Volume 6, Number 6

June 1982
ISSN 0007-1056

BRITISH JOURNAL OF HERPETOLOGY

Published by
The British Herpetological Society

BRITISH JOURNAL OF HERPETOLOGY

Volume 6, Number 6 June 1982

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EDITORIAL:

Published by the British Herpetological Society
and printed in Great Britain by Spottiswoode Ballantyne Ltd., Colchester and London

EDITORIAL

Dr J. F. D. Frazer

Dr Frazer retired as President of the British Herpetological Society in 1981, having held the post since 1955. The Committee has unanimously resolved that this issue of *British Journal of Herpetology* should be dedicated to him, as a mark of our esteem and in appreciation of his long period of service to the Society.

EDITORIAL REPORT FOR 1981

Seventeen papers and ten letters to the Editor were published during 1981. Mean publication time has been reduced, and all papers relating to British herpetofauna (which receive priority) were published less than one year from their receipt. Sixteen manuscripts were not accepted for publication (37%).

The Editor is grateful to the following people who kindly reviewed manscripts during the year: R. A. Avery, B. I. Baker, T. J. C. Beebee, A. d'A. Bellairs, H. R. Bustard, B. Clarke, A. S. Cooke, T. R. Halliday, L. S. Kelleway, M. R. K. Lambert, K. Simkiss, I. F. Spellerberg, I. R. Swingland, T. E. Thompson, D. W. Yalden, P. J. Wisniewski, D. M. Woolley. The Index for Volume 5 was compiled by D. R. Blatchford.

CORRIGENDA

Meek, R. & Inskeep, R. 1981 Aspects of the field biology of a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *British Journal of Herpetology* 6, 159–164. The equations *should read*

page 161: Carapace length $= 0.29 \times$ body mass$^{0.35 \pm 0.14}$
page 163: Carapace length $\propto$ body mass$^{0.36}$

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 186–187 (1982)

TEMPERATURE TOLERANCE IN THREE POPULATIONS OF SALAMANDERS, *SALAMANDRA SALAMANDRA* (L.)

GAD DEGANI

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(*Received* 12 *March* 1981)

SUMMARY

The heat tolerance of salamanders (*Salamandra salamandra*) from three different habitats was studied. Two are semi-arid habitats, with very cold winters and dry, hot summers. One is a moist habitat where water is available throughout the year and the water temperature is very constant.

The critical thermal maxima (CTM) of larvae from semi-arid habitats were significantly higher than the CTM of larvae from moist habitats after one month of growth, at each of the acclimation temperatures. However, the CTM of adult salamanders from semi-arid habitats were significantly greater than those of adult salamanders from the moist habitat only after the salamanders were acclimated at 30°C, indicating adaptation to long and hot summers in semi-arid habitats.

INTRODUCTION

Thermal acclimation and tolerance of Urodela have been studied by many investigators. Most of them have used the critical thermal maximum (CTM) as a measure of temperature tolerance (*e.g* Hutchison, 1961; Pough & Wilson, 1970; Hutchison & Rowlan, 1975; Claussen, 1977). Only a few studies have considered intraspecific CTM variation (Hutchison, 1961; Gatz, 1973; Claussen, 1977). The CTM of juvenile *S. salamandra* from one population was studied by Warburg (1971).

S. salamandra is found in Israel in three different habitats in isolated populations. One population is found on Mt Carmel and in central Galilee, both of which are semi-arid habitats, with cold winters and dry, hot summers (Degani & Warburg, 1978). In contrast, the Tel Dan population is found around the Dan stream, where water is available throughout the year and the water temperature at 15–17°C is very constant (Degani & Mendelssohn, 1979).

There is no information however, regarding the comparative temperature tolerance of larval and post metamorphosis *S. salamandra* from these different habitats.

MATERIALS AND METHODS

The adult salamanders were collected from Mt Carmel, Galilee and Tel Dan, as described previously by Degani & Warburg (1978). Females were allowed to bear their young in aquaria as described previously by Warburg, Degani & Warburg (1979). Larvae from Galilee and Tel Dan which were born at the same time were grown at 10°C and at 20°C, while larvae from Galilee and from Mt Carmel were grown at 20°C and at 30°C.

The heat resistance of adult salamanders from Galilee, Mt Carmel, and Tel Dan and of juvenile salamanders from Galilee was studied after each group of salamanders had been acclimated for 21 days at 10°C, 20°C and 30°C.

The CTM of larvae was studied as described previously by Hutchison (1961). The water was aerated and stirred while being heated at a rate of 1°C min by means of a heating tape. Water temperature was measured by a certified mercury thermometer of ± 0.1°C accuracy. The CTMs of adult and juvenile salamanders were studied by methods similar to those of Claussen (1977). The body was heated at a rate of 0.7°C/min by means of a heating tape and the temperature measured by a thermocouple probe inserted through the cloaca and connected to a thermocouple thermometer (Spidomax-Leeds and Northrup). All CTM measurements were initiated between 9:00 a.m. and 1:00 p.m.

RESULTS

The thermal tolerance (CTM) of *S. salamandra* larvae from all the populations increased during development (Tables I, II). Moreover, the CTM of larvae from Galilee was significantly greater ($P < 0.05$; *t*-test) than that of larvae from Tel Dan after one month of growth, at different acclimation temperatures (10°C and 20°C). No significant differences were found between the larvae of Mt Carmel and of Galilee. The CTM of larvae grown at 20°C was significantly ($P < 0.001$; *t*-test) higher than the CTM of larvae grown at 10°C. Similar differences were found between larvae grown at 20°C and at 30°C.

No difference was found between the CTM of adult *S. salamandra* from the three populations, Galilee, Mt. Carmel and Tel Dan, that were acclimated at 10°C (Table III). Although the Galilee and Mt Carmel salamanders that were acclimated at 20°C had a greater mean CTM temperature than the Tel Dan population, the difference was not significant ($P > 0.1$). The CTMs of salamanders from mountain pop-

TABLE I. Critical thermal maxima (CTM) of larvae at different acclimation temperatures during growth ($5 < N < 10$)

		Galilee		Dan	
Date	Acclimation temp (°C)	Weight (g) ± SD	CRM	Weight (g) ± SD	CTM
16.6.77	10	0.3 ± 0.1	30.3 ± 0.7	0.3 ± 0.1	30.1 ± 0.6
29.6.77	10	0.5 ± 0.1	32.0 ± 0.3	0.3 ± 0.0	31.3 ± 0.4
11.7.77	10	0.7 ± 0.1	33.0 ± 0.4	0.4 ± 0.1	31.4 ± 0.4
12.6.77	20	0.6 ± 0.1	34.0 ± 0.5	0.4 ± 0.1	33.2 ± 0.9
29.6.77	20	1.1 ± 0.1	34.0 ± 0.5	0.6 ± 0.1	33.9 ± 0.6
11.7.77	20	1.9 ± 0.1	35.9 ± 0.6	0.6 ± 0.1	34.9 ± 0.2

TABLE II. Critical thermal maxima of larvae at different acclimation temperatures during growth ($N = 5$)

Date	Acclimation Temp. (°C)	Galilee CTM	Carmel CTM
28.12.77	20	32.5 ± 0.3	32.7 ± 0.3
10.1.78	20	33.3 ± 0.6	33.0 ± 0.3
28.12.77	30	35.0 ± 0.0	35.1 ± 0.2
10.1.78	30	35.4 ± 0.2	35.4 ± 0.2

TABLE III. Critical thermal maxima (CTM) of adult salamanders at different acclimation temperatures ($N > 5$)

Acclimation temp. (°C)	Galilee juveniles CTM ± SD	Galilee adults CTM ± SD	Carmel adults CTM ± SD	Dan adults CTM ± SD
10	31.8 ± 1.1	32.7 ± 0.6	32.0 ± 0.7	32.5 ± 0.8
20	33.9 ± 0.3	34.8 ± 0.9	34.5 ± 0.7	33.8 ± 0.9
30	35.7 ± 0.5	36.2 ± 0.5	36.2 ± 0.2	35.6 ± 0.3

ulations (Galilee and Mt Carmel) that were acclimated at 30°C were, however, significantly higher than the CTM of salamanders from the Tel Dan population that were acclimated at the same temperature. Although the adult salamanders from Galilee had a greater mean CTM temperature than the juvenile salamanders from the same population, the difference was not significant ($P > 0.05$).

DISCUSSION

The intraspecific CTM differences of *S. salamandra* are correlated with the temperature ranges in the different habitats. The CTM of larvae from the Tel Dan population increased more slowly during development than the CTM of larvae from Galilee. The temperature in the Dan stream is very constant (Degani & Mendelssohn, 1979) throughout the year, that of the water bodies in Galilee and Mt Carmel is not. The temperature in semi-arid habitats (Galilee and Mt Carmel) are lower in winter and hotter in summer. The difference between CTMs of larvae from Galilee and larvae from Tel Dan was significant only after 1 month's growth. Those findings agree with those of Keen & Schroeder (1975). They report that the CTM of larval Ambystomids increases with size. Hutchison (1961), Gatz (1971) and Claussen (1977) suggest that there are no significant intraspecific side effects in *Ambystoma*. Significant intraspecific CTM, however, was found in *Notophthalmus viridescens* (Hutchison 1961).

Both larvae and terrestrial salamanders from all the populations show a significant acclimation response between 10°C and 30°C, similar to that demonstrated for a wide variety of other Urodela (*e.g.* Hutchison, 1961; Pough & Wilson, 1970; Claussen, 1977). The higher CTM of adult salamanders from semi-arid habitats was found only after they had been acclimated at 30°C, indicating adaptation of *S. salamandra* to long and hot summers in semi-arid habitats.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 188–194 (1982)

RHYTHMIC ACTIVITY IN YOUNG RED-EARED TERRAPINS (*PSEUDEMYS SCRIPTA ELEGANS*)

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(*Received* 8 *April* 1981)

SUMMARY

Young *Pseudemys scripta elegans* did not show marked diurnal rhythms of activity either under room conditions or under controlled lighting (L:D/12:12), although they were mainly active during the first few hours of illumination. Activity was largely suppressed at 30°C but reappeared when the temperature was lowered to 20°C. A clear rhythm was occasionally seen when the animals were exposed to 12 h ultra-violet light followed by 12 h darkness. The rhythm is endogenous and circadian, free-running more obviously in darkness (DD) than in constant light (LL). It was expressed more clearly in groups of three terrapins than in pairs or individual animals. The implications of these results are discussed.

INTRODUCTION

Although numerous qualitative observations have been made on daily rhythms of locomotory activity in reptiles, surprisingly little quantitative information is available, especially in relation to aquatic terrapins (cf. Cloudsley-Thompson, 1971), with the possible exception of *Pseudemys scripta elegans* (Wied). Brett (1971) recorded spontaneous locomotory activity in six small terrapins belonging to this species and showed that, in normal day–night conditions, above average activity began just before sunrise at 05.00 h and lasted until 10.00 h. Both caged and control animals exhibited a persistent solar rhythm in constant low illumination, and there was some indication of a persistent lunar day rhythm as well. Brett did not, however, investigate advancement or retardation of the onset of activity when the rhythm was free-running. Quay (1967) demonstrated 24-h rhythms in cerebral and brainstem content of 5-hydroxytryptamine in baby *P. scripta elegans* under a standard artificial daily photoperiod (04.00–18.00 hr), while De Rosa & Taylor (1978) found that *Chrysemys picta* (Schneider) exhibits time-compensated sun-compass orientation. The experiments described below were undertaken to investigate the effects of alternating light and darkness (LD) and fluctuating temperatures in synchronizing or entraining the circadian rhythm of locomotory activity in baby *P. scripta elegans* in the laboratory.

MATERIAL AND METHODS

Experiments were carried out in the laboratory on 8 juvenile red-eared terrapins (*Pseudemys scripta elegans* (Wied)) over a period of about six months. The animals were obtained from a dealer. They measured approximately 35 × 35 mm and weighed about 7.5–8.5 g. When not being used in experiments, they were fed and cared for as recommended by Boycott & Robins (1960).

Activity was monitored by means of aktograph apparatus devised by Constantinou (1980). The terrapins were placed singly, or in groups, in crystallizing dishes containing water to a depth of about 2 cm and a stone onto which they could climb. Above each dish was a lid made of two copper sheets insulated from one another by rods of Perspex 1 cm in length. The upper sheets were connected to the negative pole of a 24 V d.c. power supply, the lower to a multi-channel event recorder. The electric circuits incorporating the activity cages, power supply, and event recorder, were made or broken by steel pins suspended from the upper sheets of the lids and passing through holes in the lower sheets. As the terrapins moved in the crystallizing dishes, they touched the suspended pins and deflected them so that contact was made with the lower halves of the lids, thus completing the electrical circuits. The lower portions of the pins, which dipped into the water, were covered with fine plastic tubing both to insulate and to soften them.

The aktographs were placed on a window bench when activity under room conditions was being monitored; or in a growth cabinet within which both light and temperature were controlled automatically. The intensity of illumination falling on the crystallizing dishes where they were illuminated in the cabinet was approximately 600 lux.

RESULTS

The juvenile terrapins did not show any very marked rhythm of activity. Under room conditions, they were mainly active during the early hours of daylight, but the rhythm soon broke down in constant darkness (DD) (Fig. 1). Nor was it particularly marked under controlled conditions of 12 h light (600 lux) followed by 12 h darkness (L:D/12:12) (Fig. 2). No effect on the

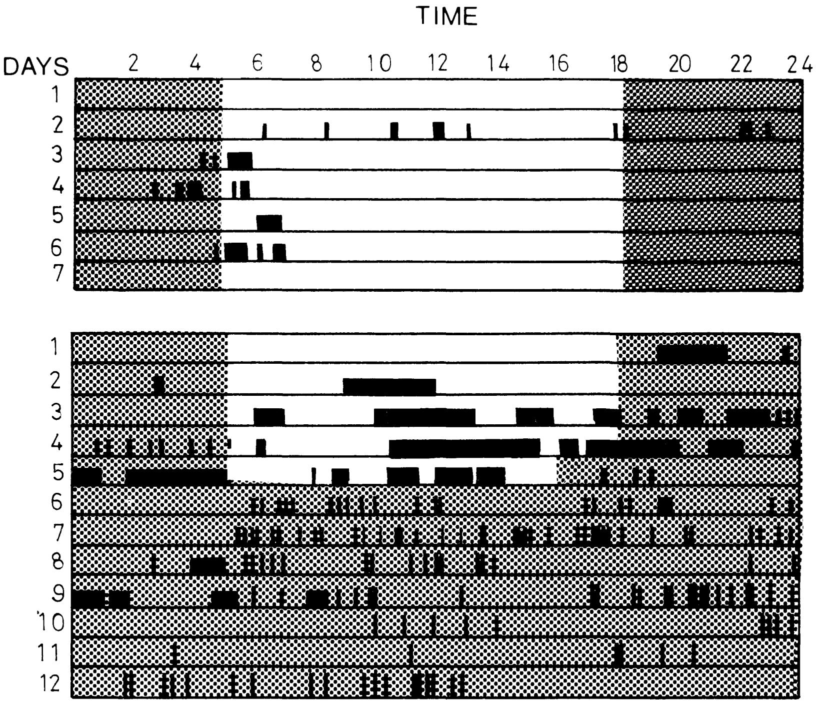


FIG 1 (a). Activity of a single *P. scripta elegans* in room conditions (*c.* 21°C). Ordinates: days, Abscissa: time (h).

FIG. 1 (b). Activity of a group of four terrapins for 5 days in room conditions (*c.* 21°C) followed by constant darkness (DD) (days 6–12).

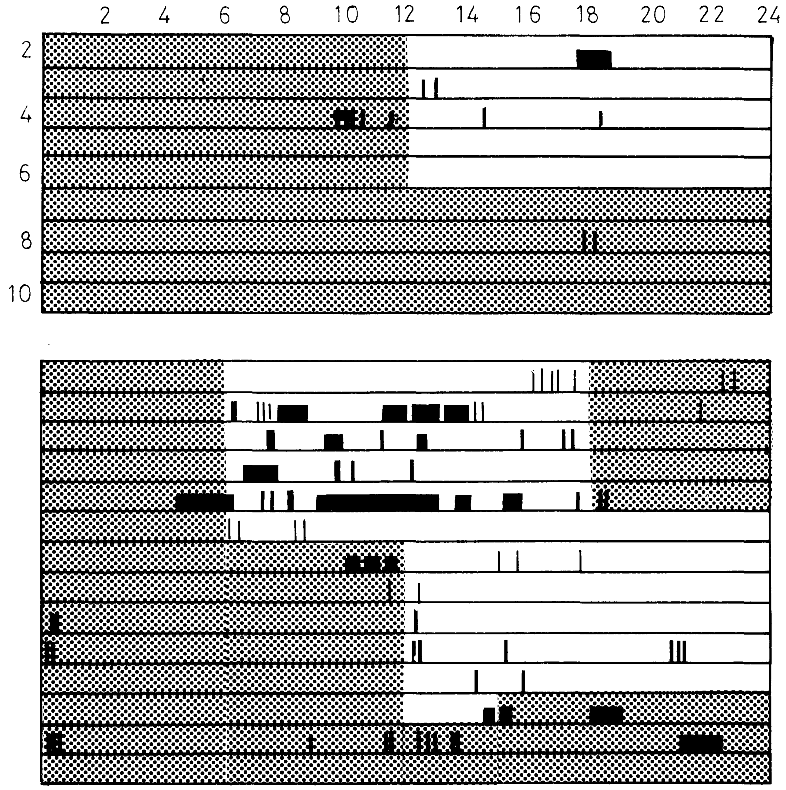


FIG. 2 (a). Activity of a pair of terrapins at 23°C in L:D/12:12 followed by DD.

FIG. 2 (b). Activity of a pair of terrapins in L:D/12:12 (20°C in dark, 30°C in light) followed by DD (20°C).

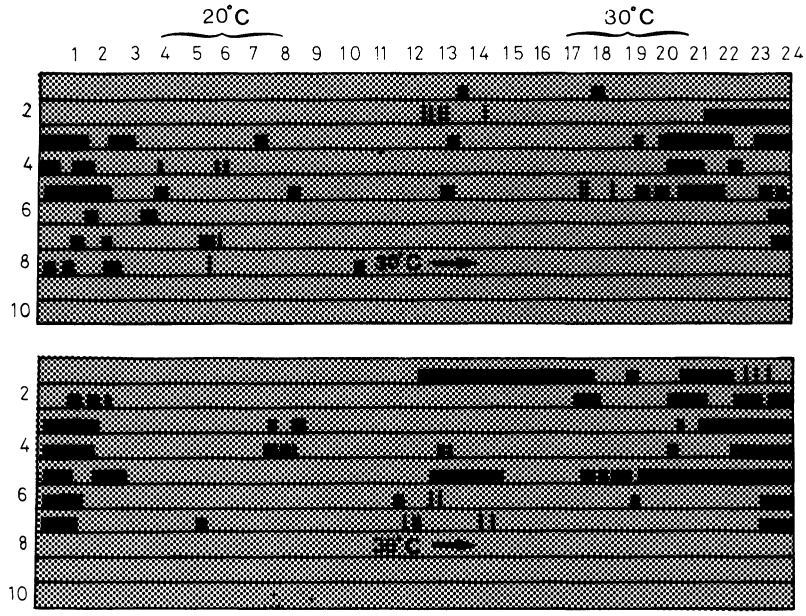


Fig. 3 (a). Activity of a pair of terrapins in DD with 12 h at 20°C alternating with 12 h at 30°C.

Fig. 3 (b). Replicate experiment with another pair of terrapins.

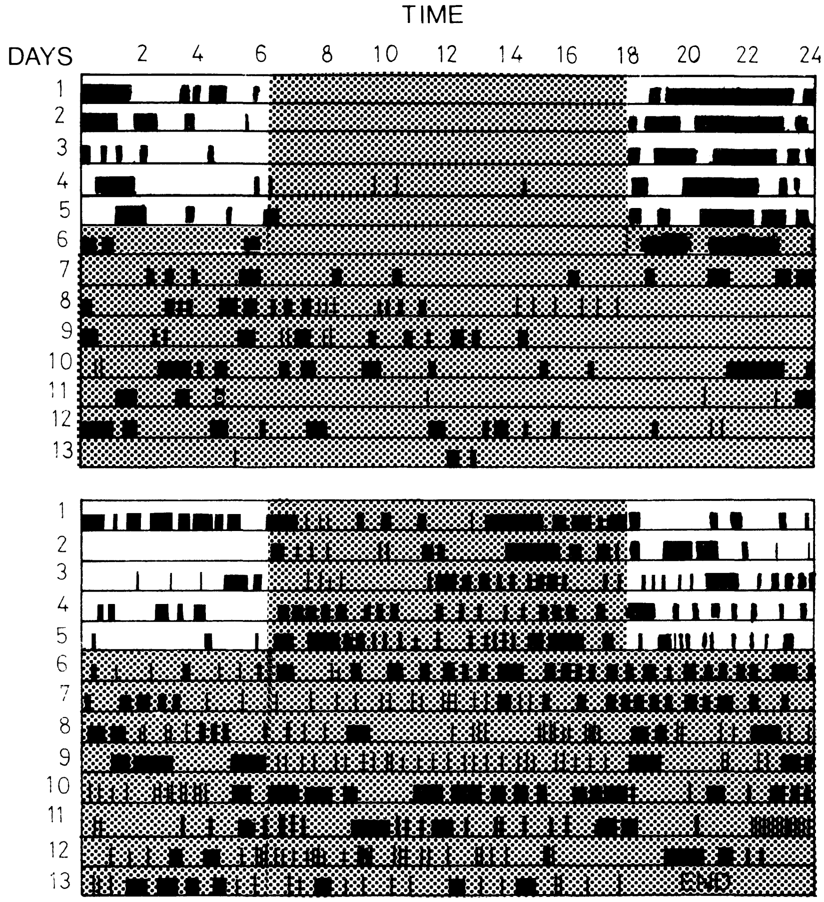
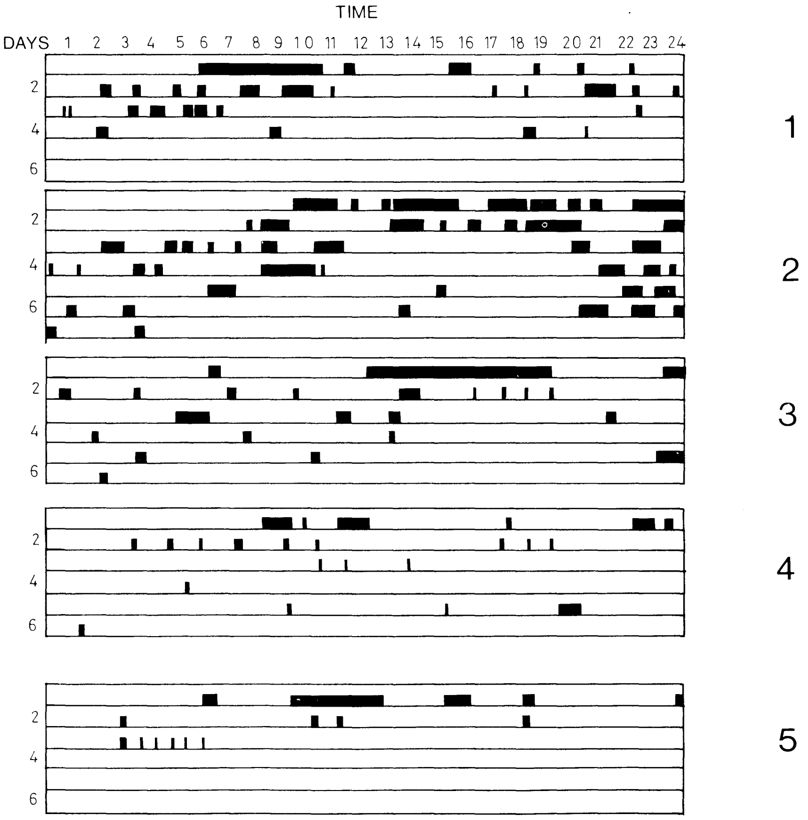


Fig. 4 (a). Activity of a single terrapin exposed daily to 12 h ultra-violet light alternating with 12 h darkness at 20°C, followed by DD.

