working bench and a microscope may be interested to see the titles of two books which might help them with their histopathology and which are, by present day standards, not too expensive. One would not expect either of these books to be written primarily for herpetologists, but herpetological pathology being a branch of veterinary science, the general rules of procedure and interpretation are very much the same for both.

Few herpetologists realise the enormous part played by parasites in the lives of lower vertebrates. In particular the importance of the protozoa is not always sufficiently appreciated because they cannot be seen with the naked eye and like the bacteria, they often need sophisticated methods to be detected. The first of the two titles quoted above contains all the information needed and is a perfect guide for anybody who has the chance to investigate material fresh enough to produce reliable results.

The second title deals with histopathology generally where the requirements are perhaps not quite so stringent and where we can sometimes obtain fair results from material not as ideally fixed as we should like it to be. The book is concise and up to date but none of the illustrations are in colour. Considering that, as the title indicates, the book deals with 'Stains' examples of what these various stains can do and what they cannot would have have been welcome even if most pathologists effectively ruin the efforts of their technicians by using yellow tungsten light without filters instead of daylight, which is often available in laboratories with large windows.

The two books mentioned are of course by no means the only ones on their subject, but I thought they deserved to be mentioned here because they are concise, cover the subject well, particularly for beginners and . . . are not too expensive.

E. ELKAN.

Gans, Carl. (1974). *Biomechanics. An Approach to Vertebrate Biology.* J. B. Lippincott, Philadelphia, Toronto. Pp 261. Paperback £3.30, hardback £6.25.

The application of mechanical principles to the study of animal functions such as locomotion and feeding has often yielded rewarding results. All too often, however, works on biomechanics are almost incomprehensible to the many naturalists who lack a mathematical background. Dr. Carl Gans, familiar to herpetologists both from his original work and his editorship of *Biology of the Reptilia,* has managed to write a highly significant book with a refreshingly sparing use of formulae. Originally trained as an engineer, he brings the principles of engineering to bear on such topics as egg-eating snakes, the vocalisation of frogs, and the locomotion of snake-like reptiles; he pays particular attention to the burrowing of amphisbaenians, those fascinating worm-like reptiles which he has studied so effectively for many years. Indeed, the majority of his masterly analyses, explained in lucid text and illustrated by outstanding photographs and attractive line drawings, are concerned with herpetological problems. One great virtue of the book is that the author never loses sight of the living animal and the adaptations which it shows to its natural surroundings. Indeed the work is as much an exercise in functional anatomy as in biomechanics, and beautifully exemplifies what so many of our zoological contemporaries have forgotten; the contribution which anatomy can make to our understanding and appreciation of the lives of animals.

A. d'A. BELLAIRS.

Gans, Carl. (1975). *Reptiles of the World.* Ridge Press/Bantam Books, Toronto, New York, London. Pp 159. 173 colour photos. $1.95.

Gans has scored another bullseye, on a different target. This little paperback is exceptionally good value with its excellent colour photos. It shows many rare or little known types of reptiles which are seldom illustrated. such as the shield-tail, pipe and sunbeam snakes, all primitive forms of great interest to students of ophidian evolution. The groups and species mentioned have been well selected to show the diversity of the class; they are described in short but authoritative notes which contain much out of the way information based on original study. No one interested in reptiles should be without this book.

A. d'A. BELLAIRS.

Gans, C. and Parsons, T. S. (editors) (1973). *Biology of the Reptiles.* Volume 4, Morphology D. Pp. V + 539. Academic Press, London. Publication date February 1974. £14 ($39.50).

This is the fourth volume of the series on the reptiles, dealing with a wide variety of aspects of the group. The present volume (there is to be a companion volume on similar subjects) is concerned with osteology and myology of different reptilian orders and contains, as the editors state, a "remarkable assemblage of data". If it is still inadequate then future workers have a valuable springboard for further contributions in this field. The volume includes: "The locomotor apparatus of Testudines" by Warren F. Walker; "The head muscles and hyolaryngeal skeleton of turtles and crocodilians" by Gert Horst Schumacher; "The skull of the Crocodilia" by N. N. Iordansky, "The crocodilian skull in historical perspective" by Wann Langston and "The muscles of the jaws and associated structures in the Rhynchocephalia and Squamata" by Georg Haas.

