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SEASONAL MOVEMENT OF THE SNAKES *CORONELLA AUSTRIACA, VIPERA BERUS* AND *NATRIX NATRIX* IN SOUTHERN ENGLAND

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SUMMARY

During 1974 a programme of research, directed towards an ecological study of high density smooth snake populations, was extended to include the study of both the adder and the grass snake. Distinct seasonal movement was recorded for both the adder and the grass snake and both species were seen to occupy two distinct habitat types. Seasonal movement was not observed in the smooth snake and only one habitat type was seen to be utilised during the study period. Adders were observed not to encroach on the dry heath areas, but grass snakes were regularly encountered within the smooth snake populations. Food resources and competition are discussed and some potential prey species mentioned. The local distribution of the three species and the implications for management and conservation are discussed.

INTRODUCTION

The distribution of the smooth snake, *Coronella austriaca*, in England has now been defined and the species is known to be locally distributed on parts of our southern heathland (Biological Records Centre, 1973). Various ecological aspects are currently being studied by a number of workers, and some work has already been published (Spellerberg and Phelps, 1975; Spellerberg and Phelps, 1977). Prior to this there were no ecological accounts of the smooth snake in England although there are various general articles, most of which have been reviewed by Taylor (1948) and McClellan (1975).

Current studies of the smooth snake have revealed that actual numbers found within populations vary considerably, and results indicate that the population density is possibly influenced by the nature of the prevailing habitat. Optimum habitat conditions for the smooth snake are not yet fully known and it is probable that some undiscovered factor, or combination of factors, is responsible for the fact that in a number of cases the species exists in high concentrations.

Fragmentation of the southern heaths has resulted in some smooth snake populations existing in much smaller areas than those that were formerly occupied. High density smooth snake populations all occur within areas of major afforestation, and in these areas mature pine forest is thought to be an effective barrier for a species which exhibits a low dispersal capability. Even so, high concentrations of smooth snakes have been seen to maintain their numbers for at least four seasons. The occurrence of high density smooth snake populations in England is rare, and in most parts of the species range it is more thinly dispersed.

During the study of these high concentrations of smooth snakes, the adder (*Vipera berus*) was only recorded within the area of habitat occupied by the smooth snakes on rare occasions. The grass snake (*Natrix natrix*) was observed more frequently but sightings fluctuated throughout the active season. This phenomenon was seen to be consistent for a number of years, and during 1974 ultimately prompted the present study to discover how the adder and the grass snake were disposed in areas of high smooth snake concentrations.

STUDY AREAS AND METHOD

Two areas in south-east Dorset were known to contain high numbers of smooth snakes, and, in addition, these smooth snake populations had already been the subject of intensive research for at least four seasons (Spellerberg and Phelps, 1975, 1977). The scope of research was enlarged during 1974 and all the habitat types in the general area were given consideration in the context of the range and distribution for the three snake species.

Both study areas had distinct wet and dry areas. The dry areas were typified by elevated south-facing slopes covered with thick heather, *Calluna vulgaris*, which ranged from 50–60 cm in height. Young heather plants were infrequent in the dry habitat and open areas existed throughout either in the form of bare patches of sand or banks and ridges colonised by dwarf gorse, *Ulex minor*. The two study areas had not been subject to any serious forestry programme, but young *Pinus pinaster* were prominent within the dry areas.

The dry areas of sloping heath graduated into a wet area, typified by *Erica* spp., and ultimately a bog system, *Molinia*, with a well-defined stream in the centre of one study area. The wet heath and bog system were known to form part of the summer range for the grass snake and the adder.

The individual identification of snakes was achieved by clipping the ventral scales in accordance with a code, a method used by Prestt (1971). Furthermore, each snake was given a hypothetical field number, and a record index card was established for each individual. Many of the smooth snakes had already been marked prior to the present study and Table I shows the number of snakes marked between 1972 and 1977.