Fig. 4 (b). Replicate experiment with another terrapin.



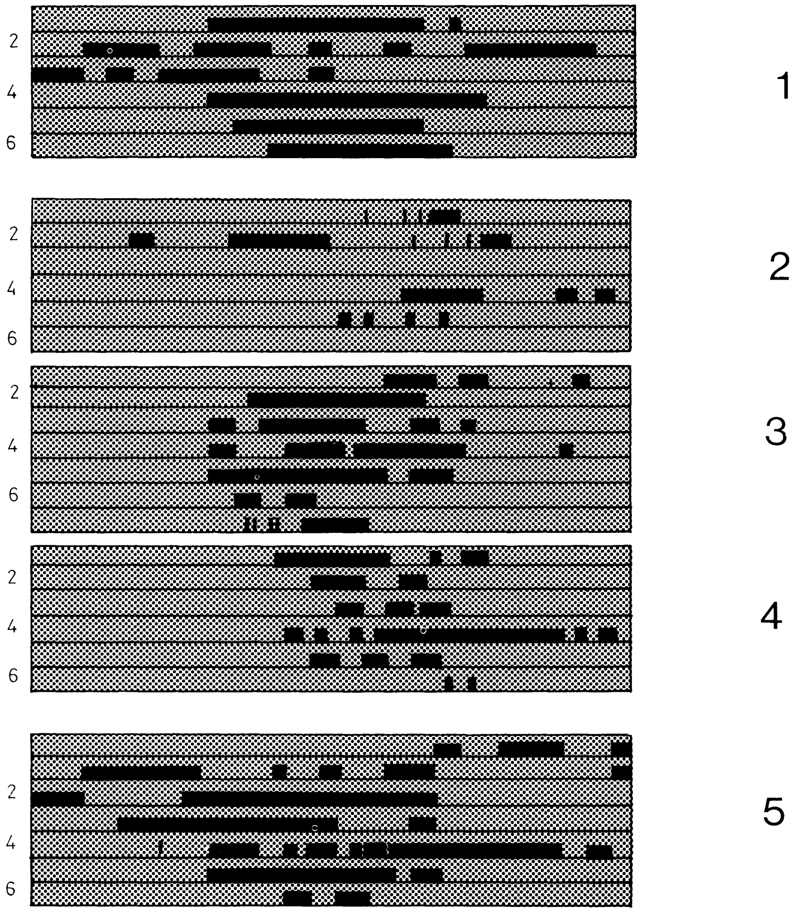


FIG. 5 (a). Activity of isolated terrapins in LL at 23°C after entrainment in L:D/12:12.
FIG. 5 (b). Activity of isolated terrapins in DD at 23°C after entrainment in L:D/12:12.

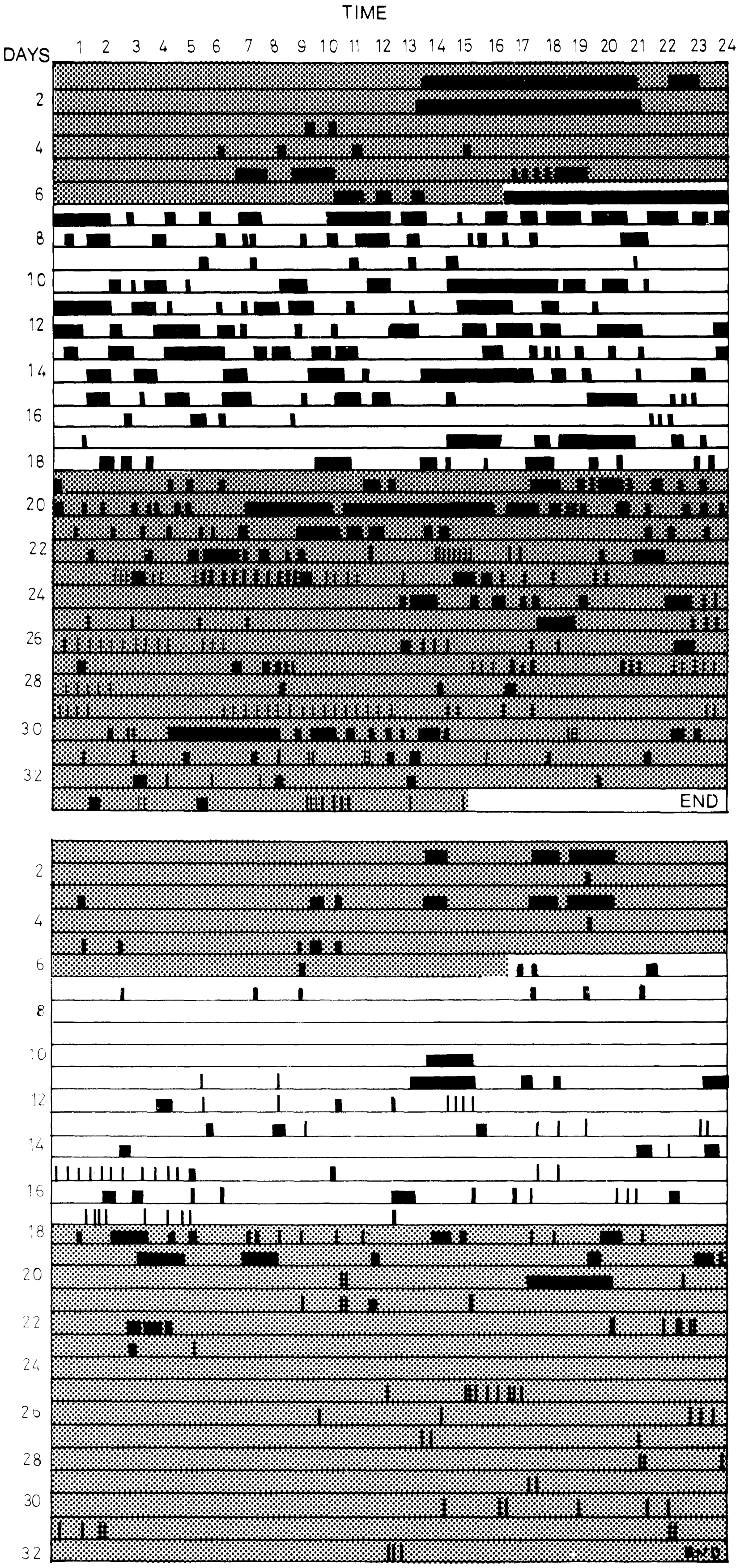


FIG. 6 (a). Activity of a group of three terrapins (entrainment to L:D/12:12) at 22°C in DD for 5 days 16 h followed by LL for 12 days and then DD for a further 15 days.
FIG. 6 (b). Replicate experiment with a pair of terrapins.

rhythm was noted when one side of the crystallizing dish was surrounded with black plastic and a black curtain suspended from the lid across the centre, almost excluding light from one half of the arena. (The object of this experiment was to allow the terrapins a choice of light or darkness during the light period so that their activity rhythm should not be influenced by light stimulation from which no escape was possible.)

Activity was largely suppressed at 30°C, but reappeared when the temperature was lowered to 20°C. This effect was clearly shown in experiments in which 12 h at 20°C alternated with 12 h at 30°C in DD. As can be seen in Fig. 3, the bulk of activity occurred during the last few hours at 20°C when the water in the crystallizing dishes had cooled, and during the first few hours at 30°C before it had fully warmed up.

When exposed to ultra-violet light from 06.00–18.00 h, a clear rhythm was occasionally, but by no means always to be seen. In these conditions, when a rhythm did appear, the bulk of activity took place in the UV light (Fig. 4).

Experiments were carried out in continuous light (LL) or darkness (DD) at constant temperatures (23°C) to determine whether or not the activity rhythm was endogenous and free-ran under constant laboratory conditions. As can be seen from Fig. 5 this was, indeed, sometimes the case, the rhythm free-running more obviously in DD (Fig. 5b) than in LL (Fig. 5a). After free-running in darkness for several days the rhythm broke up completely when the juvenile terrapins were maintained in constant light (Fig. 6a), but there was some indication that the rhythm was resynchronized when the animals were returned to DD. The rhythms were usually clearer and more activity expressed in groups of three terrapins than in a parallel experiment, in which the animals were in pairs or else separated from one another (Fig. 6b).

The records selected for presentation in Figs. 1–2 are those which illustrate most convincingly the effects described.

DISCUSSION

Unlike many reptiles, which exhibit clear rhythms of locomotory activity (*vide* Cloudsley-Thompson, 1971), juvenile *P. scripta elegans* do not show very well marked 24-h rhythms—either exogenous or circadian. In contrast, Ernst (1976) noted that, in the field, activity of the spotted turtle *Clemmys guttata* (Schneider) is limited to the hours of daylight. As darkness approaches the animals burrow into the muddy bottom of some waterway, or crawl into muskrat burrows where they remain immobile until dawn. Only nesting females are active after dark. Babcock (1919) reported that captive turtles preferred to sleep out of water—possibly an adaptation against predation by raccoons. When the sun rose, however, they left their nesting places and either basked until warm or foraged for food.

The influence of temperature on circadian activity in terrapins is probably more complex than it might, at first, seem. That is to say, its effect is more than one of simple thresholds of activity. For instance, Ernst (1972) recorded cloacal temperatures in wild adult *Chrysemys picta* during various phases of the normal activities throughout the year. He calculated that the optimum temperature was 20.5°C, and that the normal activity range was 8–26.8°C—below 30°C at which activity is inhibited in *P. scripta elegans*. The critical thermal maximum for *C. picta* was 41.5°C. Again, Gatten (1974) found that, after feeding, the thermal preferendum of red-eared terrapins increased from 24.6°C to 29.1°C. On the other hand, replete specimens of *Terrapene ornata* (Agassiz) exhibited less variability of body temperature than did fasting individuals, but had a thermal preferendum of 29.8°C, only 1.5°C above that of animals deprived of food for 7–14 days. Nutritional status thus significantly affects thermoregulatory behaviour, but differently in different species of chelonians. A distinct phase response of locomotory activity to temperature has been found in the turtles *C. picta*, *Clemmys guttata* and *Sternotherus odoratus* (Latr.). Bimodal rhythms were evident at higher temperatures (25°C) and unimodal patterns at lower temperatures (15°C). In the case of *Emys* [*Emydoidea*] *blandingii* (Holbrook), a similar effect was noted. At the same time, the phase response appeared to be adaptive because, at a given temperature, activity was greatest at times when ambient temperature in the field might be most conducive for activity (Graham, 1979).

Activity rhythms are frequently less marked in juvenile than in older animals of the same species. This may account for the fact that Brett (1971), who worked on larger specimens, obtained a clearer rhythm than that described here among younger individuals of *P. scripta elegans*. It is possible that circadian rhythmicity may take some time to develop and mature. The adaptive functions of circadian rhythms have been studied comparatively little (Cloudsley-Thompson, 1980). It may be of significance, however, that the activity of young red-eared terrapins is sometimes markedly increased in UV light: Brett & Robins (1960) have pointed out that ultra-violet light is essential for proper growth. It is obvious that low temperature must impose a threshold to the activity of poikilothermic animals. In *Testudo graeca* (L), above about 25°C, there is an excess of metabolic heat production over evaporative heat loss (Cloudsley-Thompson & Butt, 1977). If the same is true of *P. scripta elegans*, as may well be the case, the cessation of activity at higher temperatures (30°C) could well be a method of minimizing the excess heat load.

ACKNOWLEDGEMENT

My thanks are due to Eileen Bergh for typing this manuscript and to Roy Abrahams for drawing the figures.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 194–197 (1982)

BODY TEMPERATURES AND ACTIVITY PATTERNS OF *TESTUDO GRAECA* IN NORTH WEST AFRICA

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(*Received* 4 *July* 1981)

SUMMARY

Field observations were made on the behaviour and body temperatures of four individual *Testudo graeca* in their scrubland habitat in North West Africa. To regulate body temperature *Testudo graeca* spends a large part of the day shuttling between sunlit and shaded areas. Throughout the morning and early afternoon much of the tortoises' time is spent either at basking sites close to shade or moving around in more open areas. This behaviour results in increases in body temperature. By early afternoon maximum body temperatures are reached and a period of stability in body temperature begins. Within this stable phase the tortoises more evenly divide their time between the various types of activity. Although feeding takes place throughout most of the day there is no strong tendency for this to occur during any particular time period. During the late afternoon much of the tortoises' time is spent in the shade, resulting in a decline in body temperature.

INTRODUCTION

The spur-thighed tortoise *Testudo graeca* has an extensive distribution over Europe, Asia and North Africa. In the warm dry region of North Africa it appears to favour the sunny scrub covered hillsides where there are good basking and shaded areas. During the summer months, however, the populations inhabiting the coastal regions of North West Africa are subject to persistant sea mists which drift inland during the late afternoon and which may remain until late morning or early afternoon the following day. The effects of these mists are that they reduce the heat levels in the tortoise habitat to much lower levels than are experienced on days when the skies are clear. This paper is concerned with the thermoregulatory behaviour of *Testudo graeca* under these conditions as observed during late May and early June.

In the laboratory, thermoregulation and thermoregulatory behaviour in *Testudo graeca* has been reported by Bannikov (1951) and Cloudsley-Thompson (1974) and in both laboratory and in the field by Lambert (1981). The closely related *T. hermanni* has been dealt with by Cherchi (1956, 1960) and Cherchi, Holzer, Scortecci & Serrato (1958).

METHODS, MATERIALS AND STUDY SITE

The field work was carried out during late May and early June 1980 on four individual *T. graeca*. The

TABLE I. Body masses, carapace lengths and sexes of the four tortoises

Code	Sex	Mass (g)	Carapace length (mm)
T1	Male	640	137
T2	Male	720	144
T3	Male	660	145
T4	Female	1370	185

tortoises were located in an area of dry scrubland on the coast of Southern Morocco and were marked for future identification with the codes T1, T2, T3 or T4 on the backs of the carapaces with Indian ink. The lengths (measured as a straight line from the nuchal to the supracaudal scute), body masses and sexes of the animals are shown in Table I. Body temperatures were recorded by inserting a mercury bulb thermometer into the cloaca. Soil and ambient air temperatures were recorded simultaneously; soil temperatures by inserting the bulb 8 mm into the soil, air temperatures with the bulb shaded.

Behavioural patterns were monitored by locating the animals when possible at approximately 15-min intervals and noting their particular behaviour. Behavioural patterns were defined in the following manner: *basking*, inactive at a particular site which was fully exposed to the suns rays. *Shade*, situated in a shaded area where no sunlight penetrated. *Feeding*, which may have taken place in a shaded or sunlit area therefore an additional data point was awarded to either shade or active data to allow for the possible effects of the tortoises' position on its body temperature. *Active*: we observed essentially two types of "active" behaviour: (a) when the animals were found moving around the study site in open areas. Movement here was irregular consisting of periods of walking interupted by longer periods of inactivity. This type of behaviour usually occurred during the earlier part of the day. (b) Extended activity, consisting of much longer periods of walking when the tortoises appeared to be investigating their habitat perhaps in search of food plants. This behaviour was typical of afternoon "activity".

RESULTS

BEHAVIOUR

Shuttling between basking sites and shaded areas was an important part of daily behaviour and accounted for 62·9% of the total daily activity recorded over 3 days ($n = 108$). The greatest amount of time was spent in the shade (35.3%) with basking time slightly less (27.6%). Movement around the habitat (walking) accounted for 26.4% of the time while feeding amounted to 12.3%. Figure 1 is a histogram of a single day's observations ($n = 69$) on these behavioural patterns

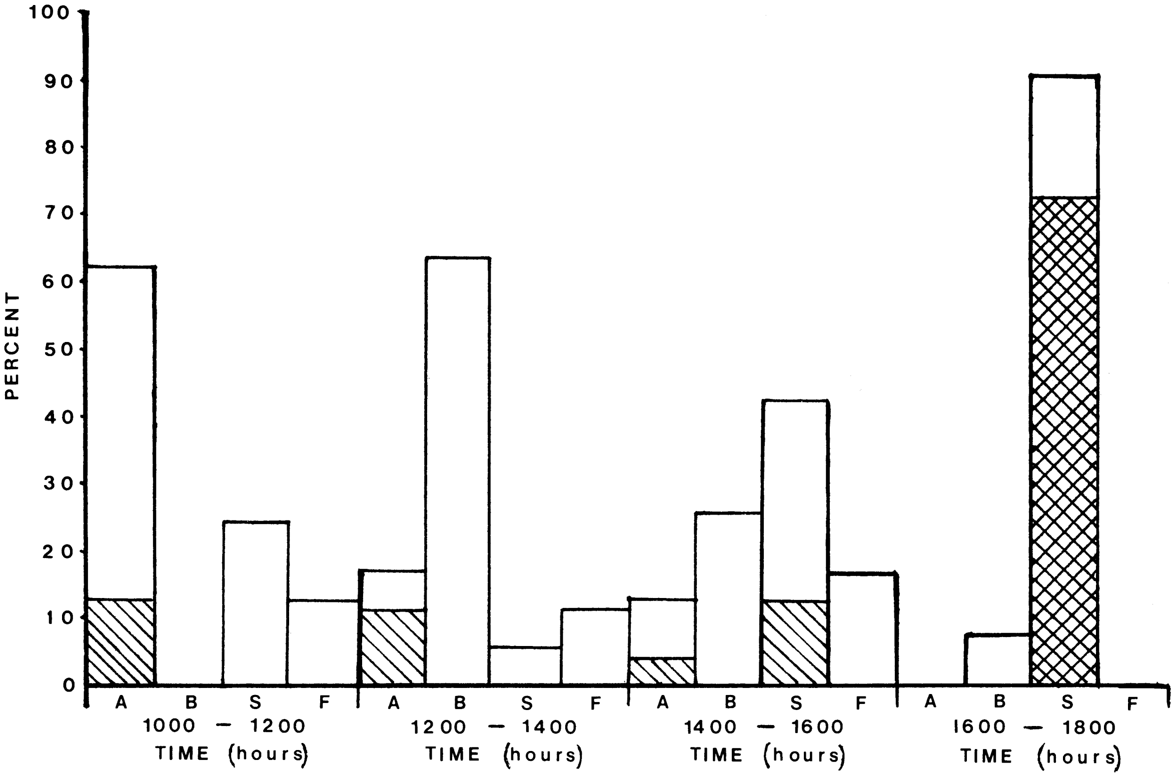

FIG. 1. Histogram of daily behaviour patterns in *Testudo graeca* recorded over one day ($n = 69$) in which each particular behaviour is shown as a percentage of the total observed behaviour within 2 hourly unit periods. Between 1000–1600 h the hatched areas represent the distribution of feeding data on active or shade data. The cross hatched area on shade data during the last time period shows the amount of data recorded after all four tortoises had retreated into shade, which may represent the end of daily activity. A = active; B = basking; S = shade; F = feeding.

sectioned into 2 hourly unit periods. This shows that movement around the habitat took place mainly between 1000–1200 h (62%). Basking was performed mostly between 1200–1400 h when it amounted to 64% of the period. The amount of time spent in the shade increased to 93% during the last period of activity (1600–1800 h) during which time the animals retreated to their nightly resting spots. Feeding was observed to occur in either shaded or open areas throughout most of the day except within the period between 1600–1800 h during which time the sea mist began to drift inshore (Fig. 2). Time spent feeding never accounted for more than 18% of the total of any time period.

Body Temperatures

Basking was normally performed in a secluded but exposed site close to cover. Figure 2 shows the relationship between the body temperatures of the four tortoises over a single daily period in relation to air and soil temperatures. On this day a range of body temperatures from 22–35°C ($\bar{x} = 29.8$°C, $n = 54$) was recorded. Body temperatures were highest (33–35°C) between 1300–1700 h, the time when the skies were mostly free of the sea mist. From a comparison of the data shown in Figs. 1 and 2 it can be seen that increases in body temperature took place mainly in the morning and early afternoon but increased steeply between 1200–1400 h, the time during which basking was most pronounced. There then followed a period of body temperature stability which began after maximum body temperatures are reached. The amount of time spent in the shade increased in the late afternoon and as a result body temperatures began to decline.

Soil temperatures were the highest environmental variable and only 16.6% of the body temperature records exceeded them. The greatest temperature differential between body and soil temperatures was never at any time more than 3°C. However 87% of body temperatures where in excess of air temperatures and here the differential could be as high as 11.5°C. For most of the day body temperatures lay between soil and air temperatures (68.5%).

DISCUSSION

The relationship between the thermal environment and reptilian behaviour has been described by many workers (for reviews see Templeton, 1970; Cloudsley-Thompson, 1971; Heatwole, 1976). These show that most heliothermic reptiles perform a somewhat predictable sequence of behavioural patterns which enable them to successfully maintain stable body temperatures for at least part of the day. The present results indicate that despite the inclement weather conditions, *T. graeca*, can, by adopting set behavioural routines, elevate and maintain body temperatures to within narrow limits. Figure 2 shows that body temperatures approximately fall into three stages: (i) a heating phase,

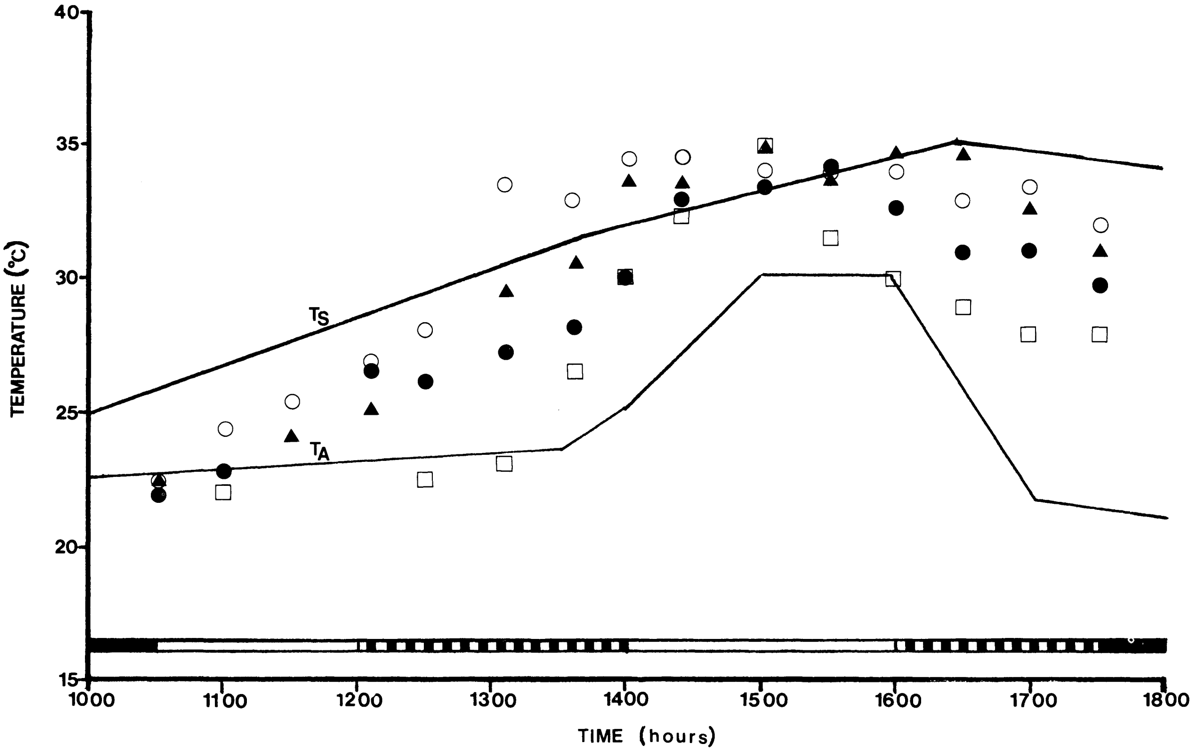

Fig. 2. Sample of body temperatures of four individual *Testudo graeca* in relation to changes in air temperature (Ta), soil temperature (Ts) and weather conditions recorded over a single daily period. Weather conditions are shown as a horizontal bar at the lower end of the graph. The light section represents the time when clear cloudless skies prevailed, the dark section when the sky was mostly covered in mist and the stippled area when clear and misty skies were alternating. The key to the symbols for the tortoises are T1 = ●, T2 = ○, T3 = ▲, T4 = □.