On the whole apart from Walker's chapter on the locomotor apparatus, the descriptions emphasise the origin, development and morphological relationships of the various muscle, nerve and skeletal components, rather than functional anatomy. As Gans writes "We still lack electronmyographic studies of locomotor or feeding patterns in any reptile". Yet the tendency nowadays is to concentrate more on the functional implications of morphological structure, a subject in which the senior editor has made substantial contributions.

Perusing the pages of this book, which is indeed somewhat heavy going for those who are not specialists in the various subjects therein, one can only marvel at the erudition and dedication of the authors. The detailed prose is a delight to read, the illustrations are of high quality and adequately labelled and explained and the bibliographies are ranging and extensive. It is probable that this series on the reptiles will turn out to be the finest ever produced on any vertebrate group. I'm sure Tom Parsons and all his industrious colleagues associated with this series will be the first to acknowledge the meticulous care and talent and the enormous energy of the presiding senior editor Carl Gans.

All herpetological libraries and institutions who have not purchased the first four volumes or who have not budgeted for those to come, will suffer a serious omission in their library lists: Certainly they will not be bang up to date. The price is high—there is a nasty word inflation—but the book is still of inestimable value for those who wish to learn.

H. FOX.

Bellairs, A. d'A. and Attridge, J. (1975). *Reptiles.* Pp X + 240. Fourth edition. Hutchinson, London. Paperback, £2.75.

Since this book was first published in 1957, reprinted in 1966 and then released again as second and third editions in 1968 and 1970, there has been, as the authors state, "a tremendous increase in the number of publications dealing with reptiles". The original author, the well-known expert on reptiles A. d'A. Bellairs, is now joined by John Attridge, who is mainly concerned with reptilian palaeontology, a difficult and complex field of zoology though one which is still rapidly developing notwithstanding the recent death of its greatest researcher A. S. Romer.

The 12 chapters introduce the reptiles and describe their general features, their origin and radiation, ancestry and the earlier offshoot derivations into the birds and mammals. The chapters on fossil reptiles, the ichthiosaurs, plesiosaurs, archosaurs, dinosaurs and pterosaurs etc. are quite detailed for a book of this size and the reader should not assume that this book is a pleasant harmless digression from the hard stuff. The work is indeed serious, detailed, albeit shortened and thus of necessity a limited account of the reptiles, but it should serve as a firm basis for anyone wishing to delve more deeply into specified aspects of the group.

The authors are really up to date too, for on page 153 an addendum quotes *The Times*, 13 March, 1975, on a recently discovered flying reptile in Texas, with a wingspan of 51 feet.

There is a useful bibliography and numerous black and white line drawings. At £2.75 it is unhesitatingly recommended.

H. Fox.

Cloudsley-Thompson, J. L. *Crocodiles and Alligators*. The Bodley Head New Biology. Publication date August 1975. Hardback, £1.75.

This short book of only 47 pages is obviously aimed at the young who wish to enjoy reading about interesting animals. The author describes the subjects of the book in clear, precise prose and supplies many stimulating facts within a minimum of space.

I hadn't thought about it before but the very narrow snout of the gharial is an adaptation for fish eating. Catching fish with a sideways sweep the narrow snout has a reduced resistance to the water. It seems that from the egg, which is eaten by a variety of predators to the adult, which may be trampled to death by elephants, crocodilians do live dangerously and probably only about one per cent of the young survive to reach maturity; they are thus not always the predators.

Most young crocodiles are inoffensive says the author; nevertheless if any young person reading this book ever gets within reach of a crocodile it would be unwise to pat its head. The book is nicely illustrated by Joyce Bee and elegantly presented. If the reader thinks the book expensive then think what it costs to send a parcel.

H. Fox.

Romer, J. D. *Annoted Checklist with Keys to the Lizards of Hong Kong.* Memoirs of the Hong Kong Natural History Society. No. 10. 15 April 1975.

Copies of this publication may be obtained on application to: The Hong Kong Natural History Society, c/o The Department of Zoology, University of Hong Kong, Hong Kong. A crossed postal order for 80p should be enclosed to cover the cost of a single copy sent by surface mail.

Published by the British Herpetological Society and
Printed by Fox Publications Limited, London, N.15, England