TABLE I. Number of snakes marked, 1972–1977

Study Area One

	Males	Females	Immature	Total
C. austriaca	24	18	5	47
V. berus	14	12	2	28
N. natrix	5	7	4	16

Study Area Two

	Males	Females	Immature	Total
C. austriaca	16	14	3	33
V. berus	11	9	1	21
N. natrix	9	12	3	24

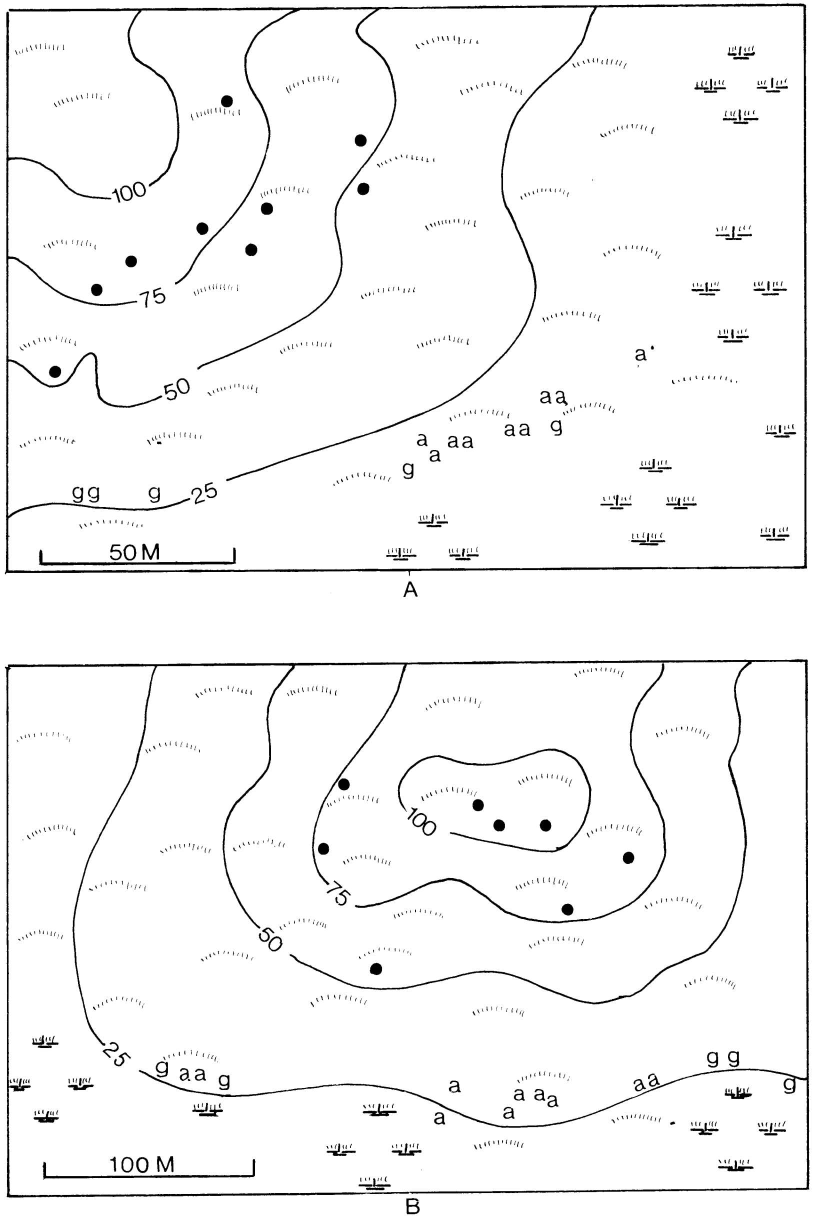

FIG. 1. Distribution of the three snake species plotted during the spring of 1975. A, Study Area One; B, Study Area Two. ●, Smooth Snake; a, Adder; g, Grass Snake.

Snakes were located by careful searches of the ground and by scanning wet areas with binoculars during the summer months. The capture of smooth snakes was enhanced by the use of funnel traps (Prestt, 1971) and by the laying of square quarry tiles throughout the dry areas.

During the present study period, each snake captured was plotted on a large-scale map and the distance moved, if any, recorded.

RESULTS

Figure 1 shows the distribution of the three snake species for the two study areas plotted during the spring of 1975. This recorded local distribution was found to be consistent throughout the study period.

Adders were extremely localised on emergence from hibernation and adult males were seen to occupy surface dens identical to those utilised during previous years. The tenacity to the surface den by male adders has been observed in other areas (Prestt, 1971). Adult female adders emerged 9–15 days after the males and established surface dens some distance away from the adult males. The differences in dates of emergence for the snake species for the two study areas was negligible and Table II shows the earliest recordings for the three snake species during the study period.