(ii) a stable phase and (iii) a cooling phase. Under the climatic conditions during the period that the data were gathered, increases in body temperature occurred throughout the morning and early afternoon when the tortoises spent the greatest amount of their time exposed to solar radiation (either when they were basking or moving around in exposed areas of their habitat). The stable phase was entered around 1400 h and lasted until about 1630 h. During this period maximum voluntary body temperatures were reached and the animals more evenly devoted their time to other functions such as feeding. Entry into the cooling phase began in the late afternoon when the sea mists shifted back inland.

The maximum voluntary body temperature of 33–35°C selected by our animals compares with a maximum voluntary temperature of 35°C selected by a captive *T. graeca* living in a greenhouse in southern Britain (Lambert, 1981). This is several degrees below the critical thermal maximum of 42.8–43.6°C recorded for *T. graeca* by Hutchison, Vinegar & Kosh (1966) and the 39.5°C at which thermoregulatory salivation is initiated (Cloudsley-Thompson, 1974). The maximum voluntary temperature in *T. graeca* closely approximates that found for the related *T. hermanni* in the laboratory (32°C; Cherchi, 1956) and field (34°C; Meek & Inskeep, 1981), which are also several degrees below the critical thermal maximum of 39–42°C and lethal maximum of 44–45°C recorded for this species (Cherchi, 1956).

Swingland & Frazier (1979) found that on cloudy days the Aldabran giant tortoise (*Geochelone gigantea*) is active all day, but operates at lower body temperatures than on days when the skies are clear. By using a spot survey technique on North African, Eastern European and Western Asian populations of *T. graeca*, Lambert (1981) found that basking took place during the earlier part of the morning when the skies were clear but that basking could persist until the middle of the day when the skies had been clouded over earlier. Our data in Fig. 1 shows that with the presence of sea mists, basking did not begin until mid-day, although the tortoises were to some extent active in the morning. However, this situation may be a result of our interpretation of behaviour, since it is possible that the behaviour which we defined as "early morning activity" is in fact partly a basking strategy perhaps employed when climatic conditions are less than favourable.

ACKNOWLEDGEMENTS

We thank Professor R. McNiell Alexander for critically reviewing the manuscript, Mr K. Umpleby for assistance in the field and Mrs Helen Meek for typing the manuscript. We should also like to thank Dr I. R. Swingland and Dr M. R. K. Lambert for sending us reprints of their papers on tortoises.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 198–199 (1982)

ALLOMETRY IN CHELONIANS

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(*Received* 25 *July* 1981)

SUMMARY

Measurements have been made on the relationship between body mass and carapace length in four species of chelonian. The results, in the form of allometric equations, show that in general carapace length is proportional to body mass$^{0.34}$.

INTRODUCTION

Jackson (1978, 1980) has reported on a relationship between carapace length and body mass in *Testudo graeca* and *Testudo hermanni*. His method of determining this relationship, by dividing mass by the carapace length, produced a series of ratios ranging from 0.39 to 7.90 in *T. graeca* and from 1.99 to 9.19 in *T. hermanni*. By comparing data from sick tortoises, Jackson (1980) argued that it should be possible to determine the health of each individual animal by use of these ratios. Recently Lawrence (1981) using Jackson's method, has produced ratios for several species of Chelonia from data held in the stock records of the Association for the Study of Reptilia and Amphibia. With these data, which in addition to measurements on *T. graeca* and *T. hermanni* included two freshwater species of Chelonia, Lawrence produced ratios which unfortunately appear to vary in even greater extent to those supplied in Jackson's (1980) paper.

The purpose of this paper is to produce a single mathematical formula for each species in the form of allometric equations which can be equally applied to either adults, sub-adults or juveniles. It is demonstrated that by the use of standard statistical techniques for dealing with length–body mass data, equations can be produced which in comparison to the methods used by Jackson (1978, 1980) and Lawrence (1981) give a clearer and more accurate definition of the allometric growth relationships. The principles of allometry and examples of its uses with other types of biological data have been described by Alexander (1971).

METHODS

Data from four species of Chelonia from the ASRA stock records detailed by Lawrence (1981) were used in the analysis. These species were: *Testudo graeca* (78–2381 g), *Testudo hermanni* (796–2198 g), *Emys orbicularis* (60–595 g) and *Chrysemys* (=*Pseudemys*) *scripta elegans* (25–1276 g). The standard method for measuring carapace length in chelonians is by taking a straight line from the nuchal to the supracaudal scute; it is assumed here that the measurements given by Lawrence (1981) are of this form. Allometric equations were obtained from the data by least-squares regression after transforming the data to logarithmic form (Bailey, 1959). The t distribution was used to assign 95% confidence limits to the exponents. Body mass was treated as the independent variable and carapace length as the dependent variable.

RESULTS

Figure 1 shows the data for all four species plotted on logarithmic coordinates. The allometric equations that have been derived from these data are of the form $y = ax^b$. This is where y = carapace length in mm, a = the intercept and b an exponent of the mass x in g.

This gave for *Emys orbicularis*,

$$y = 10.84 \times \text{mass}^{0.41\pm0.06} \quad r = 0.99, n = 7,$$

Chrysemys scripta,

$$y = 15.25 \times \text{mass}^{0.36\pm0.01} \quad r = 0.99, n = 26,$$

Testudo graeca,

$$y = 21.43 \times \text{mass}^{0.30\pm0.03} \quad r = 0.97, n = 28,$$

Testudo hermanni,

$$y = 11.87 \times \text{mass}^{0.38\pm0.11} \quad r = 0.94, n = 9.$$

r = correlation coefficient, n = the number of data points. A comprehensive equation obtained by combining all four data sets gives

$$y = 16.77 \times \text{mass}^{0.34\pm0.01} \quad r = 0.98, n = 70.$$

The line predicted by the constants in this equation in relation to all four data sets on logarithmic coordinates is shown in Fig. 1.

DISCUSSION

The study of allometric growth curves provides a useful basis for establishing the relationship between body mass and carapace length in chelonians. The availability of the data sets from the ASRA stock records has enabled the calculation of allometric equations which define the growth relationships of four commonly kept species of chelonian. By use of these

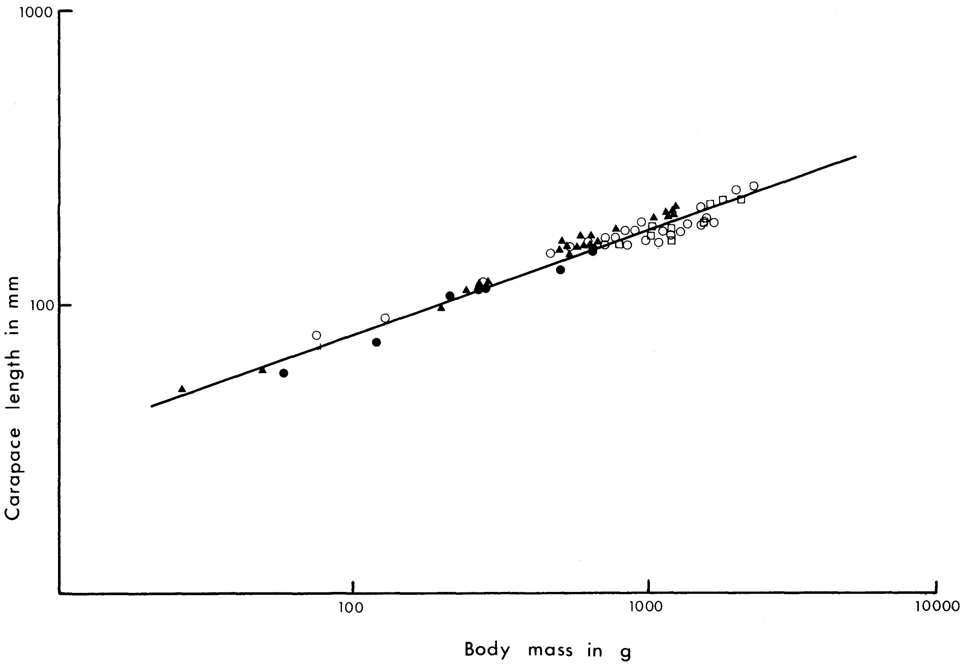

FIG. 1. A graph on logarithmic coordinates showing body mass plotted against carapace length in all four species of Chelonian discussed in the text. The line taken through the data is derived from the constants in the comprehensive equation. The symbols for each species are *T. graeca* = ○, *T. hermanni* = □, *E. orbicularis* = ●, *C. scripta* = ▲.

equations it is possible to determine whether a given individual has a typical body mass–carapace length relationship for its species. Although the equations are based on only small samples, it can be seen from the graph and the high correlation coefficients that the equations provide a reliable description of the data that has been analysed. If it can be assumed that this is typical data for the captive chelonians dealt with in this paper and that there is no radical change in growth strategy then the equations should also be reliable for size ranges not included in the samples.

The equations can also be used to compare the growth relationships between species or populations. Here when two exponents are compared the lower value indicates a relatively greater increase in body mass in relation to increases in carapace length; an exponent of 0.33 indicates geometric similarity. In this respect it is interesting to compare the data for captive animals with those for wild tortoises, since differences in diet, food availability, and perhaps seasonal changes in climate, may produce fluctuations in body mass. Data are available for wild *T. hermanni* from Yugoslavia and Greece. Meek & Inskeep (1981) working with a Yugoslavian population found an exponent of 0.35 in their animals which when allowing for the confidence limits suggests that they do not differ too greatly from the captive tortoises. Stubbs, Hailey, Tyler & Pulford (1981) have published data for Greek populations but have not quantified the relationship. However, from their graph it is estimated that,

$$y \approx 16.00 \times \text{mass}^{0.35}.$$

This equation is closer to the one for other wild *T. hermanni* than that for captive animals.

Exponents of 0.35 and 0.38 have been found for wild *Mauremys caspica* in North Africa (Meek, in preparation); these agree well with the exponent for captive *Chrysemys scripta* but are lower than that found for captive *Emys orbicularis*.

ACKNOWLEDGEMENTS

I thank Professor R. McNeill Alexander and A. S. Jayes for reading the manuscript, and my wife Helen for the typing.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 200–202 (1982)

SEMEN COLLECTION BY ELECTROEJACULATION OF THE GREEN TURTLE, *CHELONIA MYDAS*

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(*Received* 8 *August* 1981)

SUMMARY

Electroejaculation was used to obtain motile sperm from farm reared green turtles, *Chelonia mydas*, at the breeding facilities of Cayman Turtle Farm Ltd. Motility and volume was variable depending upon time and frequency of ejaculation and the individual male used. Total sperm counts up to 66 × 10^8 were observed with percent motility as high as 90%. Of over 70 attempts, 60% yielded motile sperm. This technique was employed with males nine to 14 years old and weighing 110 to 175 kg. Semen collection is the first step in a continuing programme to develop a successful technique of artificial insemination.

INTRODUCTION

Since 1973, mating and subsequent nesting has occurred among the captive breeding colony of green turtles *Chelonia mydas* at the facilities of Cayman Turtle Farm, Ltd., a commercial sea turtle farm in the British West Indies (Wood & Wood, 1980). A programme to develop the means to collect semen and artificially inseminate turtles on the farm was initiated in 1978. This programme was designed to compliment the on-going reproductive programme by providing information on the sperm production capabilities of the males, by enabling artificial insemination of nesting females whose first nests in a season show no signs of embryonic development, and by eventually allowing for controlled and selective breeding among the farm's stock. Initial collection attempts and description of the turtle spermatozoa morphology have been previously presented (Platz, Mengden, Quinn, Wood & Wood, 1980).

MATERIALS AND METHODS

Male green turtles hatched and reared to maturity at Cayman Turtle Farm Ltd. were maintained in one of two excavated ponds each containing approximately one million gallons of constantly flowing sea water. These turtles ranged in age from nine to 14 years and weighed from 110 to 175 kg. The turtles were fed a commercial high protein (35%) pelleted diet. The males were kept with the females in the pond from March through November for the breeding season. Female to male ratio varied from 4.3:1 to 8.6:1, depending on the year. During the remaining months, the males were kept separated either in a fenced section of the pond or in stock tanks. Data presented were collected from April 1979 through July 1981.

The following procedure was routinely followed for collection and evaluation of ejaculate:

1. The male was removed from the water and lifted onto a metal rack, approximately 50 cm high, and secured to the rack with ropes from all four flippers. The tail was allowed to hang unsupported from the edge of the rack. Anesthesia was not used in the collections. The tail was rinsed with sea water to remove any sand or particular matter.
2. The electroejaculator (constructed by C. Platz) was an AC 60 Hz stimulator. The rectal probe consisted of a PVC tube 70 cm long and 2.5 cm in diameter containing three stainless steel electrodes, 13 cm long running within 1.0 cm parallel to each other at the end of the probe. The probe was coated with petroleum jelly and inserted through the cloaca into the rectum 40–60 cm, depending upon the size of the male.
3. Normal stimulus consisted of 15 stimuli, 4–8 volts in intensity, effective amperage 0.15–0.40 amperes. Stimulus duration was 3–4 seconds from 0 to peak voltage to 0 again without pause at peak voltage. Approximately 2 seconds rest was allowed between stimuli. The series of 15 stimuli was repeated at four to five depths as the probe was withdrawn 8 to 10 cm at a time. Following removal of the probe, the tail and penis, if extended, was milked manually to aid in removal of any remaining ejaculate. The turtle was then returned to the water.
4. The semen was collected in 5 ml of normal saline and examined immediately for percent motility, progressive motility and total sperm count (Platz & Seager, 1977; Platz, Wildt & Seager, 1978).

RESULTS AND DISCUSSION

Table I summarizes 74 attempted collections. Ejaculate containing sperm was obtained in 55 attempts. Fourteen of these 55 collections had no motile sperm or the total count was so low as to indicate that the ejaculate would be inadequate for fertilization of a female. No abnormal spermatozoa were observed in samples which were examined at high magnifications. The ejaculate was often quite viscous and frequently contained clumps of material, which when manually broken apart contained millions of spermatozoa. The volume of ejaculate varied between 1 to 2 ml up to 100 ml.

The physical response of the male to stimulus was variable among the males. In some instances the penis would be extended as the male was secured to the rack. In other instances, the penis was extended following the initial stimulus. Ejaculates containing viable sperm were also obtained without the penis ever being exposed. Urination was also variable, some urinating before or after stimulation and others not at all. In a few instances the turtle defecated on partial insertion of the probe, in which cases, the turtle was released because clean samples were unable to be obtained afterwards. In addition to the 74 attempted collections summarized in Table I, several males were secured on the rack, but insertion of the probe caused minor bleeding and the turtle was released. These turtles showed no continued bleeding or ill effects when observed in the water following the attempts.

Although the normal electroejaculation procedure consisted of a series of stimuli, in some instances, the male would ejaculate without any electrical stimulus. This occurred during six separate attempts when the male ejaculated as the probe was inserted. In approximately 10% of the collections, an ejaculate was obtained after only a few stimuli. To minimize stress to the male, no further stimulus other than manual milking of the tail and penis was applied once an ejaculate containing motile sperm was obtained.

TABLE I. Summary of semen collections

Number of attempted collections	74
Number of collections with sperm	55
Volume of ejaculate, range	1–100 ml
% motility, range	0–90%
Average motility (55 collections)	36%
Total sperm count in ejaculate, range	0–6600 × 10^6
Average count (55 collections)	470 × 10^6
Age of males (28 males)	9–14 years
Size of males (28 males)	110–175 kg

TABLE II. Successive electroejaculation of three males

	Day				
Male	1	2	3	4	5
118					
% Motility	0	5	0	0	5
Total sperm count, $\times 10^6$	0	5	30	30	33
124					
% Motility	5	25	65	0	0
Total sperm count, $\times 10^6$	48	1	182	15	0
253					
% motility	10	65	80	0	35
Total sperm count, $\times 10^6$	645	487	450	88	530

Muscular response of the males to electrical stimulus consisted of curling of the rear flippers, tensing of the neck, and a sharp intake of breath. More active movement against the restraints of the ropes and the position would occur with or without electrical stimulation. In initial electroejaculation trials described previously by Platz *et al.* (1980) higher voltages up to 30 volts (0.90 amperes) were used. However, with successive trials, the lower voltages appeared to be sufficiently effective and to have less chance of harming the turtle.

Observations on the farm's breeding stock show that the turtles mate for hours and days at a time. Three males were electroejaculated 5 days in succession to determine if sperm production is limited or time dependent over such an interval. Table II lists the results of this trial. Obviously, the variability among males is considerable, but for male 253, viable sperm with reasonable motility was collected four of five successive days.

In addition, the same male is often observed to mate throughout the season with several different females. Two males electroejaculated in successive months during 1979 demonstrated continued sperm production until October. Males nos. 288 and 10 showed respective total sperm counts (and percent motilities) in April, May, July, and October of 130 × 10^6 (20%), 350 × 10^6 (10%), 1900 × 10^6 (40%), 0 (0%); and 280 × 10^6 (80%), 100 × 10^6 (50%), 20 × 10^6 (5%), 0 (0%). Although these two males showed no sperm production in October (which is beyond the mating season of April through July), other males yielded ejaculates in October with good motility and high counts as summarized in Table III.

Data reported in this paper were obtained using males nine to 14 years of age. Only two of the 28 different males failed to produce an ejaculate containing sperm. Green turtle males of this age would appear physiologically capable of fertilizing the female. The data presented also indicated that one male would be capable of fertilizing several females in one season. There is considerable variability encountered in the electroejaculation attempts among the different males used and among the different times of the season when the collections were made. Further investigations are

TABLE III Seasonal production of sperm. Number in parentheses is actual number of attempted collections

	Feb.	April	May	June	July	Aug.	Oct.
Number of collections	1 (1)	8 (9)	15 (18)	7 (8)	12 (16)	2 (3)	11 (19)
% Motility							
Average	45	20	27	62	34	35	52
Range	—	5–80	0–80	0–90	5–60	5–70	0–80
Total sperm count, $\times 10^6$							
Average	1355	81	198	313	491	260	1035
Range	—	10–280	1–645	1–1176	10–1900	1–520	10–6600

necessary to determine if the variability is due to technical, environmental, or physiological parameters.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 202–205 (1982)

A COMPARISON OF DATES OF BREEDING ACTIVITY FOR THE FROG (*RANA TEMPORARIA*) AND THE TOAD (*BUFO BUFO*) AT A SITE IN CAMBRIDGESHIRE, 1971–1981

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(*Received* 28 *September* 1981)

SUMMARY

Dates of spawning and general breeding activity were monitored for populations of frogs (*Rana temporaria*) and toads (*Bufo bufo*) at a site in Cambridgeshire from 1971 to 1981. The relationship between the spawning dates of the two species was not statistically significant, mainly because in three of the years frogs spawned early but cold weather then delayed the onset of the toad spawning season. Periods of intense spawn production by frogs were associated with daytime maximum air temperatures of at least 5°C and night-time minima of at least 0°C. Toads assembled for spawning when temperatures were approximately 5°C higher. There was a significant relationship between the date of peak spawning activity by frogs and the date on which the largest aggregation of toads was recorded.

INTRODUCTION

Collating information collected by Dr J. F. D. Frazer during the 1950s, I found that a significant relationship existed between spawning dates of the frog (*Rana temporaria*) and the toad (*Bufo bufo*) for different parts of the country (Cooke, 1976). Thus in areas such as the mild south west of England, both species spawned relatively early, whereas in regions with more severe winters and springs, such as Yorkshire or East Anglia, both species spawned later. Information for a single site at Iwerne Minster in Dorset collected by H. J. Moore from 1950 until 1957 also fitted this pattern. In Dorset, frogs and toads spawn moderately early and the range of first spawn dates reported by Moore was considerable, especially for the frog.

From 1971 to 1981 inclusive, I monitored the breeding events for the frog and toad populations utilizing St Neots Common, Cambridgeshire. This is the most important breeding site in what used to be the old county of Huntingdonshire, a relatively impoverished area for anuran species (refer to Cooke and Ferguson, 1974). To give some idea of the size of the breeding populations: total counts of spawn clumps for the frog varied between 81 and 225 per year, and annual maximum counts of breeding toads ranged from 49 to 1080 (a mark/recapture estimate in 1980 indicated that about half of the toads present on a single day were actually counted). One purpose of the study at St Neots was to determine whether breeding events for the two species were related temporally, taking into account the weather conditions prevalent at the time. Unlike the site at Iwerne Minster, St Neots is in a region in which both species spawn relatively late.

Several authors have studied the breeding of frogs or toads in relation to weather conditions (*e.g.* Moore, 1954; Savage, 1961; Frazer, 1966; Heusser, 1969; van Gelder & Hoedemaekers, 1971; Kowalewski, 1974; Obert, 1976; Gittins, Parker & Slater, 1980; Wisniewski, Paull & Slater, 1981). But each of these studies has been concerned with one or other of the two species (with the exception of that of Kowalewski, 1974) and has been of relatively short duration.

OBSERVATIONS

A description of the site will be given elsewhere (Cooke, in preparation). Frogs appear to be resident on the Common, whereas in recent years toads have tended to overwinter away from the Common, and spring migration to the breeding sites involves the crossing of roads when many toads are killed. The appearance of toad carcases on the roads serves to indicate that toads are migrating and breeding activity may be imminent.