During the latter half of June, at Study Area One, male adders dispersed to the wet areas and became difficult to locate. It is known that throughout part of its range at least, the female adder has a biennial breeding cycle, and that during any one season the subsequent breeding and non-breeding females show marked differences in habits (Prestt, 1971).

TABLE II. Earliest dates of emergence for the three snake species

Study Area One

1974

	Male	Female	Immature
C. austriaca	Mar. 20	Apr. 2	Mar. 24
V. berus	Feb. 20	Mar. 18	Mar. 5
N. natrix	Mar. 10	Mar. 30	Mar. 18

1975

	Male	Female	Immature
C. austriaca	Mar. 31	Apr. 5	Apr. 2
V. berus	Mar. 12	Mar. 24	Mar. 9
N. natrix	Mar. 8	Mar. 31	Mar. 8

Study Area Two

1974

	Male	Female	Immature
C. austriaca	Apr. 1	Apr. 4	Apr. 2
V. berus	Mar. 1	Mar. 22	Mar. 9
N. natrix	Mar. 18	Apr. 3	Mar. 30

1975

	Male	Female	Immature
C. austriaca	Apr. 4	Apr. 10	Apr. 3
V. berus	Mar. 9	Mar. 18	Mar. 15
N. natrix	Mar. 22	Mar. 30	Mar. 22

The non-breeding females were observed to disperse to the summer areas shortly after the males at both study areas. Breeding females at Study Area One dispersed 15–20 days after the adult males. Breeding females at Study Area Two showed a limited amount of dispersal and during 1975 four females were observed to remain in the hibernation area throughout the active period.

The return to the hibernation bank reached a peak during the early part of September. The pregnant females were the first to return and gave birth in the hibernation area.

On emergence from hibernation, grass snakes were observed to remain for much shorter periods, and usually vacated surface dens at both study areas during early April. From this period, the movements of grass snakes became erratic, and individuals, at both study areas, were recorded within the confines of the smooth snake area. All these were notably small individuals (between 300 and 450 mm in length).

During the latter half of May, mating pairs were found grouped in the wet areas. The highest incidence of mating pairs was observed at Study Area Two, where fifteen separate copulating pairs were seen in five days. At both study areas mating was observed to take place in the wet heath areas, although smaller, probably immature, grass snakes persisted on the dry heath. At the end of June, the close of the mating period, the grass snakes were seen to disperse into the bog. The return to the hibernation bank coincided with that of the adder, and both species were often observed in close proximity to each other.

Smooth snakes emerged from hibernation later than both the adder and the grass snake (Table II).

Records of individual smooth snakes during the spring were notably singular, and observations of communal lying out were restricted to the adder and the grass snake in the respective hibernation areas.

In addition to later emergence, the daily cycle of the smooth snake during the spring was much shorter than that of the other two species. On most days lying out would not commence until 11.00 hr or later.

Prior to the beginning of the mating period, which commenced about the middle of May, adult smooth snakes were observed to be sedentary and at this time their location could be determined with some accuracy. During the mating period adult male smooth snakes became secretive and difficult to locate. Adult females were in evidence throughout the active season, and the monitoring of their movements showed that they existed within definite home ranges.

Distinct seasonal movement which involves the occupation of more than one habitat type is a common feature of the annual cycle for many snake species (Fitch, 1960; Burkett, 1966; Prestt, 1971). Seasonal movement of both the adder and grass snake was a notable occurrence at the two study areas.

The occupation of different habitat types was not recorded for the smooth snake at any time during the study period, and all recorded movement at both study areas was confined within the boundaries of the areas of dry heath.

DISCUSSION

Past literature has mentioned that smooth snake populations are often found near water (Appleby, 1971; Steward, 1971). Furthermore, recent studies have included populations where individuals have been found in sphagnum bog (Spellerberg and Phelps, 1977). Therefore it may appear surprising that during the current study of the two smooth snake populations the species showed no inclination to utilise the wet habitat. Potential food for the smooth snake was plentiful and the dry heath contained such species as the bank vole (*Clethrionomys glareolus*), common shrew (*Sorex araneus*), meadow pipit (*Anthus pratensis*) and the sand lizard (*Lacerta agilis*). Although smooth snakes have been observed to feed upon immature sand lizards, results indicate that adult sand lizards are not a major source of food (Spellerberg and Phelps, 1977).