Dates when the first spawn was seen are given in Table I. In 1973, no toad spawn was located although tadpoles were found subsequently. The mean dates (frog, 13 March; toad, 30 March) fitted the relationship between mean spawning dates for the two species throughout the country (Cooke, 1976). For St Neots Common, however, the relationship for individual years was not statistically significant, although a positive trend was evident (Spearman Rank Correlation Coefficient, $R_{10} = 0.494$, $0.05 < P < 0.1$). Closer examination of the data revealed that in the four years when frogs spawned comparatively early (1975, 1977, 1978, 1980), the data did not conform to the general pattern. In 1977, the weather remained mild until near the end of March enabling toads to begin spawning very soon after the frogs. In 1975, 1978 and 1980, toad mortality on the roads was noted in early March, but in each year the weather turned cold before breeding could begin and remained cold until around the end of March. In each of these three seasons, toads spawned rather late. Events in 1975 are used to illustrate the effect of weather conditions on breeding; 1975 has been selected because this was the year with the longest interval between spawning dates of the two species (32 days). Meteorological data were recorded daily at Monks Wood Experimental Station, about 18 km to the north of St Neots Common.

The first 10 days of March 1975 were mild (maximum air temperatures 6–13°C, minimum temperatures 1–6°C) and wet (Fig. 1). The following three days were also wet, but although the nights were relatively mild, day temperature failed to rise above 6°C. From around 13 March to 18 March, the Common was extensively flooded. Although the frog population began to spawn on 7 March, breeding had been delayed by 10 March and there was little spawning during the flooding period. Frogs rarely favour this temporary floodwater for spawning at St Neots. From the road mortality data, there was evidently some early movement of toads, but this soon ceased. After 20th, until about 27 March, the weather became milder with maxima of 5 to 10°C and minima of 1 to 4°C, except for the night of 26/27 March, when the temperature fell below zero. This was the main spawning period for frogs. On 27 March, a few toads were observed on the Common, but from then until 10 April it became colder again with night-time temperatures of −3 to 4°C, and toads only appeared sporadically in their main breeding site. A little toad spawn was seen on 8 April. After 10 April the weather became much milder. On the night of 11–12 April, minimum temperature exceeded 5°C for the first time for more than a month, and mass movement of toads appears to have begun at all the main breeding sites in the area. At St Neots, the toad breeding season was late and of short duration with a peak count on 14 April.

TABLE I. Dates when the first spawn and peak breeding activity were recorded

	Dates of first spawn			Dates of peak breeding activity		
	Frog	Toad	Interval (days)	Frog: median spawn date	Toad: peak numbers	Interval (days)
1971	16.3	3.4	18	17.3	31.3	14
1972	16.3	30.3	14	16.3	22.3	6
1973	13.3	—	—	19.3	27.3	8
1974	13.3	22.3	9	18.3	26.3	8
1975	7.3	8.4	32	27.3	14.4	18
1976	22.3	7.4	16	26.3	7.4	12
1977	4.3	8.3	4	11.3	11.3	0
1978	6.3	30.3	24	13.3	3.4	21
1979	28.3	14.4	16	6.4	12.4	6
1980	3.3	2.4	30	11.3	2.4	22
1981	10.3	23.3	13	17.3	23.3	6
Mean	13.3	30.3	18	19.3	30.3	11
Range	3.3–28.3	8.3–14.4	4–32	11.3–6.4	11.3–14.4	0–22

Thus the flooding and low temperatures in the middle of March interrupted the frog breeding season and lengthened it considerably. The duration of the spawning period was estimated at 34 days for 1975 compared, for instance, to a range of 8 to 19 days for the years 1971–1974. Average daily mean temperature during the spawning period was 3.3°C in 1975 and 3.8 to 6.6°C for 1971–1974. Judging from (1) the appearance of dead toads on the roads from 10 March and live toads in the breeding site from 27 March and (2) the dates of spawning in other years (Table I), toads would presumably have gathered to spawn earlier in 1975 had the weather been milder.

In 1975, the main frog spawning season was associated with maximum temperatures of 5 to 10°C and minimum temperatures of 0 to 4°C. Analysis of weather data for 1971–1974 generally showed similar ranges for the main spawning periods: 1971, maxima 7 to 12°C, minima −1 to 6°C; 1972, 3 to 9°C, −1 to 7°C; 1973, 11 to 17°C, −1 to 5°C; 1974, 4 to 13°C, −3 to 5°C. The start of spawning usually coincided with an increase in daily mean temperature. Amounts of rainfall during spawning were variable. From 1971 to 1975, the main movement of toads coming in to spawn was usually associated with day-time maxima of 10°C or more, and nightly minimum temperatures of at least 5°C. Often there was considerable rain during the days preceding movement, but only little rain actually during movement. In no years was there a significant delay in spawning once the main influx of toads had occurred. Indeed as can be seen in Table I, the mean dates of first spawn and peak numbers coincided on 30 March. As a general rule, peak frog spawning was associated with daytime maxima of at least 5°C and night-time minima of at least 0°C, while toad movement and subsequent spawning was accompanied by temperatures about 5°C higher.

Where temperature data can be directly compared with details given by the authors quoted in the Introduction, there is reasonable agreement. The study of Obert (1976) is of particular interest because he observed a frog population near Bonn, Germany,

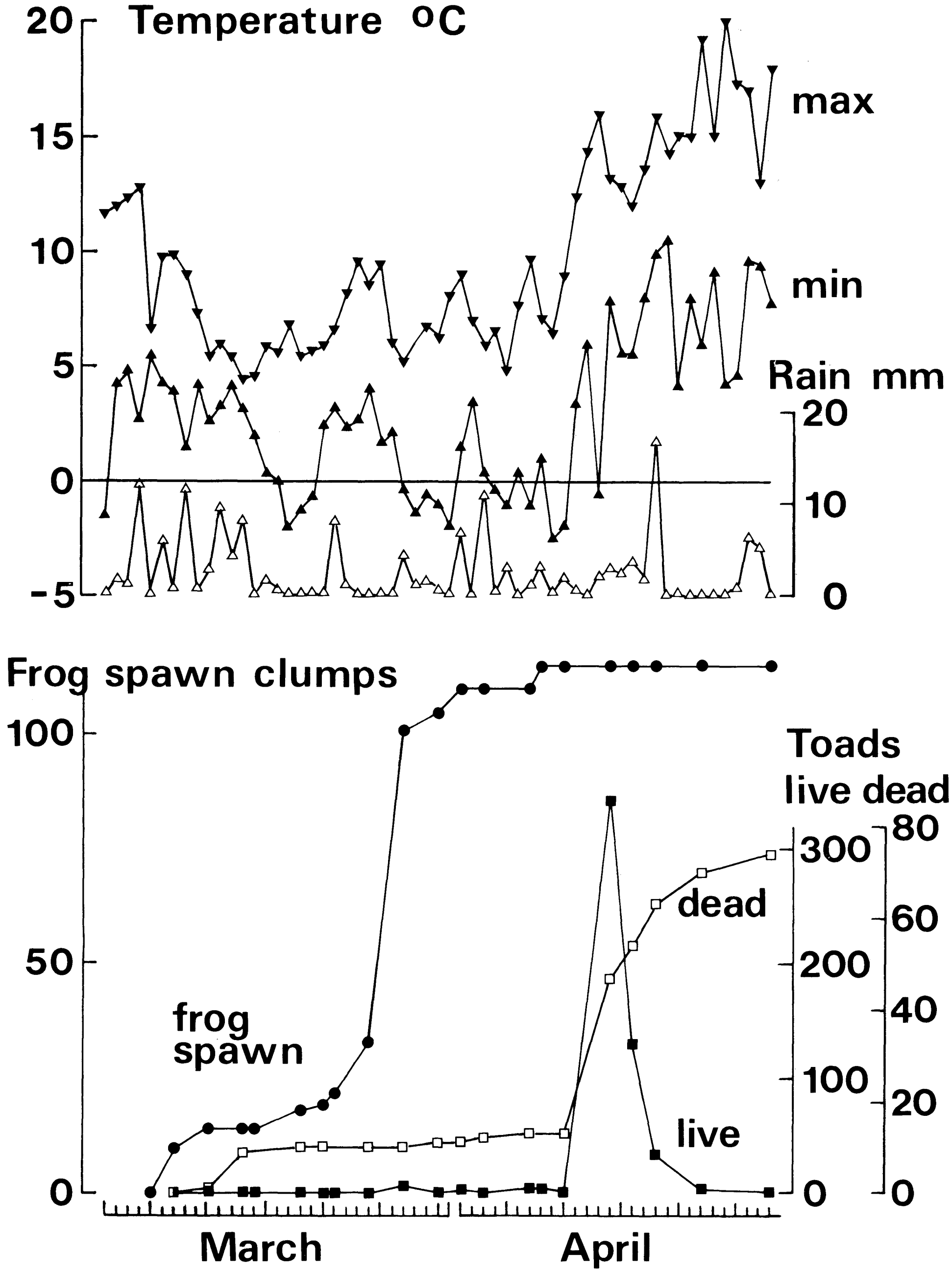

FIG. 1. Relationship between breeding activity of the frog and the toad on St Neots Common and weather conditions recorded at Monks Wood, 1 March 1975–28 April 1975. Maximum temperature of day *n* (▼). Minimum temperature of night *n* — 1/*n* (▲). Rainfall 9 a.m. day *n* to 9 a.m. day *n* + 1 (△). Cumulative total frog spawn clumps (●). Counts of live toads on the Common (■). Cumulative total of dead toads on road (□).

during the early 1970s, including 1975. During March 1975, the maximum and minimum temperatures at Bonn and St Neots showed very similar trends, but temperatures at Bonn tended to be several degrees higher. Spawning at Bonn appears to have been completed by 10 March just before the cold weather set in. By this time at St Neots, very little frog spawn had been laid and spawning was then interrupted (Fig. 1). This early spawning at St Neots may be equivalent to the "pre-spawning period" discussed by Obert (1976). Wisniewski *et al.* (1981) found, following a detailed study at a Welsh site, that air temperature needed to be 3°C or more in order for toad migration to occur. As pointed out by Frazer (1966), this critical temperature does appear to vary somewhat between colonies. The critical temperature for toads at St Neots (minimum air temperature 5°C) fell within the range given for other sites.

In view of the protracted nature of the frog breeding season during several years at St Neots, it was hardly surprising that the relationship between dates when the two species began to spawn was not statistically significant. It was considered that there might be a significant relationship between times of peak breeding activity for the two species. Peak breeding activity can be most conveniently represented for the toad by the date on which maximum numbers were recorded in the breeding sites, and for the frog by the date by which half the spawn clumps were recorded (frogs are exceedingly wary and difficult to count at St Neots). The relationship between these two series of dates (Table 1) was significant (Spearman Rank Correlation Coefficient $R_{11} = 0.609$, $P < 0.05$).

Previously (Cooke, 1976) it was found that for populations throughout the country, where the frog tended to spawn later so the interval between the spawn dates of the two species diminished. This relationship did not hold for St Neots, either for spawn dates or for times of peak activity (Table I). The reason for this may have been connected with the fact that at St Neots, both species spawn relatively late at times which are fairly predictable from year to year. The range of spawn dates for the frog was only 3–28 March at St Neots (11 years) whereas it was 3 February–23 March at Iwerne Minster (8 years). Thus perhaps at St Neots, variation in spawn dates between years was relatively small compared to perturbations in the relationship between spawn dates for the two species caused by extreme weather conditions.

ACKNOWLEDGEMENTS

For most of the period I worked at Monks Wood Experimental Station (formerly part of the Nature Conservancy, and later the Institute of Terrestrial Ecology). My thanks are due to many past and present colleagues for their help and encouragement over the years.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 206–207 (1982)

NATIONAL CHANGES IN STATUS OF THE COMMONER BRITISH AMPHIBIANS AND REPTILES BEFORE 1974

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(*Received* 20 *March* 1982)

During deliberations on the parliamentary bill, which eventually appeared as the Wildlife and Countryside Act 1981, we analysed data collected by the Biological Records Centre to try to derive information on changes in national populations of the commoner species. Data have been assimilated by BRC for many years, a provisional atlas being published in 1973 (Arnold, 1973). On the maps, presence on a 10 km square basis is indicated by symbols:

○ present up to 1959
● present 1960–1973

One problem with this dot system is that, from the maps, one does not know whether a ● covers a ○. We therefore started with the raw data and compiled a new map for each species up to 1959, for comparison with the 1960–1973 distributions indicated in Arnold (1973).

It is not possible to compare records of two species during the same time period, say smooth newt *Triturus vulgaris* and slow worm *Anguis fragilis*, because some species are easier to find and therefore more likely to be recorded than others. However, it is probably a fair assumption that the effort put into recording smooth newts relative to slow worms changed little during the two time periods. Therefore, it is reasonable to compare the ratio of sightings, 1960–1973: up to 1959, between different species to determine which were relatively infrequently recorded after 1960 (Table 1). Ratios for the common frog *Rana temporaria* and common toad *Bufo bufo* cannot be compared with those for the other species, as these species were the subject of an extensive survey (Cooke, 1972), data from which were incorporated into the BRC maps (hence the high ratios for these two species). None of the other seven species had such an injection of extra information into the BRC scheme. Ratios for the seven non-anuran species varied from 0.67 for the palmate newt *T. helveticus* to 1.28 for the smooth newt.

The lower the value of the ratio, the more likely the species is to have declined in numbers over the period 1960–1973, although these ratios alone tell us nothing about absolute changes in status. National surveys have been carried out on two of the seven species in the main list in Table 1: on the warty newt *T. cristatus* (Beebee, 1975) and on the grass snake *Natrix natrix* (Spellerberg, 1975). Both surveys relied on correspondents completing questionnaires; more than 100 forms were returned for each survey. The overall views were that both species declined during the 1960s and through into the 1970s. Lesser decreases were noted in the 1950s. Thus these surveys indicated widespread declines for the grass snake and warty newt. From the ratios given in Table I, it would be reasonable to suggest that the palmate newt, adder *Vipera berus* and slow worm also declined. Although many of the correspondents of Beebee (1975) reported coincidental changes in status of all newt species, there was no reason to suggest that the palmate newt had declined more severely than the warty newt (which might be suggested from the ratios in Table I). The explanation for this may involve one of the limitations of the BRC data. The distribution maps only give information on presence or absence in a 10 km square; they provide no information on abundance in occupied squares. Although the range of the palmate newt may have contracted, it is still frequently very common where it does occur. Local declines in the slow worm and adder have been noted (see Prestt, Cooke & Corbett, 1974).

The two species in the main list with the highest ratios, the common lizard *Lacerta vivipara* and smooth newt, are generally considered to be fairly adaptable to the changing environment. Whether national populations have declined significantly is open to debate, but some local declines have occurred (Prestt *et al.*, 1974; Beebee, 1975; Buckley, 1975).

The two species treated separately in Table I, the common frog and common toad, appeared from the

Table I. No. of 10 km squares* in which the commoner species of amphibians and reptiles were recorded (i) up to 1959, (ii) 1960–1973

	(i)	(ii)	(ii)/(i)
Palmate newt	279	186	0.67
Adder	497	359	0.72
Grass snake	365	362	0.99
Slow worm	367	390	1.06
Warty newt	213	232	1.09
Common lizard	439	490	1.12
Smooth newt	252	322	1.28
Common frog	465	1233	2.65
Common toad	280	806	2.88
Total no. of squares with records	1297	1614	

* British mainland and adjacent offshore islands only.

survey of Cooke (1972) to have suffered widespread declines, especially during the 1960s.

In conclusion, surveys already published on four species indicated widespread population declines during the 1960s and into the 1970s. BRC data suggest that at least three of the remaining five species also declined during this period. There is an urgent need for more up-to-date information, and in 1982 NCC is organizing a broad survey into status changes of all nine species.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 207–213 (1982)

CHOICE OF SUBSTRATE AND HEATING RATE IN *LACERTA VIVIPARA*

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(*Received* 22 *March* 1982)

SUMMARY

Common lizards (*Lacerta vivipara*) in summer basked mostly on dry grass during sunny weather, but on pieces of wood when the sunshine was interspersed with periods of cloud cover (changeable weather). In order to determine whether this switch in behaviour could be interpreted as a cost-benefit situation, the effects of different substrates on heating rates at high and low irradiance were investigated. Basking times on wood were related to a number of environmental thermal variables.

Heating curves were fitted to a logistic model, which allows description of the complete curve from two basic parameters. Other parameters, such as rate of heating at any temperature, time interval for any temperature interval (or vice versa), and thermal half time, are easily derived from these.

INTRODUCTION

The ecology of the common lizard (*Lacerta vivipara*) has been well studied, particularly its population ecology (Avery, 1975; Pilorge & Castanet, 1981; Bauwens & Thoen, 1981a) and energetics (*e.g.* Avery, 1971, 1976; Patterson & Davies, 1978a). Studies on the behaviour of wild lizards have been limited to those aspects requiring short periods of observation, such as emergence times (Avery & McArdle, 1973) and flight distances (Bauwens & Thoen, 1981b). This is largely due to their preference for densely vegetated heath and grassland (Smith, 1973) in which observation of an individual for more than a few minutes is rare. Studies of thermoregulation are limited to those on animals in enclosures (Avery, 1971) or in the laboratory (Avery, 1976; Patterson & Davies, 1978b).

The present work was prompted by seeing common lizards using habitual basking sites, which were piles of wood, and returning to these between forays into the surrounding grassland. Activity patterns of individuals were observed at these sites. It became apparent that in summer wood was only used in changeable weather; on sunny days lizards basked on small patches of dry grass. This difference in basking substrate selection was interpreted as a cost-benefit situation, and the benefits of heating on different substrates were hence investigated. A new method of describing heating rates, more applicable to ecological problems than those previously devised, was developed.

METHODS

FIELD OBSERVATIONS

The study area was a field of rough grassland (*Arrhenatherum* and *Anthoxanthum*) at Leavenheath, Suffolk. In 1978 and previous years lizards basked on

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small piles of old timber in the grass. These were too structurally complex to allow easy spotting of the lizards, and so all were replaced in March 1979 by two halves of an old unpainted door, each 1 m × 1 m in size, placed 25 m apart. There were no other wood sites within 50 m, and it was probable that: (a) all lizards on the wood were seen by the observer nearby; (b) lizards returning to the wood at reasonable intervals were not using other wood sites in between.

Intensive observations were made at these sites during periods of changeable weather in early July and mid August 1979. The presence and activity of each lizard was noted every 15 seconds during observation periods of 1 to 3 hours. Individuals were recognized by natural marks. Basking was defined by dorso-ventral body flattening.

Shade air temperature 30 cm above the ground (T_A), temperature of the upper surface of the wood (T_W) and temperature of a blackened probe in the sun at 30 cm (T_{BB}) were measured every 10 minutes with a thermistor thermometer. The meter and observer were hidden in grass 3 m from the wood, and observation from this distance had no noticeable effect on lizard behaviour provided that no sudden movements were made.

Using the same probes, ($T_{BB} - T_A$) was calibrated against a photoelectric solarimeter under artificial light to give a measure of irradiance.

In addition to intensive observations, the area was examined daily from July to September 1979 and the pattern of lizard activity noted.

Heating Rates

Heating rates of a 3.45 g adult common lizard were measured on wood and straw substrates at thermal equilibrium under known irradiance. Straw was used in place of dry grass for reasons of supply, the wood was weathered timber similar to that used in the field. Irradiance was produced by a 275 W infra red reflector lamp.

Two levels of irradiance were used, 0.013 and 0.026 J cm^{-2} s^{-1}. At the lower, T_A and T_W were comparable to values recorded in the field. At the higher, T_A was kept down to a similar level to that for low irradiance, and T_A and T_W were lower than those associated with high irradiance in the field. This was to separate the effect of irradiance and substrate from differences due to air temperature.

The lizard was slowly cooled to 18–20°C in the light. Its body temperature (T_B) was measured, and it was placed in a low wire mesh arena directly under the lamp, on wood or straw. Basking usually followed; the trial was discarded if the lizard climbed from the arena or burrowed into the straw. After 5 minutes the lizard was removed, and T_B measured. The lizard was then replaced, this being repeated until there was no further rise in temperature. T_B was measured with a quick reading 1.5 mm diameter thermistor probe, inserted cloacally, the lizard held by the base of the tail to minimize hand warming. This took 15 seconds; time out of the arena was not included in heating time.

Heating rates under 0.026 J cm^{-2} s^{-1} and 0.5 m s^{-1} of wind from a desk fan, and cooling rates in still air and 0.5 m s^{-1} of wind were also measured. For the latter the lizard was warmed in an open box under 0.5 J cm^{-2} s^{-1} irradiance, T_B measured, and the fall in T_B measured every 5 minutes during activity in a large cage. Heating rates of a 6.2 g *Podarcis muralis* and a 16.6 g *Lacerta viridis* were also measured in all three conditions on both substrates.

RESULTS

Field Observations

The proportion of time that individual lizards spent in basking was calculated for 30 minute intervals, a time scale appropriate to that of lizard activity and of variation in cloud cover, which was the main cause of variation in the thermal conditions. The percentage of this interval spent basking (% B) is shown against mean T_A and irradiance during the interval in Fig. 1.

Correlations between % B and the thermal variables are given in Table I, excluding incomplete cases or intervals when no lizards basked on the wood. Significance of correlation between % B and each

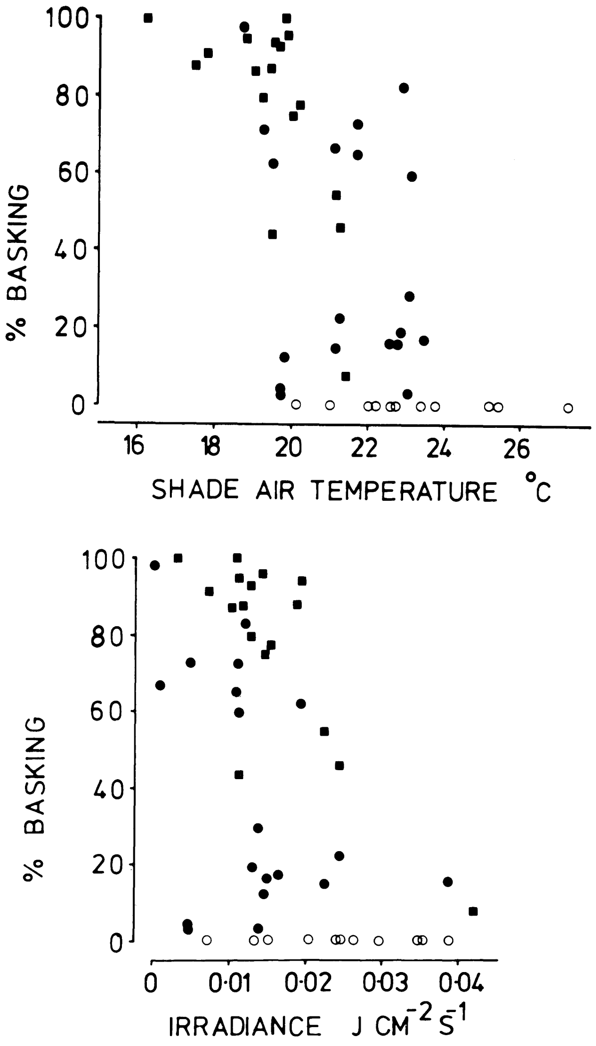

Fig. 1. Variation of percentage of time spend basking with (a) shade air temperature, and (b) irradiance. ■ juveniles, ● adults, ○ no lizards basking. Each point is one 30 minute interval.

thermal variable is investigated by Spearman rank correlation coefficient (r_s), as some of the variables were not normally distributed or easily transformed to normality (Sokal & Rohlf, 1969).

The coefficient of determination (proportion of total variation explained by the correlation) is also given, both for zero order correlations between % B and each thermal variable, and for second order correlations between % B and each variable after adjusting for the effect of the other two variables. This is the Pearson product moment correlation coefficient, squared (r^2) (Sokal & Rohlf, 1969). All correlations were performed using SPSS (Nie, Hull, Jenkins, Steinbrennen & Brent, 1975).

TABLE I. Correlation of percentage of time spent basking with thermal variables

Total (n = 33)	Shade air temperature	Substrate (wood) temperature	Irradiance
r_s	−0.520	−0.633	−0.305
P	0.001	0.001	0.042
Zero order r^2	0.276	0.331	0.126
Second order r^2	0.003	0.081	0.053
Adults (n = 19)			
r_s	−0.142	−0.248	−0.370
P	0.281	0.153	0.059
Zero order r^2	0.056	0.132	0.160
Second order r^2	0.021	0.068	0.096
Juveniles (n = 14)			
r_s	−0.504	−0.508	−0.511
P	0.033	0.032	0.031
Zero order r^2	0.552	0.619	0.645
Second order r^2	0.026	0.169	0.121

r_s is the Spearman rank correlation coefficient; r^2 (coefficient of determination) is the Pearson product-moment correlation coefficient, squared.

Basking period was calculated as the duration of a period of uninterrupted basking. Variation of this is shown with mean irradiance and T_W during the period in Fig. 2. Short basking periods occurred in all conditions, long periods only when it was cooler.

The three thermal variables were mutually correlated, and related by the equations

$$\text{irradiance in J cm}^{-2}\,\text{s}^{-1} = 0.00253T_A - 0.037 \quad (r^2 = 0.302)$$

$$T_W = 1.82T_A - 8.3 \quad (r^2 = 0.706).$$

Most basking on wood was at T_A below 24°C, irradiance below 0.025 J cm^{-2} s^{-1}, and T_W below 36°C (Figs. 1 and 2). These conditions were exceeded, often considerably, on sunny summer days, and extensive observations indicated that lizards used small patches of dead grass in hot weather. They moved through the area of grassland, apparently not returning to any particular place habitually.

HEATING RATES

Heating curves of a 3.45 g common lizard under high and low irradiance on wood and straw substrates are shown in Fig. 3. The means of several trials are fitted to a curve with a logistic limitation to the rate of heating, such that at any temperature, T°C;

$$r_T = r_0 \frac{(K - T)}{K} \tag{1}$$

where r_T is the rate of increase of temperature per unit time (dT/dt) at T°C, r_0 is the rate at 0°C, and K is the equilibrium body temperature under the conditions. The assumptions of this model are noted in the discussion.

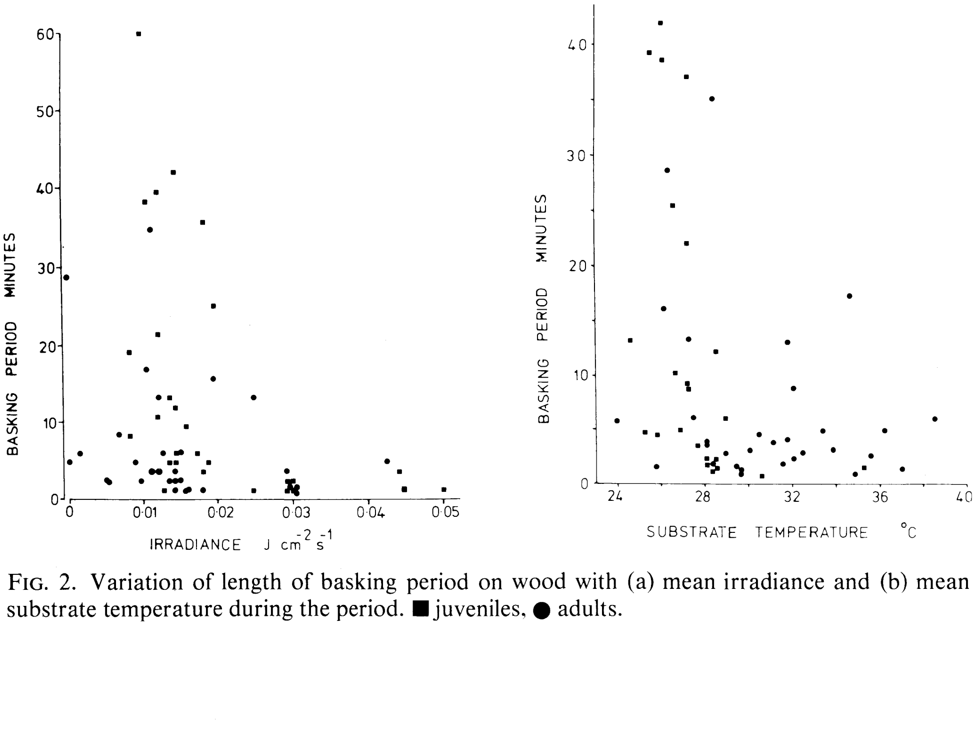

FIG. 2. Variation of length of basking period on wood with (a) mean irradiance and (b) mean substrate temperature during the period. ■ juveniles, ● adults.

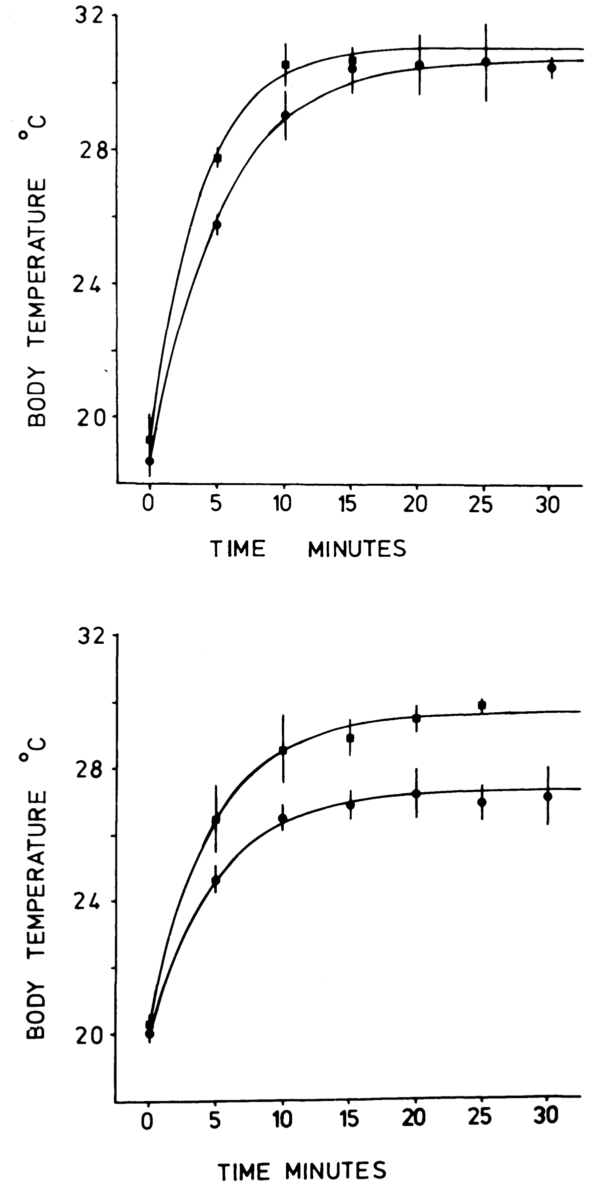

FIG. 3. Heating curves of a 3.45 g adult common lizard. Irradiance (a) 0.026 J cm^{-2} s^{-1}, (b) 0.013 J cm^{-2} s^{-1}. Both still air. ■ on wood, ● on straw. Vertical bars are 95% confidence limits of the mean.

The fitted curves are equation 1 integrated with respect to time (t)

$$T_t = K - (K - T_0)\, e^{(-r_0/K)t} \tag{2}$$

where T_0 is the starting temperature in °C, t the time from the start in minutes, and e the base of natural logarithms.

Where data are in the form of a series of temperatures at a fixed time interval (in this case, five minutes), the parameters K and r_0 may be estimated by linear regression (a) of $(T_{t+5} - T_t)$ on T_t gives K as the intercept on the abscissa; (b) of ln $(K - T)$ on t, where ln is the logarithm to the base e, gives r_0 as ($-$ slope) K for temperatures below equilibrium (modified from Caughley 1977: 182). Small errors in measurement of T or estimation of K will cause large errors where $(K - T)$ is small, and only values of $(K - T)$ over 2°C were used.

A FORTRAN program was developed to calculate K and r_0 by performing these regressions in turn on data supplied as a series of body temperatures at a given fixed time interval. This simple fitting method is unreliable where few points are involved, but produces starting values which may be modified to improve the fit.

Cooling curves were fitted from a baseline of 40°C, defining $\bar{T}_t = 40 - T_t$, $\bar{K} = 40 - K$, and r_{40} as the rate of cooling at 40°C. The curves were then fitted as above, replacing T_t, K and r_0 by $\bar{T}_t$, $\bar{K}$ and r_{40}. The cooling curve is then described by

$$T_t = K + (T_0 - K)\, e^{(-r_{40}/\bar{K})t} \tag{3}$$

Table II shows the parameters K and r for all the heating and cooling conditions, together with some secondary parameters.

DISCUSSION

SUBSTRATE CHOICE

During changeable weather when lizards were basking on wood, the percentage of time spent basking was significantly negatively correlated with all three thermal variables (Table I). Correlations for juveniles were higher than for adults, indeed for the latter only

TABLE II. Parameters of heating and cooling curves for an adult common lizard

Irradiance J cm^{-2} s^{-1}	0.013		0.026		0.026		0	
Windspeed m s^{-1}	0		0		0.5		0	0.5
Air temperature °C	22–23		20–21		22–23		21–22	
Substrate	wood	straw	wood	straw	wood	straw	wood	straw
n	5	5	5	5	10	10	10	10
Substrate temperature °C	26–27	23–25	28–30	23–25	28–30	26–28	21–22	
r_0 or r_{40}°C minute^{-1}	6.25	5.47	8.14	5.53	8.88	7.00	4.50	4.97
K°C	29.7	27.4	31.2	31.2	31.9	31.3	22.2	21.3
Δt_{21-25} minutes	2.9	4.9	1.9	2.8	1.6	2.2	—	—
r_{15}°C minute^{-1}	3.1	2.5	4.2	2.9	4.7	3.6	—	—
Δt_{15-25} minutes	5.4	8.2	3.7	5.4	3.2	4.3	—	—
Half time minutes	3.3	3.5	2.7	3.9	2.5	3.1	2.7	2.6

r_x is the rate of change of temperature per unit time at x°C; $tx - y$ is the time to heat or cool from x°C to y°C. Lizard used for cooling was slightly smaller than the one used for heating.

irradiance had an effect approaching significance. Zero order correlations do not show a clear pattern of which variables have the greatest effect. Second order partial correlations show that air temperature has a much smaller effect than irradiance or substrate temperature, for adults, juveniles, and the combined results.

Extensive observations produced only occasional sighting of lizards basking on grass in changeable weather; most were on wood. On sunny days they were on patches of dry grass and none were seen basking on wood. This was interpreted in terms of the costs and benefits of moving to and basking on different substrates. Wood sites were much less numerous, and would involve greater movement costs (time and energy) to lizards returning to them, and restriction to a relatively limited foraging area (central place foraging—see Orians & Pearson, 1979).

The proposed benefit was increased rate of heating, thus reducing the time spent basking. The substrate selected should switch where the extra cost of moving to wood is the same as the benefit of less time basking once there. The transition from changeable to sunny weather was thought to cause this switch, with the benefit of wood being greater in low or fluctuating irradiance.

The cost will depend on the T_B at which return to the basking site occurs (and the lizard's performance at that T_B), and the distance moved to reach the basking site. On sunny days lizards will reach a higher T_B, and as a result may go further while foraging. They will also start back at a higher T_B (as they are cooling to a higher ambient temperature), and so the cost of moving back to the basking site is probably relatively independent of the weather.

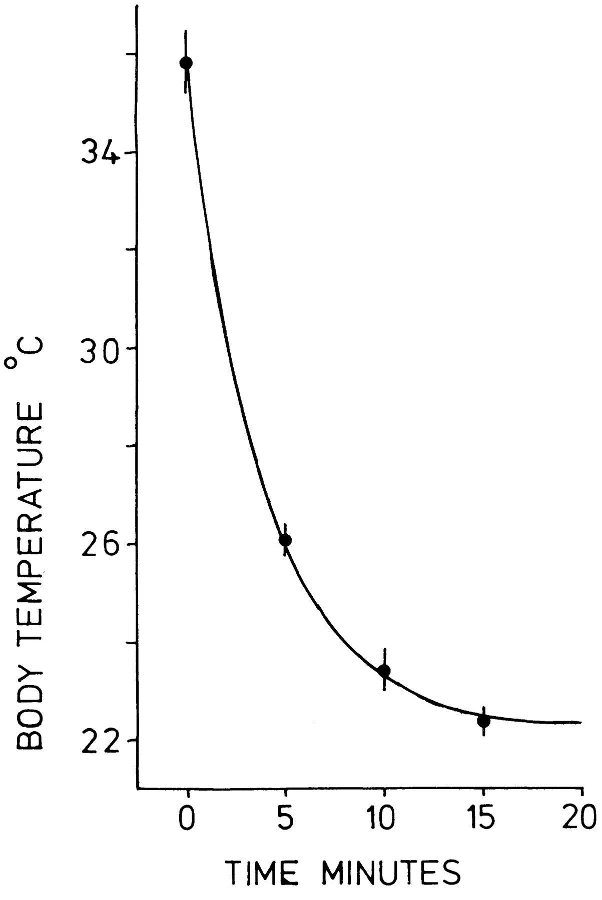

FIG. 4. Cooling curve of an adult common lizard in still air. T_A 21–22°C. Vertical bars are 95% confidence limits of the mean.

Figure 3 shows that the benefit of a wood substrate appears greater at low irradiance. This benefit may be expressed in two ways:

(1) The time saved in heating over a specified temperature range. The time saved heating from T_A (about 21°C) to 25°C is 2 minutes at 0.013 J cm^{-2} s^{-1}, 1 minute at 0.026 J cm^{-2} s^{-1} (Table II, Δt_{21-25}). At higher irradiance the absolute size of this saving will be reduced still further as heating rates increase on both substrates.

(2) A higher temperature may be reached. This may be particularly important at low irradiance during prolonged basking (see below). At higher irradiances, lizards will resume activity before K is reached (on sunny days, T_W was over 40°C).

Adult common lizards were studied in a large cage under combinations of irradiance and basking site availability thought to favour a basking substrate switch. However, inability to provide both a sufficiently large area (costs of moving to the wood too low), and sufficient numbers of small prey to stimulate continued foraging, produced activity/basking patterns which could not be considered normal (Hailey, 1980). Demonstration of a change in basking substrate choice with irradiance in controlled conditions is therefore lacking.

BASKING PERIODS

The pattern of basking period decreasing exponentially with increasing irradiance (Fig. 2) is similar to that for the time to heat over a given temperature interval (see Avery & McArdle, 1973; Avery, 1976). In practice the temperature interval over which a lizard basks will change with conditions, lizards returning to bask and reaching a higher temperature in hot weather.

Avery (1971) found that daily food consumption of *L. vivipara* in changeable weather was only about half that in sunny weather, and later implied (Avery, 1976: 252) that this was due to limitation of foraging time. This is apparently contradicted by the long basking periods (over 20 minutes) observed in changeable weather during this study (Fig. 2). At these times, little increase in T_B can be expected as K is approached, and any small rise will be lost rapidly on activity (Fig. 4). This apparent waste of time when time is limiting could have several possible explanations:

(1) Lizards are waiting for irradiance to increase. Such an increase may be rapid during changeable weather in summer, and can be taken advantage of immediately. Bauwens & Thoen (1981b) found that stationary common lizards face little risk of predation.

(2) Lizards switch from active foraging to sentinel predation. Continued basking will enable lizards to maintain a high T_B to respond efficiently to prey passing near (this was seen twice). Continued basking thus allows high T_B to be saved for pursuit and not lost while searching for prey.

(3) Basking may increase the amount of food that can be processed on changeable days. Avery (1971) found that on sunny days, food intake was limited by the ability to process rather than catch prey. Food through-put rate is temperature-dependent in Lacertids (McClelland, pers. comm.) as in other reptiles (Skoczylas, 1978). It is possible that lizards still feed maximally on changeable days but processing limits this to half that on sunny days. Under such conditions, further basking would be more advantageous than further foraging.

These possibilities are not mutually exclusive. Use of substrates which enable a higher K to be maintained and also act as heat stores in fluctuating conditions will be particularly advantageous in changeable weather. Demonstration of long basking periods when time is thought to be limiting highlights the importance of studying behaviour of individuals—this would not be suspected from studying what the population generally is doing at any time.

Description of Heating Rates

Description of heating rates has a complex literature. Three parameters have been used previously:

(1) The time taken to heat over a specified temperature interval, Δt_{T1-T2} (*e.g.* Avery & McArdle, 1973; Hailey, 1980). This is unsatisfactory where the upper limit approaches K, as a small change in the value chosen (usually somewhat arbitrarily) will cause a large, non linear change in Δt.

(2) The rate of heating at a specified temperature (*e.g.* Bartholomew & Tucker, 1963; Avery & McArdle, 1973; Claussen & Art, 1981). This rate will depend on the temperature chosen as well as the conditions.

(3) The half time or time constant. The half time is that for the elimination of 50% of the ΔT between body and ambient temperature (Spigarelli, Romberg, Prepejchal & Thommes, 1974; McKenna & Packard, 1975; Glidewell, Beitinger & Fitzpatrick, 1981). The time constant (Spotila, Lommen, Bakken & Gates, 1973; Smith, 1976), is a similar measure, using 63% of the ΔT, and is equal to the half time × 1.44 (Glidewell *et al.*, 1981). These parameters are useful in step transfer conditions (where K is fixed) and in the study of the scaling of heat change with body mass (see also alternative time constant of Bell, 1980). They are less useful in ecological discussion, however, as a lizard of given size will have approximately constant half time, independent of conditions (see below).

The logistic model proposed here has the major advantage that the *complete curve* is described by two parameters, K and r_0. Given these, it is simple to calculate any of the other parameters, though the reverse is not possible.

The time interval for a given temperature interval is calculated from equation 2, or the modified form:

$$\Delta t_{T_U} - T_L = \left[-\ln \frac{(K - T_U)}{(K - T_L)} \right] . \frac{K}{r_0} \qquad (4)$$

where T_U and T_L are the upper and lower limits. For cooling curves, K, T_U, T_L and r_0 are replaced by $\bar{K}$, $\bar{T}_U$, $\bar{T}_L$ and r_{40}.

The rate of heating at a given temperature, r_T, is calculated from equation 1.

The half time is calculated from equation 4 modified as:

$$\text{half time} = -\ln 0.5 . \frac{K}{r_0} \qquad (5)$$

replacing K and r_0 by $\bar{K}$ and r_{40} for cooling.

As with its use in population ecology (*e.g.* Caughley, 1977), the logistic model assumes that the rate of change is directly proportional to $(K - T)$. This is also assumed for half times and time constants, and is approximately valid over small (in physicist's terms) temperature ranges (Whelan & Hodgson, 1971). Table III shows the mean fit of 180 heating curves calculated using the double regression method by computer. There is a significant departure at 10 minutes, but this is extremely small (less than the accuracy of the thermistor used), and may be an artifact of the periodic handling experimental technique or fitting by regression.

The half time varies with body mass—mean half times of the three lizards used were:

L. vivipara	(3.45 g)	3.2 minutes
P. muralis	(6.21 g)	4.6 minutes
L. viridia	(16.6 g)	6.9 minutes

It also varies with the means of heat exchange, being reduced by the extra conduction component from wood (Table 2) [see also Bell's (1980) comparison of temperature change in air and water]. However, in conditions differing only by the size or position of the temperature interval (T_0 to K) it will be constant.

It is hoped that the economy with which the logistic model described heating curves and the ease with which other parameters may be calculated from it will prove useful in the study of reptile thermal ecology.

Substrate and Morning Emergence

r_{15} for *L. vivipara* is higher, and Δt_{15-25} lower, (Table II) than that found by Avery & McArdle (1973) at the same irradiance, though their lizards were slightly smaller. There are two obvious reasons for this:

(1) Their lizards were strapped to a block of wood at 5°C, here the lizard was on a warm substrate at equilibrium under the irradiance.

Table III. Goodness of fit of the logistic model fitted by double linear regression for 180 heating curves

Time minutes	5	10	15	20
Mean (observed-calculated) °C	−0.072	+0.083	+0.060	+0.063
±1.96 standard errors	±0.106	±0.056	±0.064	±0.065

(2) Air temperature was 15°C in their experiments, 21–22°C here.

In the early morning conditions approximate to those of Avery & McArdle (1973), *i.e.* cold air and cold substrates. Later on, conditions will approach those used here as the air and substrates warm up under increasing irradiance. Δt_{15-25} will fall below that shown in Fig. 3 of Avery & McArdle (1973) as the morning progresses, and the point of levelling off may be later, as substrate heating will lag behind rises of irradiance due to thermal inertia. This may explain the observation that emergence was later than predicted from heating due to irradiance alone.

ACKNOWLEDGEMENTS

I am grateful to: Dr Bryan Turner for supervision of the project and the suggestion that heating curves might fit a logistic model. Dr Roger Avery provided lizards and advice. Dr R. Anderson provided the integrated form of the logistic model used (equation 2), and Rob Kirkwood an alternative form. Malcolm McClelland and Dr Roger Joy provided helpful discussion on lizard ecology and computer programming, respectively.

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REPTILES OF THE TURKMENIAN PLAINS (in Russian). By S. Schammakov (1981). 311 pp. Turkmenian Academy of Sciences, 2 r 60 k.

Turkmenia is the Soviet Republic to the east of the Caspian Sea, and this is a handbook to its rich (54 species) Reptile fauna. Each species is described under a standard set of subheadings: measurements, distribution, habitat, behaviour, abundance, daily and seasonal activity cycles, reproduction, population dynamics, food, enemies, hibernation; but some species do not receive this complete treatment. Distribution maps are given for each species, and this will probably be the most valuable feature of the book for those who do not read Russian; other useful features are lists of food items and diagrams of activity levels through the day, but these are not given for every species because for some, the data are not available. There are some surprising omissions—for example, there is no mention of activity temperatures. This may perhaps be because the extensive Russian work on thermoregulation (*e.g.* by N. N. Scherbak on *Eremias*) was not carried out in Turkmenia. Despite its dimensions, this book is *not* a field guide; graphs and maps are the only illustrations.

R. A. AVERY

BOOKS RECEIVED

Volumes awaiting review in the next issue include J. M. Cei *Amphibians of Argentina*, Max Sparreboom *De Amfibieën en Reptielen van Nederland, België en Luxemburg*, von Spix and Wagler *Herpetology of Brazil* (facsimile reprint) and J. E. Cooper and O. F. Jackson *Diseases of the Reptilia* 2 vols.

ANNOUNCEMENTS

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following Opinion has been published in *Bulletin of Zoological Nomenclature* 39, 21 (1982):

No. 1201 ELAPIDAE Boie, 1827: ruling to stabilize nomenclature of taxa in this family.