Food potential for the grass snake in the wet areas mainly consisted of the common toad (*Bufo bufo*) and, in addition, young grass snakes were observed feeding on three occasions on the common lizard (*Lacerta vivipara*). The adder was seen to prey heavily on the common lizard and also on the bank vole, both of which were found in and around the wet areas.

It would appear that both the smooth snake and the adder have similar food requirements. Therefore, it can be assumed that if the two species existed together in large numbers then this would result in direct competition for food.

During the present study the number of snakes of all three species remained constant throughout. Therefore, it can be stated that the three species were thriving and that no one species existed in detriment to another. It would therefore be arbitrary in the instance of the two study areas, to describe the adder habitat as marginal or sub-optimal.

The present study indicates that in areas where the smooth snake is abundant it is unlikely that the adder will colonise the habitat within the smooth snake population. Past and present results also indicate that the smooth snake exhibits a low capability of dispersal and adaptation, and that the species shows a marked dependence on heathland habitat.

The adder has shown an ability to adapt to changes in its habitat, and even to changes and fluctuations in food sources (Simms, 1972). Similarly, grass snakes have also been observed to adapt to changes in habitat and food species (Phelps, 1971).

Past and present studies have now yielded information that can be directed towards effective conservation measures. If management techniques are to be successful, then careful consideration must be given to such aspects as seasonal movement. Where the three snake species occur together, proper protection should be awarded and the area designated to include all the habitat types utilised during the annual cycle.

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AN ATTEMPT TO EXPLAIN THE DISTRIBUTIONS OF THE RARE HERPTILES *BUFO CALAMITA*, *LACERTA AGILIS* AND *CORONELLA AUSTRIACA* IN BRITAIN

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INTRODUCTION

It has been clear since the earliest attempts were made to accumulate records of the British herpetofauna (Taylor, 1948, 1963; Smith, 1951) that the distributions of the three rarest species *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* were not in any sense general but involved some form of limitations not apparent with the common species. It was also apparent early on that these limitations could be related to soil structure; all three species were confined essentially to areas of coarse sandy substratum, usually exemplified as lowland heath or coastal dune habitats. These initial observations have been confirmed by subsequent, more detailed surveys which have also provided extra information on the kinds of habitat structures utilised within these broad categories (Arnold, 1973; Prestt, Cooke and Corbett, 1974; Beebee, 1976, 1977; Beebee and Griffin, 1977). However, numerous aspects of the distribution and abundance of these animals remain unexplained. In this account, the differences rather than the similarities between the three distributions are considered and suggestions are made as to how the recent situation arose. The precarious future of the heathland habitats is also discussed.

METHODS

Data on distribution were extracted directly from the sources listed above. Only sites from which the records were known to be reliable were considered, but all such records from the times when the species were first noted in Britain (generally up to 200 years ago) were relevant to the study. Information on the distribution of heath place-names and of heaths and dunes was obtained from published atlases and ordnance maps, and by direct visitation.

RESULTS AND DISCUSSION

THE PATTERN OF RECORDS

Figure 1 illustrates the recent distributions of the three species in a zonal fashion, with arbitrary lines indicating overall limits of extent. Several features are immediately apparent. Firstly, the herptiles differ quite markedly in the extent to which they have colonised Britain in recent times. Natterjacks achieved the widest range by far, and it is notable that although elsewhere in Europe *Bufo calamita* is found farther north, the colonies in north-west England and Scottish Solway live under cooler summer conditions than those found anywhere else in the range of the species. Natterjacks probably reached virtually all of the major heathland blocks in England, but even here the situation is not completely straightforward. There are no clear records (and virtually none of any sort) from the Brecklands, a very large and well-investigated area of heathland in western East Anglia and within the overall range of the species. Furthermore, natterjacks never seem to have been widespread in the heathland areas of south-west Hampshire and Dorset, a zone from which the species disappeared completely many years ago (Beebee, 1976). This is a particularly enigmatic observation because the records are clear enough to indicate that at least one or two colonies did exist there in the nineteenth century, and because this area of heath has survived rather better than most others in terms of capacity to sustain the rare reptiles.