The Commission gives notice of the possible use of its plenary powers as follows:

Case no. 1172 *EREMIAS* Wiegmann, 1834 (Reptilia, Lacertilia), proposed designation of a type species by use of the plenary powers.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 215–219 (1982)

CONGENITAL DEFECTS IN THE GHARIAL *GAVIALIS GANGETICUS* (GMELIN)

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(*Received* 27 *April* 1981)

SUMMARY

Twelve kinds of congenital defects, namely, absence of one or both eyes, corneal defect, unsmooth pupil, squint, bent neck, hunch back, bent tail, crossed snout, absence of palatal valve, bulged belly and wrong unbilical constriction were noticed for gharial eggs incubated under simulated ideal conditions, and are believed to be naturally occurring. It is believed that a "blind" gene is present in the gharial populations from Kali-Narayani-Gandaki and Karnali rivers in Nepal.

INTRODUCTION

The biology of the gharial (*Gavialis gangeticus*) is virtually unknown (Neill, 1971). The only published data on congenital defects concern two blind gharial (Singh & Tandan, 1978; Subba Rao & Bustard, 1979). The literature on congenital defects in crocodilians is very sparse. Bustard (1969) noted an abbreviated and malformed tail in *C. novaeguineae*, Kar (1980) reported an instance of malformation at birth in *C. porosus* and Kar & Bustard (1982) reported a greatly abbreviated tail in *C. porosus*, all observations on hatchlings or full term embryos. Lynn & Ullrich (1950) described experimental production of shell abnormalities in chelonians.

In 1975 the Government of India commenced a large-scale conservation programme on the gharial (FAO 1975; Bustard, 1975). Under this programme we have incubated 1061 gharial eggs under simulated natural conditions in a hatchery designed for tropical conditions (Bustard & Singh, in press). This has given us the opportunity to study and record what we consider to be naturally occurring congenital deformities.

MATERIALS AND METHODS

Gharial eggs collected from the Kali-Narayani-Gandaki river system (1975, 1976, 1977) and the Chambal river (1979, 1980) were incubated in brick-walled cells of river sand 1 m^3 in a predator-proof wire-mesh enclosure. This method provided a mean nest temperature of 30°C (range 29–32°C). Moisture content was maintained at around 8% water content in the medium (by weight) as recommended by Bustard (1966). Yearwise incubation and successful hatching were as follows:

Year	Place of incubation	Total eggs	Total hatchlings	% hatchlings
1975	Tikerpada, Orissa	71	42	59.1
1976	Tikerpada, Orissa	230	65	28.2
1977	Royal Chitwan National Park, Nepal	590	438	74.2
1978	Royal Chitwan National Park, Nepal	—	—	—
1979	Tikerpada, Orissa	20	15	75.0
1980	Tikerpada, Orissa	150	114	76.0

In our experience gharial with congenital defects do not emerge themselves—they require to be helped out of the eggs. Our standard practice is to surgically open all unhatched but otherwise surviving eggs 3–4 days after normal hatching is complete. Using great care it is possible to remove undamaged, all living young, some of which may survive for years. At the same time we open all other eggs that have failed to hatch. Hence complete data are recorded on all embryos showing any development.

RESULTS

Congenital defects were noticed in the Kali-Narayani-Gandaki hatchlings in all years. During 1975 and 1976 the defects were restricted to the eyes but in 1977 defects pertaining to the morphology of other parts of the body were also noted. No congenital defects were recorded in 1979 and 1980 in hatchlings from Chambal-laid eggs. Frequency and types of these congenital defects are presented in Table I and described below.

EYE DEFECTS

Eye defects recorded during 1975, 1976 and 1977 occurred in respectively 9.0%, 5.0% and 5.2% of the developing hatchlings. The various defects included blindness, defects in corneal colouration, squint and unsmooth pupil.

Blindness

Complete absence of both eyes was noticed to be the most common congenital defect and of consistent

TABLE I. Occurrence of congenital defects in *G. gangeticus*

Nature of defect	Number of instances	Total number of fertile eggs incubated	Remarks*
No eyes	2	44 (1975)	1, 6, 8, 9, 11
	3	140 (1976)	
	2	476 (1977)	
One eye present	1	476	1, 5, 8, 9, 11
Corneal defect	1	190	1, 7
Unsmooth pupil	1	44	1, 7
Unsmooth pupil	1	44	1, 7
(in one or both eyes)	3	190	
	11	476	
Squint	1	44	1, 7
Bent neck	21	476	3, 7, 8, 9
Hunch back	2	476	4, 10
Bent tail	11	476	1, 5, 8
Crossed snout	2	476	1, 7, 9
Mouth valve	1	476	1, 6, 10
Bulged belly	2	476	4, 10
Umbilical constriction	1	44	1, 6

* 1, persistent; 2, not persistent; 3, persistent in a few; 4, fatal; 5, dead but the defect may not be the cause; 6, may be fatal; 7, not fatal; 8, difficulty in swimming; 9, difficulty in feeding; 10, difficulty in respiration; 11, difficulty in vision.

occurrence in the hatchlings both at Tikerpada and Nepal. A total of seven such cases resulted from incubation of 42 fertile eggs. In all cases, both eyes were completely absent (Plate 1a) without any sign of development of the embryonic eye buds.

Only one case was recorded during 1977 of a hatchling with only one eye (Plate 1b). The corresponding area on the other side showed no trace of the eye. This hatchling had an additional deformity of the snout, which was horizontally arched and longer than normal.

Corneal defect

The normal colour of the iris in gharial is light brown. In one young individual, hatched during 1976, it was yellowish-red in colour. The cornea was depressed and the pupil did not open properly in the dark. When the animal reached a length of a metre, the colour changed to light yellow. Visual response of the eye appeared to be poor.

Unsmooth pupil

In many juveniles a persistent defect was noticed with the pupil. In dark, the pupil opens wide but in light it does not close properly. The constriction of the pupil in response to light, leaves an unsmooth and slightly round margin (Plate 1c and d).

Squint eye

Only one case was noticed in 1975 where the pupil of the right eye had been shifted to the front, forming a squint (Plate 1e).

BENT NECK

Twentyone of these hatchlings had bent necks at the time of hatching during 1977 (Plate 1f). The bends were 9:12 = right:left respectively. Within 1 month the defect had disappeared in all except four hatchlings.

HUNCH BACK

Two hunch back hatchlings were surgically removed from their eggs during 1977. These juveniles had a small hunched body, about 15 cm in total length. The head was also small and deformed. Both juveniles died within 24 hours of emergence.

BENT TAIL

In this condition the tail remains permanently bent to one side or is twisted (Plate 2a). This defect was noticed with 11 hatchlings in 1977. Such hatchlings naturally faced difficulty in swimming and thus kept mostly to shallow water in the rearing pools.

CROSSED SNOUT

Two hatchlings during 1977 had a crossed snout (Plate 2b). This defect was not pronounced when they hatched, but it became evident within the next five days. In this defect the upper jaw crosses over the lower jaw and, therefore, projects to the side. When the snout was still in its "quick growing phase" at 30 days old, treatment was resorted to in an attempt to correct the defect. The hatchlings were force-fed throughout the treatment period and after feeding both jaws were tightly bound together with gauze cloth or adhesive plaster. Following nine days treatment the defect was fully corrected in one individual but reappeared after two years. In the other hatchling, however, it reappeared after 24 hours and subsequent treatment never improved the condition.

MOUTH VALVE

One case with this defect was noticed in 1977. In the region where the mouth opens into the oesophagus, it is guarded by two palatal flaps one aligned to each jaw. The internal nares open behind the upper valve. In this defect the upper valve is completely absent and thus the internal nares become visible when the jaws are kept open (Plate 2c and d). Such a gharial cannot breathe in water with its mouth open and snout tip protruding above the surface. It died of drowning.

BULGED BELLY

In 1977 two cases were noticed where the hatchlings were only about 12–15 cm in length and had a large bulged-out belly. These juveniles failed to emerge from the eggs by themselves. The belly had occupied almost all the space within the egg. Both the hatchlings died within 2 hours of emergence.

UMBILICAL CONSTRICTION

During embryogenesis the ventral closing up of the skin in the umbilical region normally encloses the yolk

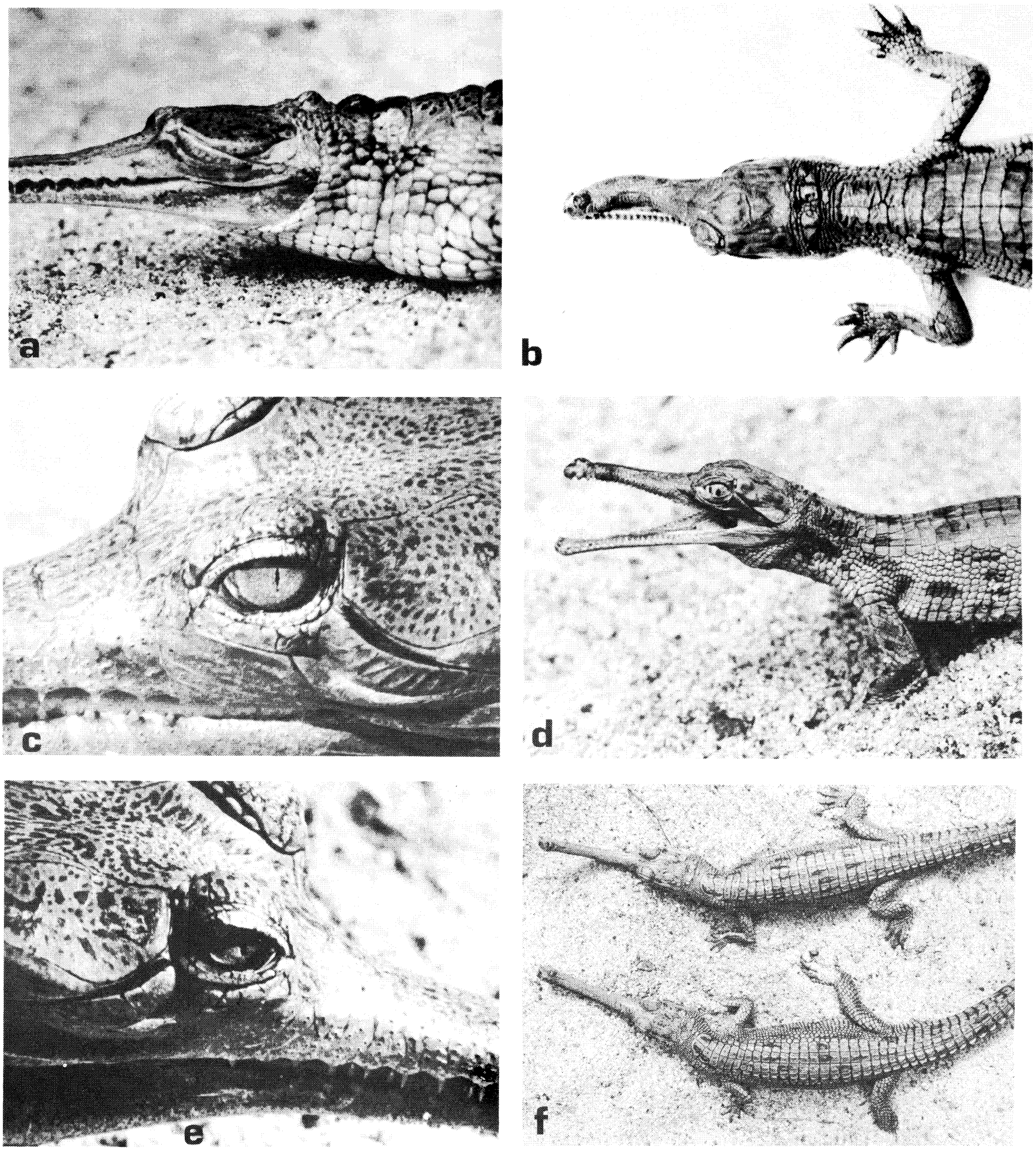

PLATE 1. (a) Blind gharial with both eyes absent. (b) Blind gharial with one eye absent. (c) Pupil of a normal gharial. (d) Pupil of a gharial showing the defect "unsmooth pupil". (e) Gharial showing squint eye. (f) "Bent neck".

mass within the abdomen. In one case in 1975 and in five cases in 1976 the skin closed on the wrong side, excluding the yolk mass. The 1975 hatchling died at about 3 months of age. All 1976 hatchlings were artificially force-fed daily after they were 5 days old. Three of these hatchlings died within 1 month while the other two survived. These were forced-fed till they were about 2 months old.

In addition to the above description of major defects, at least 200 out of the total of 438 1977 hatchlings had their tail tips curled upward (Plate 2e and f) at the time of hatching. This defect disappeared in the more vigorous of the hatchlings within 3 months of hatching, and all were very healthy. At the end of the sixth month it persisted in none of the hatchlings.

Furthermore, a juvenile of 1977 was noticed to face difficulty in walking immediately after hatching. The limbs of the right side appeared to be defective at that time. Before the third day of hatching the defect disappeared by itself.

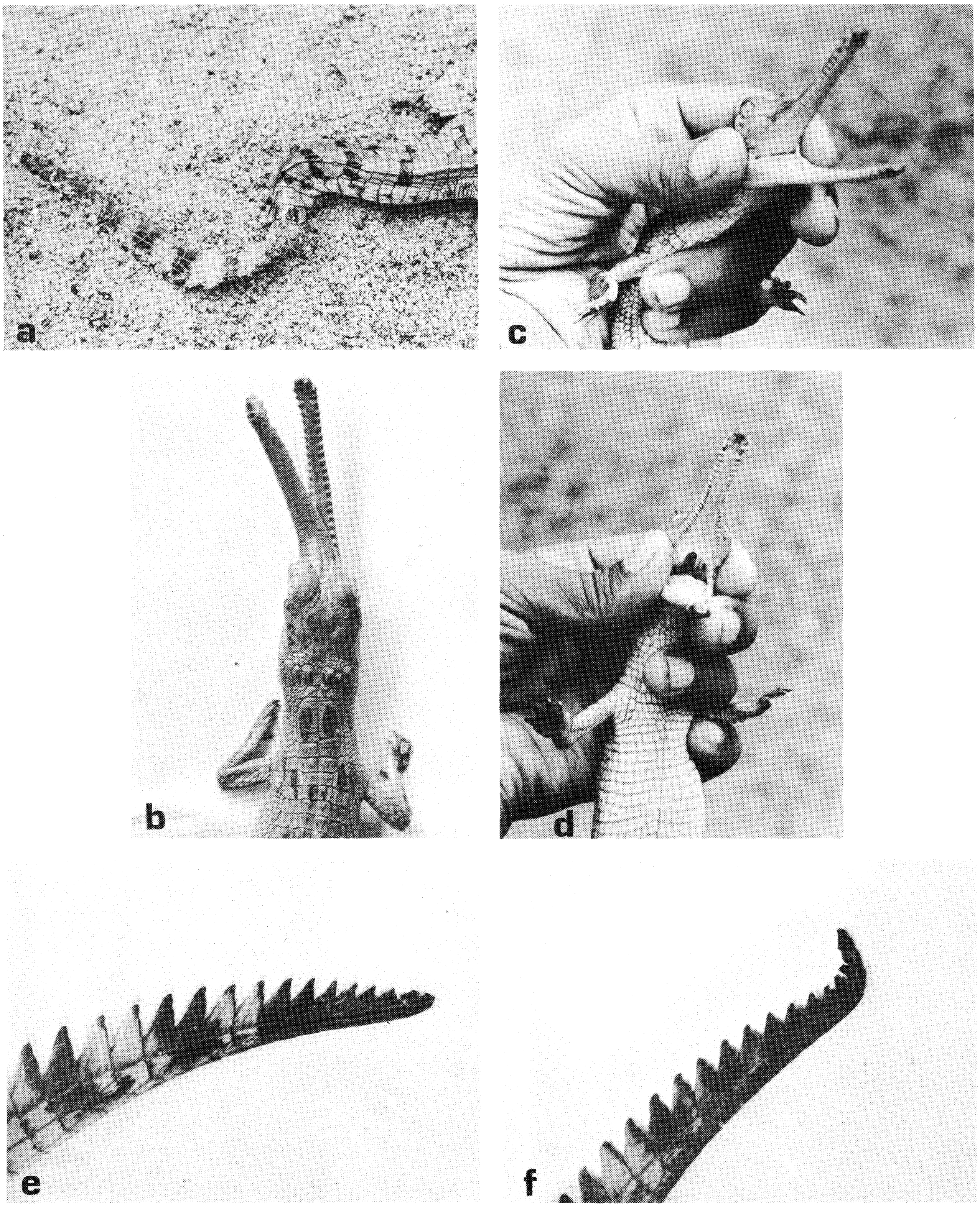

PLATE 2. (a) "Bent tail". (b) "Crossed snout". (c) Opened jaws of a gharial showing upper and lower palatal flaps intact. (d) Same showing absence of the upper flap (mouth valve defect). (e) Tail tip of a normal gharial. (f) Tail tip of a gharial showing "curling".

DISCUSSION

Only 6.1% of the total of 1061 eggs incubated showed any kind of congenital defects. This constitutes 8.2% of the fertile eggs (789) incubated. Out of the 65 instances of congenital defects there were 25 (38.4%) with eye defect(s), 34 (52.3%) with axial skeletal defects (bent neck, hunch back and bent tail), two (3.0%) with head skeleton defects (snout) and four (6.1%) of non-skeletal type (mouth valve, bulged belly and umbilical constriction).

It is interesting to note that eye defects of some kind occurred every year in eggs collected from the Kali-Narayani-Gandaki river systems originating in Nepal. An instance of a blind gharial has been recorded for eggs collected from the Girwa river gharial population (Singh & Tandan, 1978). This hatchling is similar to those reported by us above, in that there was no development of eyes whatsoever. Singh & Tandan (ibid.) record the absence of the eyeballs together with the optic stalks and optic chiasma. They explain this abnormality in terms of a deleterious gene in the genome. In this instance the young had hatched from eggs collected at Girwa river in extreme northern Uttar Pradesh, a river entering India from Nepal where it is known as the Karnali. It is believed that a "blind" gene causing the absence of one or both eyes is present in some individuals in the populations from the Kali-Narayani-Gandaki and Karnali-Girwa river systems of Nepal.

The defect involving an unsmooth pupil may be associated with defects in functioning of the ciliary muscles.

Partial desiccation of the eggs during incubation may cause skeletal distortions as is recorded for chelonians by Lynn & Ullrich (1950), in the case of gharial commonly in the form of bent necks. This problem could also be due to wrong positioning of the embryo in the egg. Choudhury (Pers. comm.) recorded instances of bent necks in hatchlings form Chambal eggs but the defect disappeared in most in due course. Minor muscular distortions, causing temporary limb defects leading to clumsy walking, may have similar causes. Only one such case was clearly noted, but gait was normal after the third day.

Bustard (1969) thought that a stunted tail in *C. novaeguineae* may have been caused by high temperature egg incubation (38°C) and recorded similar results in gekkonid lizards whose eggs were incubated at high temperatures. Similar congenital defects in *C. porosus* (Kar, 1980; Kar & Bustard, 1982) do not appear to have a temperature origin and may have been due to desiccation. We consider that the 11 individuals with bent tails (all in the 1977 sample) could be the result of desiccation. Desiccation, if present, was present during only the last 4 weeks incubation.

The defects noted in this paper were observed with young which developed from eggs incubated under simulated ideal natural conditions. The defects divide into two categories: those that are genetically determined and those that are environmentally determined. It is expected that the latter category of defects also occurs in nature, and that the frequency of these environmentally determined defects may be higher in nature than those here reported because of widely varying climatic conditions in nature compared to the provision of a more stable incubation environment in the hatchery used here.

ACKNOWLEDGEMENTS

We acknowledge support from the Government of Orissa (State Forest Department), the Government of India, and FAO/UNDP.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 220–221 (1982)

OCCURRENCE OF PARTIAL ALBINISM IN A WILD POPULATION OF THE SALTWATER CROCODILE (*CROCODYLUS POROSUS*, SCHNEIDER) IN ORISSA, INDIA

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(*Received* 2 *March* 1981)

During a population study of *Crocodylus porosus* inhabiting the tidal mangrove creeks of Bhitarkanika Wild Life Sanctuary in Cuttack District, Orissa (approximately 20° 40′ N, 86° 50′ E) the presence of several paler-coloured individuals in the population has been noticed. There is not a gradation of colour from light to dark coloration in the population but two discrete colour phases. Those comprising the majority are similar-coloured to *porosus* studied by the second author in other parts of its range in Asia, New Guinea and Australia. Those in the minority have the ground coloration replaced by a pale whitish colour. These latter individuals are well known to the local people who consider that they are a distinct species of crocodile. They refer to them in the Oriya language as "Sankhua" (which means whitish) to distinguish them from typical *porosus* (known as "Baula" in Oriya).

Like the so-called "white" tigers of former Rewa

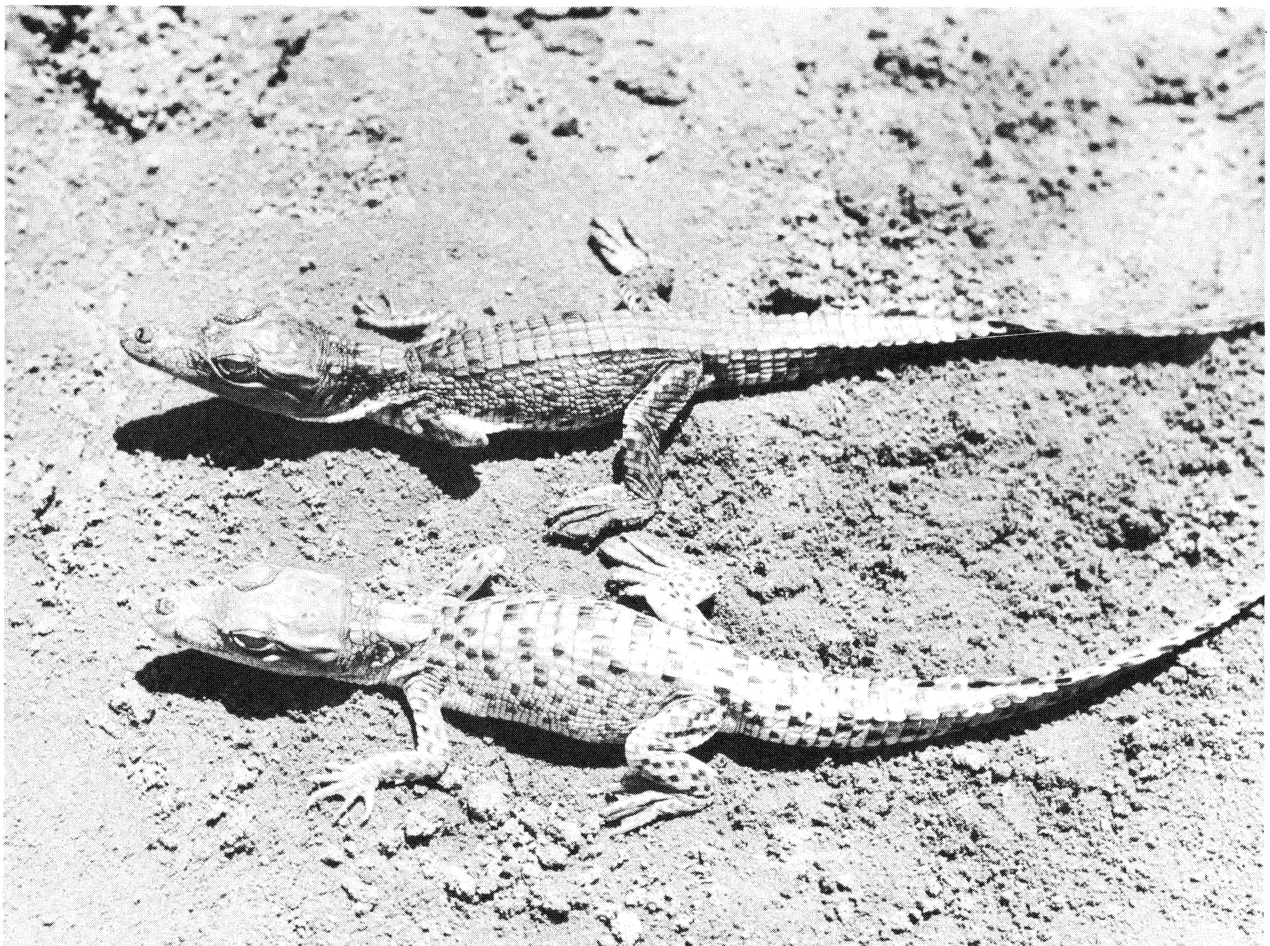

PLATE 1. Two hatchling saltwater crocodiles from the same clutch. The upper individual is of normal colour; the ground colour of the lower individual is whitish.

State in Central India (now part of Madhya Pradesh) the "white" crocodiles are not true albinos since they possess the normal black markings (spots or blotches, and stripes in crocodiles and tigers respectively). However, they both completely lack pigment in the ground colour.

At the time of the census conducted in December 1976 and January 1977, 35 adult and sub-adult saltwater crocodiles inhabited the sanctuary four of which were "white" crocodiles. These four are all present today. They comprise a female measuring 3.4–3.8 m and a juvenile (sex unknown) of about 1.2 m. A male of 5.2–5.5 m and a female of 4.0–4.3 m have a whitish face and a totally white face respectively. In adult crocodiles, the white colour is not as pale as in the baby crocodiles since, like other large reptiles, the colouring in *C. porosus* becomes dull with increasing size and age. The local people state that in very large (old) crocodiles the whitish colour of the body may become so dulled as to be indistinguishable from normal-coloured crocodiles. The face, however, is stated to remain white throughout life.

It is to be expected that the survival prospects for such albinoid individuals in the wild would be poorer than for normally coloured individuals. However, there is good evidence from local people of their occurring in the Bhitarkanika mangroves over a long time-span and the data given in the preceding paragraph show that they can recruit to the breeding cohort of the population.

A clutch of 48 eggs was collected for hatchery incubation at Kalibhanjadian within this sanctuary. The mother is thought to be the 4.0–4.3 m "white" crocodile referred to above. The clutch produced 24 hatchlings between 21–23 August 1975, one of which was a "white" crocodile. The other 23 were all normal *porosus* hatchlings. The "white" crocodile and a normal-coloured member of the same brood are shown in Plate 1.

The "white" crocodile, which is a female, has been retained in captivity at the Centre at Dangmal. It has increased its birth weight of 55 g and length of 280 mm to 45.4 kg and 2.18 m respectively (November 1980).

It is hoped in due course to breed this female at the Centre.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 221–222 (1982)

EMBRYONIC TAIL DEFORMATION IN THE SALTWATER CROCODILE (*CROCODYLUS POROSUS*, SCHNEIDER) IN ORISSA, INDIA

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(*Received* 2 *March* 1981)

The clutch of 48 eggs laid in 1975 which gave rise to a "white" hatchling described in the paper immediately preceding (Kar and Bustard, 1982) also produced one abnormal embryo. This embryo developed to full-term but died without slitting the egg shell. On examination it was found to have a deformed and stunted tail similar to that described and figured for *Crocodylus novaeguineae* by Bustard (1969), where the cause was thought to be the result of high temperature egg incubation.

Saltwater crocodile eggs are usually laid during the last week of May/first week of June in Bhitarkanika. It is assumed that this nest was laid on 1 June then it incubated for 50 days prior to collection under an imperfectly known temperature regime. The nest was collected at 11 a.m. on 20 August 1975 (monsoon season). However, there was no rain on that day or on the two preceeding days and the weather had alternated between sunny and overcast. The nest temperature at the top of the egg mass at the time of collection was 31.0°C. This compares with a mean nest temperature of 31.9°C for a sample of 25 nests (Kar, 1981). Kar found that the mean nest temperature was considerably lower than air temperature throughout the day (by a mean of 2.3°C in the morning and 2.0°C in the afternoon) presumably due to evaporative cooling. In the present case air temperature was only 31.5°C, that is 0.5°C above nest temperature, at the time of collection. This is explicable on the basis that this nest was dry, so evaporation was minimal. The nest was also very compacted with much mud used in its construction resulting in reduced gaseous exchange with the outside. The nest was located in a generally shady place which may also account for the temperature being slightly lower than normal.

The eggs were incubated in an artificially prepared mound consisting of vegetation used in the natural nest. The temperature in the nest at egg level, measured through a stoppered bamboo pipe permanently inserted into the middle of the egg mass, averaged 28.5°C (range 27–30°C) during the remaining 31–33 days of incubation. Possible morphological abnormalities resulting from low temperature incubation are not known.

It is possible, though unlikely, that water deficiency could have caused the deformity as has been described for chelonian embryos by Lynn & Ullrich (1950). However, the 24 eggs which hatched all produced normal hatchlings except for the "white" individual described in the preceeding paper. The remaining 23 eggs, which failed to hatch, were apparently infertile. Water relationships of crocodile eggs are little known. Preliminary work carried out by Bustard (1976) indicated, that eggs dessicated rapidly when water was not available in the external medium. However, Bustard noted that eggs which had lost approximately 20% of their weight as a result of dessication still produced normal hatchlings.

A detailed study of the water relationships of crocodile eggs at different developmental stages, particularly if related to the natural situation, would be most valuable.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 222–223 (1982)

CROCODILE PREDATION ON MAN

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(*Received* 24 *June* 1981)

Crocodiles are much maligned animals. Instances of human predation have been greatly exaggerated, initially by early explorers. Herpetologists, however, have also been guilty of sensationalism. For instance, Arthur Loveridge (1954) writing of the saltwater crocodile (*C. porosus*) referred to it as "this man-eating monster"—an unfortunate turn of phrase. Loveridge also stated, "... once it has found how defenceless is the average man or woman when taken unawares, the estuarine crocodile becomes as confirmed a man-eater as the most persistent man-killing tiger".

After many years of work on the ecology of this species we have no evidence to support this statement (see below).

The saltwater crocodile is widely stated to be the most dangerous crocodilian species from a human standpoint (Neill, 1971) hence it is the species in which the frequency of human predation should be investigated. It is significant, therefore, that in 10 years in Bhitarkanika, Orissa, India, where indepth ecological studies on the saltwater crocodile have been in progress since 1975, only four instances of attempted human predation have occurred. This is despite this sanctuary, declared for the saltwater crocodile, (a) holding some of the largest, if not the largest, individuals of *C. porosus* alive in the world today, and (b) there being a large human population settled in and around the sanctuary. Since it is usually very large individuals which are responsible for attempted human predation, all of which are males, all the ingredients for human predation exist in Bhitarkanika.

Since, as pointed out by Loveridge, man is well within the prey size of large saltwater crocodiles, it is surprising to us that attacks on man are so rare, since, as also pointed out by Loveridge, man is an easy victim. In Bhitarkanika people freely entered the water to fish (until fishing was banned under sanctuary legislation in 1975) as well as moving about at the water's edge.

We note, in the saltwater crocodile, the same apparent reluctance to prey on man as is observed in the tiger and also in sharks in most areas of the world. From the rarity of human predation in relation to the opportunities available for this, it is clear that not only are all these groups of animals not attracted to man, but that they appear to avoid him. It may even be that the occasional instances of human predation are cases of mispredation in which the predator does not realize at the time of attack that man is the victim.

We appreciate that as conservationists, actively engaged in the conservation of crocodilians, readers may think that we are trying to "whitewash" the saltwater crocodile. This is not the case, we merely wish to view the evidence objectively. Nor is the personal evidence presented here restricted to India but covers Bustard's extensive work with the species in Australia where many aboriginal groups with which he worked, who knew the species well, did not fear it. Significantly older members of the tribes reported instances of human predation as very rare even in the past.

The saltwater crocodile is not a "man-eating monster". It may occasionally take man, and as a master predator, like the tiger or any other large wild animal, should be treated with respect by the local people. However, *scientifically*, the interesting thing is that actual instances of predation are very rare in relation to opportunities to prey on man.

Finally, we find no scientific evidence for Loveridge's statement, quoted above, that following predation on a human, the saltwater crocodile becomes a confirmed man-eater. Similarly, we found that saltwater crocodiles which "lifted" domestic cattle did not tend to become "cattle lifters" following a successful kill (Kar & Bustard, 1981). While one crocodile was responsible for two of the four instances of human predation that occurred during the 10-year period, these were more than 3 years apart, and this crocodile could have lifted a human at fortnightly intervals throughout this period *until itself killed.* These last three words may be a key factor in the comparative scarcity of human predation by both crocodiles and tigers. So-called man-eaters are normally hunted and killed and both animals have learned to fear and avoid man. Since both animals have been in close contact with man for a very long time there has been genetic selection (as a result of killing those showing the propensity) against man-eating. In support of this theory crocodile behaviour appears to have altered considerably in the 20–30 year period of intense hunting for their skins in various parts of the world. A long-term behavioural adaptation, genetically based, tending to discourage selection of man as a prey animal, could also have developed.

We have used the word "predation" in the title and throughout the text in place of "attack" to distinguish instances in which man is the potential food item from the (more common) instances in which a nest-guarding female crocodile warns man off by biting him (Bustard & Choudhury, 1980).

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 225–230 (1982)

COMPETITION FOR MATES AND FOOD ITEMS IN *VIPERA BERUS* (L.)

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(*Received* 5 *January* 1982)

SUMMARY

Agonistic and predatory behaviours were studied using cine analysis in captive and feral populations of vipers *Vipera berus* (L.). During the normal mating season, combat seems to occur exclusively between adult males; is primed by a pheromone produced by reproductively-active females and is stimulated by visual cues from other males. Later in the active period, competition for prey elicits a similar response which involves adults and juveniles of either sex. Large size confers advantages in both situations and the fact that mating and feeding occur at different times, means that sexual selection and successful reproduction can both be facilitated.

INTRODUCTION

Social aggression (Brain, 1981) has been described in males of several snake families including the Viperidae (Shine, 1978). *Vipera berus* is widely distributed (Prestt, 1971); shows clearly-defined seasonality in such behaviour (Smith, 1951) and is sexually dimorphic in adulthood (see Fig. 2); all factors facilitating study of combat in this species.

The raison d'être for social aggression in male snakes is obscure. Such activities have been said to serve no obvious function in these animals (Morris & Morris, 1965). This is a consequence of these authors' erroneous belief that combat never leads to mating or establishment of a dominance hierarchy. Parker & Grandison (1977) also suggested that it did not result in territoriality. Klauber (1972) adds that such behaviour stems from some sexual impulse but a number of authors (Prestt, 1971; Smith, 1951; Street, 1979), dismiss it briefly as "sexual territoriality". Shaw (1951) considered combat the result of male homosexual behaviour and felt that female presence was unnecessary. Intermale combat has even been misinterpreted as mating (*e.g.* Parker, 1963); probably because it occurs during normal mating periods and sexual dimorphism is not very marked in many snakes.

More recently, observations of combat behaviour in *Bitis gabonica* (Akester, 1979) led the author to believe that physical contact between sexually aroused adult males initiated combat and that territoriality, competition for food (Sutherland, 1958), sexual dominance and homosexuality played no part.

Appleby (1971) and Phelps (1980) believe that it is always males in possession of females which are victors in combat bouts in *Vipera berus*. Andren & Nilson (1981) conclude that male vipers defend females and small areas around them during the reproductive period and that a hierarchy is established at this time between males.

The purpose of the present paper is to assess the relationship between social aggression for mates and combat over food items in the common viper (*Vipera berus* L.). The existence of these activities has been documented elsewhere (Kelleway & Brain, 1982).

MATERIALS AND METHODS

A captive population of vipers was housed in a large, circular (10 m diam.) enclosure. This terrarium was constructed to resemble the snakes' natural habitat and included a hibernation site, elevated basking sites, and a small pond in a lower area (Fig. 1). A sex ratio of 1:1 as in local wild populations (*cf.* Prestt, 1971) was maintained. Population density has important effects on reptile behaviour and was maintained at a level similar to that observed during periods of aggregation (spring and autumn) which correspond to periods of intense behavioural activity. Local feral and the captive populations were observed on a daily basis during the mating periods of 1979–1981. Cine (16 mm Kodachrome 25) and videotape records of the latter were obtained. Competition over food items was also documented later in the year. Films and tapes were subjected to detailed analysis for behavioural sequences employed and the nature of the participants.

RESULTS

In social aggression over females, initial recognition (Fig. 3) is followed by mutual elevation of the combatants' anterior regions which become engaged (Figs. 4–8) with subjects attempting to press their opponent's raised portion to the substratum. Combatants once "overtopped" by opponents move laterally and upwards to gain a height advantage (Fig. 9). This sequence is often repeated many times. The entire body lengths of combatants are often tightly "corkscrewed" around each other (Fig. 11) and such pairs often roll sideways downhill. Corkscrewing imparts considerable lateral thrust to the heads and when lateral contact is lost, they may be "catapulted" apart (Fig. 13). Actions which result in wide lateral separations of the heads (>10 cm) can be regarded as "decision points" where combatants either re-engage in combat or one individual moves off rapidly, often pursued by the victor.

Bites and striking never occur in this combat but head butts (Fig. 8) are often employed. Investigatory tongue flicking (as in courtship and predatory behaviour) rarely occurs except at decision points.

Sexual combat can last up to 1 h. Although combat postures may be maintained (Fig. 12) for short periods (10–30 sec), movement is generally continuous and may be very rapid. Encounters between males of equal size last longer than those involving unmatched subjects and encounters are longer (and slower) on cool days.

The outcome of these encounters is to temporarily establish a dominance-subordination relationship. These last around 24 h over which time subordinates encountering dominants in the presence of sexually attractive females are driven off or "freeze". Pairs subsequently meeting in similar circumstances often re-engage in fighting but this is generally of short duration. Whilst larger males are engaged in long combats, smaller individuals may court reproductive females. Copulating males are often challenged by non-intromitted males but the copulating male does not respond and the "aggressor" breaks off combat display and may even court the copulating female for a short period.

Vipers are able to raise and maintain the anterior one third of the total body length (Fig. 10). Thus larger, heavier individuals have a considerable advantage in combat situations. There is a high correlation between size and combat victory but smaller males obtain a degree of success as the mating season advances.

Male combat may be elicited in the appropriate season by any snake-like object providing it is moved with a jerky action in the presence of a reproductive female. Mobile snake models (Fig. 15) of a variety of colours, and even correctly-moved sticks (Fig. 14) will be attacked by courting males. Such males will attempt to engage their own mirror-images (Fig. 16) but not life-size photographs of themselves, other males or females regardless of mode of presentation.

Feeding, reproduction and (to some extent) sloughing are mutually exclusive in vipers. In Britain, feeding does not normally commence until late May or June when vipers in the study area feed almost exclusively on small rodents and insectivores. Larger prey are subdued/killed by envenomation and all prey is swallowed whole. Envenomated prey attract and produce feeding responses in the envenomator and other individuals (Fig. 17). In dense populations, especially at times of relative food shortage, considerable competition for available food items is evident (Fig. 18).

The normal feeding attitudes, *i.e.* raised anterior with short rapid movements adopted by both sexes, elicit combat (Fig. 19). This "predatory" combat is visually indistinguishable from intermale sexual combat but is not confined to males, involving adults and juveniles of both sexes (Figs. 20–22). Neither is it confined to two individuals (Fig. 23); indeed, groups of up to seven participants have been recorded (Fig. 24). Vipers with half-swallowed prey do not respond to threats by conspecifics.

Predatory combat appears to occur regardless of sex ratio. It can be elicited in captive populations at a density of 0.5 animals per m^2 by maintaining food at an artificially low level. There is a similar high correlation between size and combat success which is likely to result in the larger, heavier gravid females obtaining disputed food items. Predatory combat, particularly amongst females, is generally shorter in duration than sexual combat. Satiated animals show little or no response to envenomated prey and are not involved in predatory combat.

DISCUSSION AND CONCLUSIONS

As social aggression over mates in vipers only concerns the male and occurs at a time of the year when feeding is not evident, the advantages of large body size during the mating period accrues to this sex. In contrast, the increased probability of victory by gravid females under circumstances of relative food shortage, by virtue of their increasing size and weight, can be interpreted as a mechanism by which the females of this species (and hence the species itself) achieves reproductive success. Young must be produced in the short active period between spring and autumn and the females' need for available food and preferred basking sites for behavioural thermoregulation are facilitated by this relationship. Males become somewhat expendable once sperm transfer is accomplished.

Although combat in vipers has been formerly closely associated with sexual behaviour, it is suggested that competition over food items may account for the so-called out-of-season mating behaviour in this (Appleby, 1971) and some other species of snakes. These data also clearly indicate how apparently the same behaviour can be used for a variety of purposes by animals with clearly different physiologies (see Brain, 1981).

ACKNOWLEDGEMENTS

I should like to thank Dr Paul F. Brain for his critical review of the manuscript. I am grateful to Professors E. W. Knight-Jones and J. S. Ryland for the facilities provided at Swansea.

This study was funded by the S.E.R.C. from whom I am in receipt of a grant.

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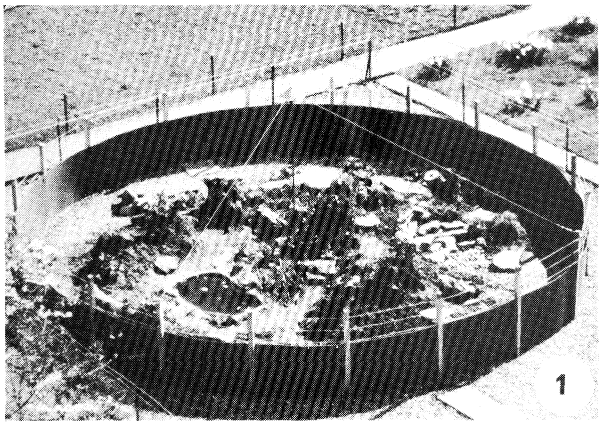
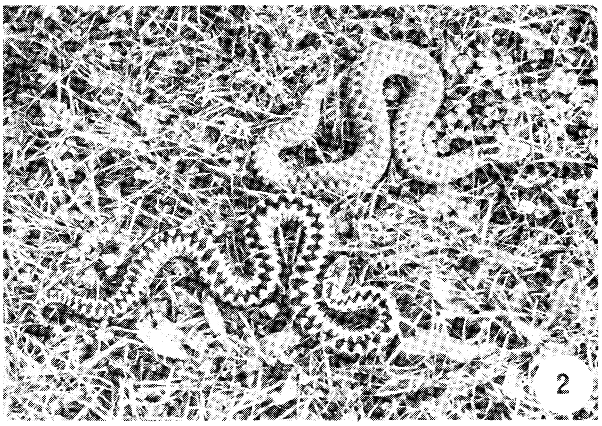
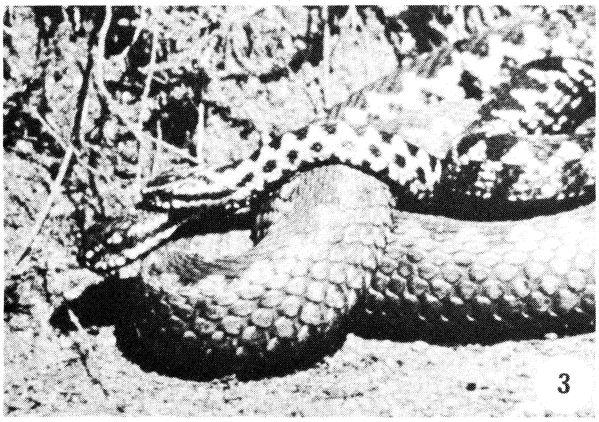
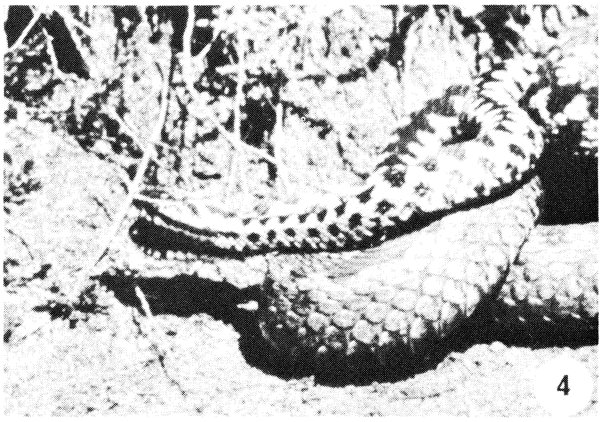
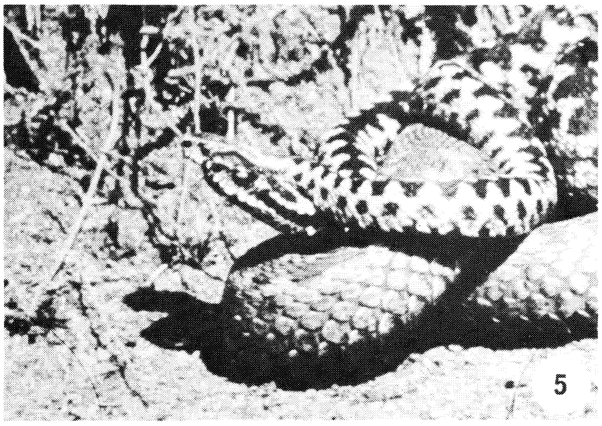
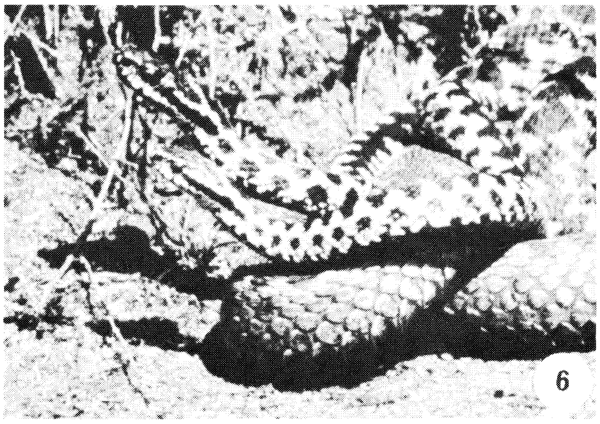


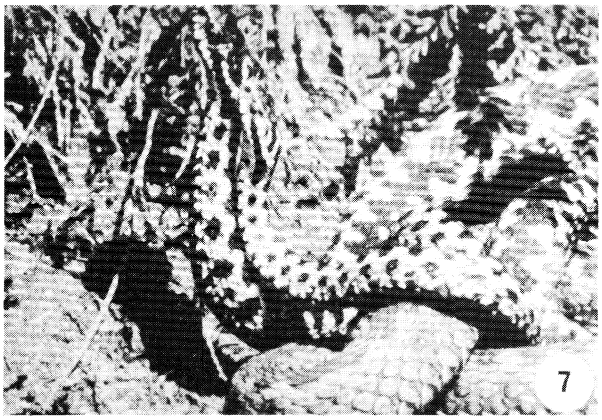


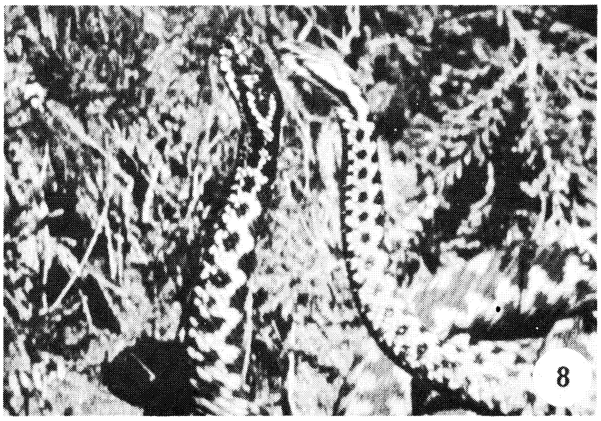






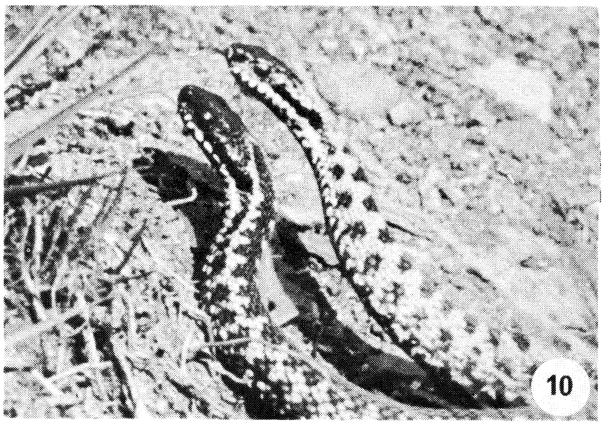






Illustrations: Figs. 3–24 are reproduced from 16 mm colour cine film shot at 24 frames per second.