The wider distribution of *Bufo calamita* is largely reflected by an ability to colonise East Anglian heaths, and more particularly the sand-dune belts of the east and north-west coasts. The situation here seems rather more straightforward in that virtually all dune systems within the overall range and with associated freshwater pools do (or did) have natterjacks. However, it is notable that dunes along the west coast of Wales and in south-west England have yielded no reliable records of the species.

Lacerta agilis, though not approaching the wide distribution of *B. calamita*, apparently occupied most of the heaths in southern England very successfully and even reached the southernmost section of the north-west coast. There are however no reliable records of sand lizards in East Anglia. This is a puzzling observation not readily explained in terms of geology, recent habitat structure or climatology.

Most restricted of the three species is *Coronella austriaca*, with no observations confirmed outside southern England. The occasional records from East Anglia are perhaps more difficult to discount than those for the sand lizard, but in the absence of a single rigorous confirmation the southern limitation for the smooth snake should probably be accepted. *Coronella* therefore does not accord with the general observation that viviparous reptiles are able to range farther north than oviparous species. Interestingly, in Scandinavia *Coronella austriaca* does range as far north or farther north than either *Lacerta agilis* or *Bufo calamita* (Curry-Lindahl, 1975).

ESTABLISHMENT OF RECENT DISTRIBUTIONS

Perhaps the first question to address was how the disjunct distributions of the rare species became established in Britain in the first place. The East Anglia and north-west coastal zones are now separated from southern English colonies by hundreds of miles, and at some point in the past it is evident that there must have been continuity between these populations. Since the climate in Britain before the onset of the sub-Atlantic period some 3000 years ago was substantially warmer than at the present time, and since all three species enjoy more general distributions still in southern Europe, it is generally believed that the current range limits were reached long ago and subsequent fragmentation has occurred as a result of climatic deterioration and resultant habitat restriction (see, for example, Spellerberg, 1975). While this is probably broadly correct, the mapping of place-names including the word "heath" shown also in Fig. 1 adds the interesting possibility that distributions may not have been so rigorously fixed for as long as previously believed. There is a clear pattern to the place-name distribution, which goes a considerable way towards linking the herptile sites in southern England with those in East Anglia and the north-west coast. Of course, the use of the word