FIG. 1. The outdoor terrarium nearing completion in the spring of 1978.
FIG. 2. Adult male and female *Vipera berus*, the female is the upper of the two.
FIGS. 3–8 show the commencement of intermale reproductive combat in sequence.
FIG. 3. Two males court the same female, initial recognition takes place and the anteriors are engaged.
FIG. 4. The upper moves to maintain its position.
FIG. 5. The lower male attempts to move laterally and upwards to gain the upper position.
FIG. 6. The positions change and anteriors become elevated as both combatants seek to maintain height advantage.
FIG. 7. The head and neck are used to try and push the lower male to the substratum.
FIG. 8. Bites or striking are never employed in combat but head-butts often are.

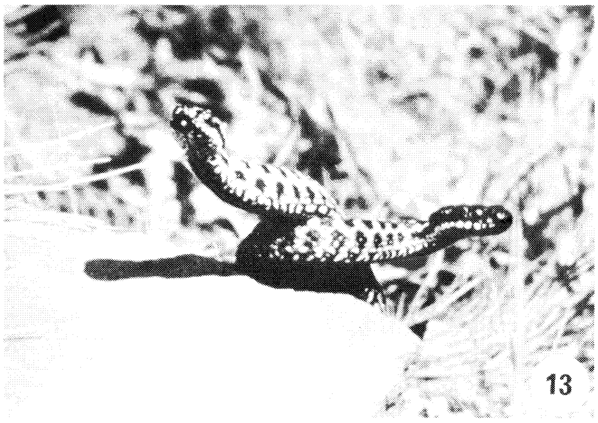
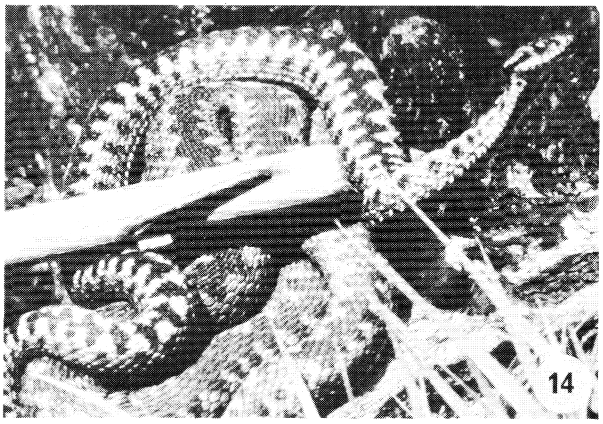
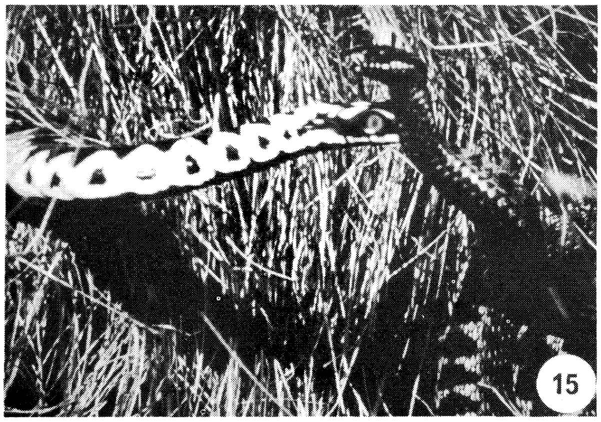
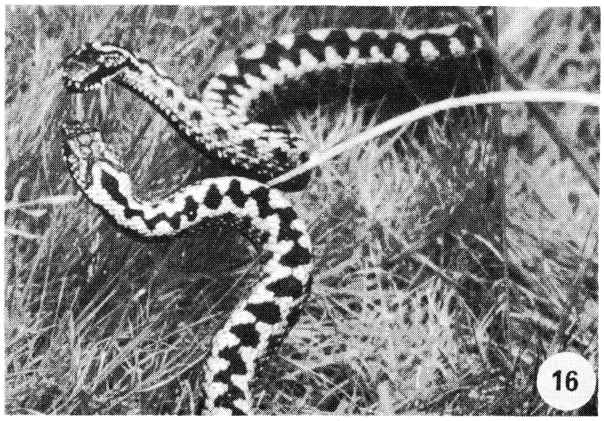






FIG. 9. The anterior portion of the body is often thrown into an "S" shape to gain greater purchase on a lower opponent.

FIG. 10. Postures are often maintained for short periods, particularly on cooler days.

FIG. 11. Combatants bodies are often tightly "corkscrewed" along their entire length.

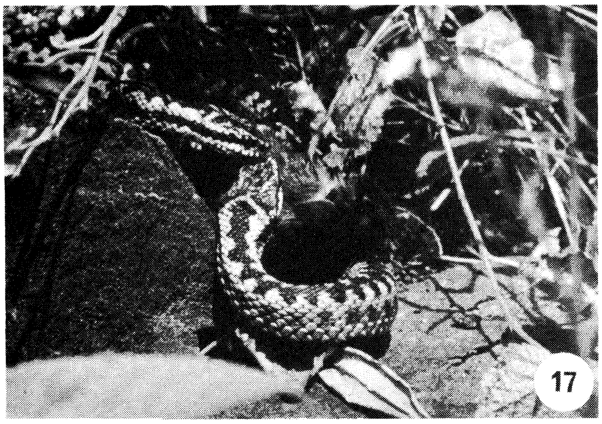
FIG. 12. Corkscrewing impedes anterior elevation and forward progress.

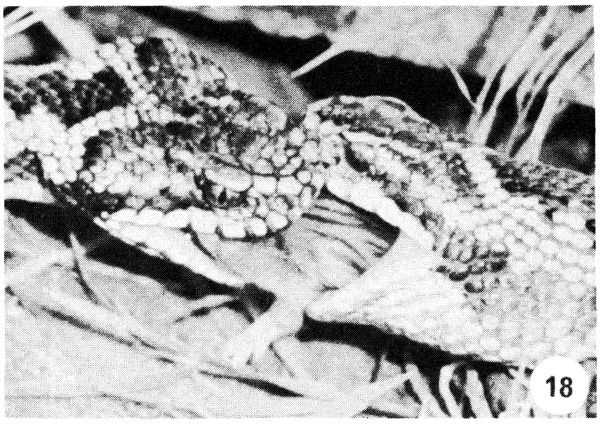
FIG. 13. Wide lateral separations of the two heads constitutes "decision points", when combat will either be terminated or continue.

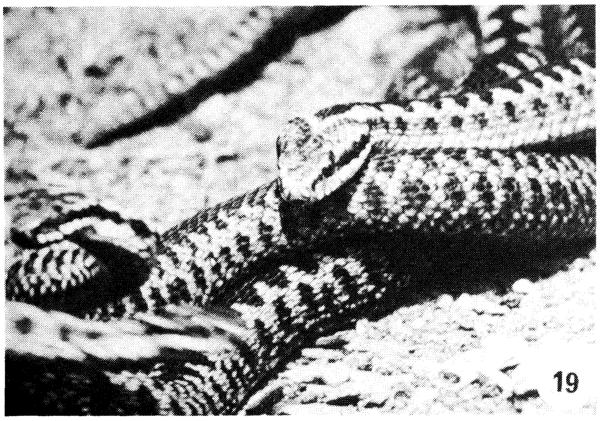
FIG. 14. Even sticks, appropriately presented, will elicit male combat in the presence of reproductive females.

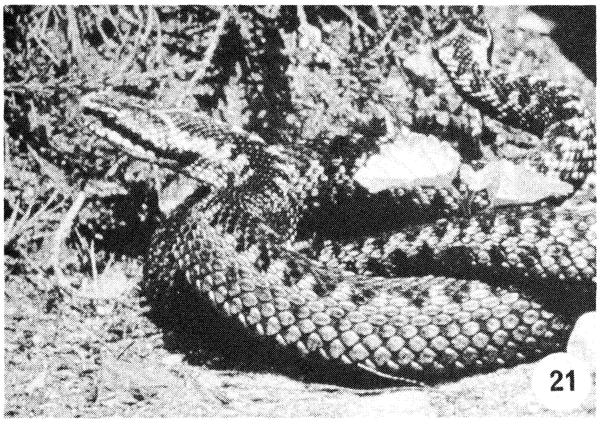
FIG. 15. Models also, regardless of colour, will be engaged in combat, providing they are moved with a jerky action.

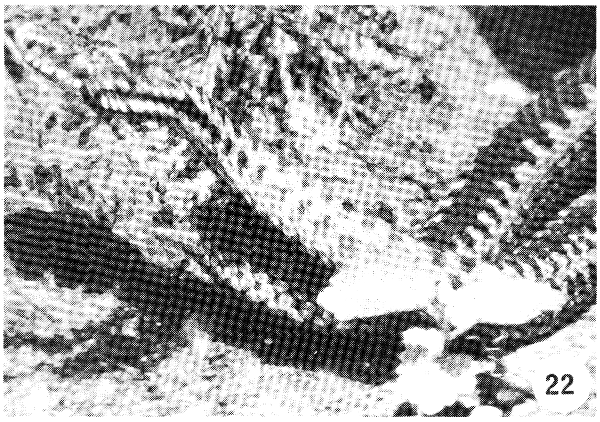
FIG. 16. Males will engage their own mirror images in the presence of reproductive females. (The edge of the mirror can be seen to the right.)











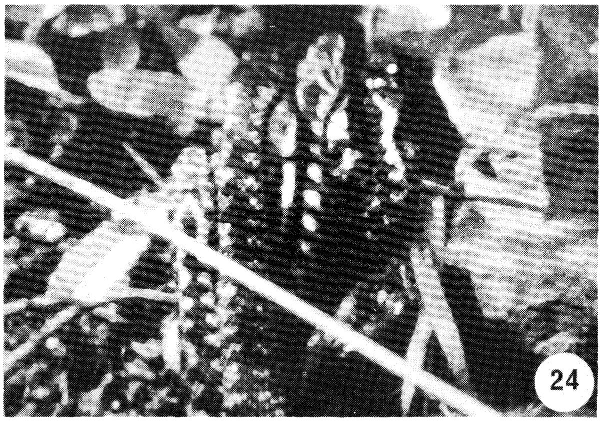


FIG. 17. Envenomated prey attracts individuals and elicits feeding behaviour.

FIG. 18. When prey are in short supply considerable competition exists for available food.

FIG. 19. Two males engaged in predatory combat are joined by a female (uppermost).

FIG. 20. A male and female engaged in combat are joined by another male.

FIG. 21. Two females combat over food showing the characteristic elevated anteriors.

FIG. 22. The attitudes of predatory and reproductive combat are visually indistinguishable. Here a male and female compete for food.

FIG. 23. Predatory combat is not confined to two individuals. Here three males show characteristic combat postures.

FIG. 24. Groups of animals have been recorded in predatory combat. Here four males and one female (one is hidden underneath) combat in late summer.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 231–232 (1982)

BOOK REVIEWS

REPTILES OF THE SOLOMON ISLANDS. By Michael McCoy (1980). 80 pp, with 8 colour and 12 monochrome plates. Wau, Papua New Guinea: Wau Ecology Institute, $US 5.00 (also available from Bishop Museum Press, Box 19000-A, Honolulu, Hawaii 86819, U.S.A.).

This is the seventh of the Wau Ecology Institute's New Guinea natural history handbooks and the first to deal with Reptiles. While only those that occur in the Solomon Islands are included, the interest and usefulness of this book extends far beyond that archipelago—at least half of the species listed here also occur in New Guinea and a quarter also occur in Indonesia. The importance of McCoy's work is further enhanced because it is the first comprehensive account of Reptiles occurring in any of the island groups that stretch from Malaya to New Guinea and beyond since Nelly de Rooij's 1915/1917 monograph "Reptiles of the Indo-Australian Archipelago".

The book's 80 pages include a brief introduction to Solomon Islands geography and some general remarks on their Reptile fauna. Following this is a short account of Reptile characteristics while an appendix explains how Reptiles may be preserved for museum collections. The rest of the book comprises a systematic account of Solomon Island Reptiles, a glossary of the technical terms used and a list of literature references.

The systematic account is detailed to the point of repetition, for example we are told that *Tribolonotus* have "lower eyelid scaly . . . head shields rugose". This statement is repeated no less than four times, under each of the *Tribolonotus* spp listed. Non-technical readers may need frequent reference to the detailed glossary and some of the terms used in the keys could have been explained in those keys, or perhaps in a footnote on the same page. Species accounts also include descriptions of the colour in life (or colours, in the case of variable species) and notes on the ecology, probably the first time that such notes have ever been published in many cases. I have one criticism here which is not entirely frivolous. I read that the snake *Loveridgelaps elapoides* is "white with black banding" but the illustration clearly shows a snake with orange and black bands. One has to read on to find that the yellow colour is restricted to the dorsal side, but surely it is the dorsal aspect of a snake that the observer usually sees first?

There are 20 pages of illustrations. Colour and monochrome are not distinguished in the list of illustrations, thus species which are illustrated both ways appear twice in the list making it necessary to go right through the list when looking for an illustration of a particular species (or else refer first to the species account, via the index and then go back to the illustrations). The illustrations are good, particularly those in colour and, despite being eight to a page, clarity is not impaired. Just thumbing through the illustrations gives one a very good idea of the diversity of small skinks in these islands.

Errors appear to be few and only one needs attention here; in the list of references, Dr. Klemmer has become 'Kelmmer'.

The criticisms that I have made largely concern the layout of the book and in no way detract from its value. Like all the Wau Institute's "Handbooks", this one is excellent value for money and is strongly recommended to anyone interested in Reptiles in general and those of the west Pacific in particular.

J. I. MENZIES

LES AMPHIBIENS DE FRANCE. By R. Guyetant. Extracts from *Revue Francaise d'Aquariologie Herpetologie*, published in a single edition by B. Conde and D. Terver. 32 pp. 7.5 F.

This short booklet, with A4-size pages, seems to be aimed at a broad market as an introduction to the species to be found in France (including Corsica). The most impressive feature is the abundance of good-quality colour photographs, some of which (such as the alpine newt on the front cover, the marbled newt and the southern spadefoot toad) I found particularly striking. The only criticism I would make of the pictures is that in the cases of the common and (especially) the crested newts, individuals with scarcely any crest were used and this does undermine the excellent technical quality of the photographs in those two instances. Apart from the photographs, there are two simple identification keys (one for urodeles, eight species, and one for anurans, only to genus level) and short descriptive texts of 100–200 words for each species. The urodele key is not really complete since it does not show how female smooth and palmate newts may be distinguished, and with the anurans the reader is expected to identify individual species from the photographs so the key is somewhat redundant. The texts are mainly accurate as far as they go, but they are very brief and generally subdivided into distribution, description, length, colour, habitat and general biology—all in 100 words! Standard texts on the European species (such as the Collins guide by Arnold, Burton & Ovenden) have to deal with many more types yet provide better information for each than does this booklet. Some of the statements are curious, and I think of little value; does the common newt breed later than the palmate? Are marbled newts less voracious than crested newts? Does *Rana iberica* get into France, and what is *Rana honnorati*? With so few words to play with, there are several instances where I feel they might have been better chosen. Text is in French throughout, and there is a short but reasonably comprehensive bibliography. To summarize, I would not recommend that anyone wishing for substantial new information on the various species either in general or in relation to France should buy this booklet but as a source of good-quality photographs alone it is worth the money.

TREVOR BEEBEE

KETTLE, R. 1981. A DISCOGRAPHY OF AMPHIBIAN SOUNDS. RECORDED SOUND 79: 51–75. Issued as a reprint by the British Institute of Recorded Sound, £1.00.

Animal sound is inherently interesting, not only to the biologist. Amphibian vocalization cannot rival bird song in terms of its melodious quality; it tends to be repetitive and interesting to the non-specialist as a curiosity rather than aesthetically pleasing in its own right. In scientific terms, however, it is of considerable interest and its significance as a mate attractant was first demonstrated, experimentally, in *Pseudacris nigrita* as recently as 1958 (Martof & Thompson). When several species breed simultaneously at one locality it is genetically important that they remain reproductively isolated. There are therefore strong selective forces maintaining the unique character of the call of each species. By contrast with many morphological characteristics, it is subject to relatively little individual variation and thus provides an excellent taxonomic tool. Taxonomic studies must take account of voice, and Kettle's work provides a most useful compendium of nearly 100 records, tapes and cassettes, published between 1931 and 1980, whose contents include the voices of amphibians.

The body of the 25-page article consists of a list of the amphibian contents of each recording; there is also a brief introduction, with sources of literature on vocalization, a species index and a helpful list of addresses from which the recordings may be obtained.

The work is unlikely to be of interest to the average amateur herpetologist, but will appeal to recording enthusiasts and to research workers. The latter are likely to find the list of sources of unpublished collections of almost as much value as the discography itself, but I was surprised here to find no mention of the important work on African species by Schiøtz (1964, 1967), or reference to his major collection of recordings. Schiøtz, amongst others, has drawn attention to the structural differences, in the calls of most species, associated with behavioural and ecological variations. Apart from calls concerned with mate attraction, for instance, there are calls apparently with territorial significance and others associated with sexual recognition. Some of the listed recordings feature these and other variations and the article would have gained enormously if reference to this fact had been made against each recording, although this would have greatly increased the author's task. Similarly some of the recordings are published together with sound spectrographs and again it might have been useful if the reader had been made aware of this.

The discography, at the modest price of £1 post free, is published as a separate by the British Institute of Recorded Sound (29 Exhibition Road, London SW7) which preserves sound recordings of all kinds from all parts of the world. These priceless archives, currently containing 1½ million recorded items, are available for use by the public at the above address.

R. S. OLDHAM

BIOLOGY OF THE REPTILIA, Volume 11. *Morphology F*, Edited by Carl Gans and Thomas Parsons (1981). 475 pp. London, New York etc.: Academic Press, £28.00.

This book contains but three chapters. A. d'A. Bellairs and the late A. M. Kamal write on "The Chondrocranium and the Development of the Skull in Recent Reptiles", K. F. Guthe on "Reptilian Muscle: Fine Structure and Physiological Parameters" and J.-P. Gasc on "Axial Musculature". All three are masterly contributions: the first and third because they review vast literatures which, although important, have been widely scattered; the second, because it combines the very different disciplines of electron microscopy and neuromuscular physiology into a novel synthetic account of the interrelationships of fine structure and function.

Ten years from now, all three of these chapters will still be used as invaluable works of reference. The reputation of *Biology of the Reptilia*, already high, is enhanced by this excellent volume.

R. A. AVERY

THE BEHAVIORAL ECOLOGY OF THE KOMODO MONITOR. By Walter Auffenberg (1981). 406 pp. Gainesville: University Presses of Florida, $45.00.

The title of this book is really a misnomer—far more topics are covered than the rather restrictive "behavioral ecology" would imply. In fact, the volume is a monographic compilation of most of what is known about the natural history of the Komodo Monitor (or "Ora"), based largely on the results of Dr Auffenberg's three expeditions to Indonesia in 1969–72. A list of the chapter headings will give some idea of the scope: morphology, relationships in time and space, ecology, activity and movement, individuals, demography, reproduction, the Ora as scavenger, the Ora as predator, feeding dynamics, coactions. The book will be of immense interest to a wide variety of herpetologists, and I urge as many as possible to read it—the review copy is, of course, now available in the British Herpetological Society library. My own reactions were admiration of the thoroughness of the work, and fascination with the practical problems of studying the biggest lizard in the world ("It required three men to manipulate lizards 1.5 m or larger . . .").

Most of the questions which I get asked about Komodo Monitors are answered here. "How big are they?" (not often more than 3 m in length); "Do they eat people?" (rarely); "What is the explanation of their curious restriction to a number of relatively small islands?" (Auffenberg thinks that they evolved there when sea levels were lower, and have now been "stranded" as an indirect result of Mio-Pliocene volcanism) and "Is their future secure?" (the author is guardedly optimistic—he writes a lot of very good sense about the problems and priorities for conservation in an increasingly overcrowded world).

R. A. AVERY

BRITISH JOURNAL OF HERPETOLOGY

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3. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed double-spaced with wide margins all round; good quality paper is essential for the top copy. Except for short notes, papers should be divided into sections. The first sub-head will be centered in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.
4. For all papers the title should be followed by the name(s) of the author(s) and the address or name of the Institution in which the work was done. For major papers a short summary is required before the body of the paper. Acknowledgements should be included before the list of references.
5. The usual rules of zoological nomenclature apply.
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7. Line drawings and half-tones are numbered in sequence in arabic numerals, e.g. Fig. 1. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied for uniform reduction by one-half on A4 size paper to fully occupy the width of the paper. Drawings should be in Indian ink on good quality tracing material, Bristol board or faintly *blue*-lined graph paper; photographic prints may be submitted. For half-tones high quality glossy prints are required. All labelling should be applied to illustrations using stencils or transfers. A metric scale must be inserted in micrographs, etc.; a figure for magnification in the legend is not acceptable. Legends for illustrations should be typed on separate sheets, one sheet for each illustration.
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   Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206–210.

   Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

   Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American Journal of Physiology* **216**, 995–1002.
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