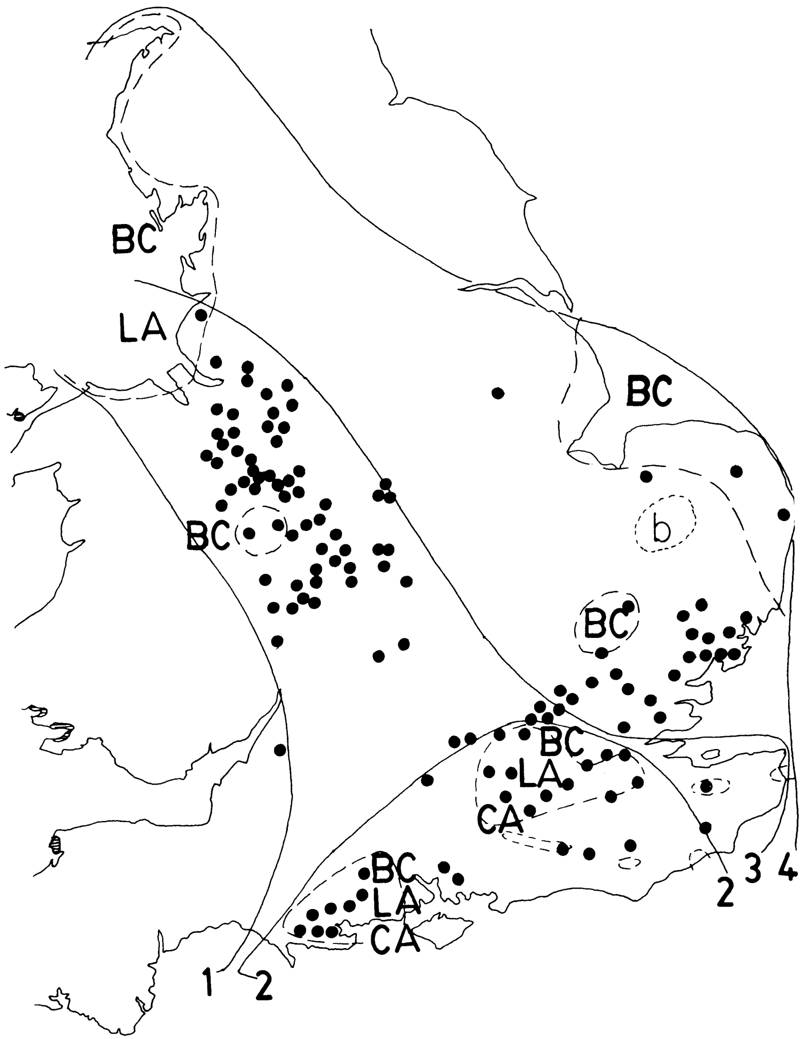

FIG. 1. Distribution of rare herptiles. ——— Boundaries of zones with reliable records for rare species *Bufo calamita* (BC), *Lacerta agilis* (LA) and *Coronella austriaca* (CA) within the last 200 years. ------ (b) = Breckland; ▤ examples of unoccupied west-coast dunes. ● Heath place-names (including a few actual heaths, mainly in Dorset and Surrey). Limit-lines for distributions are: 1 = LA and BC, west; 2 = CA; 3 = LA, east; 4 = BC, east.

"heath" in a place-name does not define the habitat in a way comparable to our present understanding of the term, but even if the flora was different from typical Callunetum all the historical evidence suggests that heath has always meant an open waste; if habitat structure is the most important factor for the herptiles, any form of undisturbed open (unforested) waste might have been acceptable as an ecosystem. Also, it should be stressed that there is no indication that heath has ever been contiguous between the zones (the geology alone makes this extremely unlikely), only that the gaps may have been smaller than previously supposed. This could mean that fairly short-term improvements in climate within the last few hundred years might have permitted significant contact between otherwise isolated populations. There are several small pieces of evidence which can be interpreted as supporting this view. Firstly, the lack of any of the rare herptiles in the extensive dune systems of western Wales, Devon and Cornwall is not easily explained on climatic grounds and it seems unlikely that all of these dunes are geologically younger than those on the inhabited coasts. Yet this is the expected result if the corridors indicated by the place-names have provided the most recent determinants of distribution. Secondly, following on from this, it seems intrinsically unlikely that so complete an occupation of the north-west dune systems would have been maintained in isolation for thousands of years without some random losses of species from some sites; but this does not appear to have happened, virtually all of the dunes on both east and north-west coasts having maintained natterjacks up to the beginning of the present century. The most likely explanation of this must surely involve periods of greater population mobility. The western and south-western dunes, on the other hand, are remote from these corridors and even if occupied in the post-glacial period would be likely to have lost their populations by chance without opportunity for recolonisation. The same argument could explain the existence of the Kerry natterjacks in Ireland, this being the only section of coast which by chance has maintained suitable conditions for natterjack toads throughout post-glacial history. Thirdly, there is fragmentary evidence at least in the case of the natterjack that within the last two centuries there has been some occupation of more general habitats; thus Bell (1849) reports the presence of natterjacks in Selbourne, some 3 miles from the nearest heath, during the middle of the nineteenth century; he also records their disappearance, and this together with the failure of Gilbert White to record them there gives the observation the expected properties of a short-term proliferation into marginal habitats. It is also of some interest that at the turn of the century Forrest (1908) reported the presence of natterjack toads in three Shropshire localities; this is the only evidence I know of concerning recent occupation of a corridor region, but the reliability of these reports remains uncertain. However, it might be pointed out that an observer in 1978 with no historical information at hand would essentially rule out all of southern England as natterjack toad habitat, since with the exception of one tiny relict population this area has been completely deserted over the last 30 years; but before that time we know for certain that it was a major stronghold of the species (Beebee, 1976, 1977).

Factors Influencing Recent Distributions

Another question not adequately answered is the distribution of the three species and its variability within the overall ranges. In particular, why has *Bufo calamita* not been reported from Breckland and only rarely from Dorset? And why are the two reptiles absent from East Anglia? Table I summarises the rather different geologies of the three major remaining heathland areas, East Anglia, the London Basin and Wealden edge, and south-west Hampshire and Dorset, in terms of the major soil components. The data imply that in the case of the reptiles at least the underlying geology is of little importance as long as some type of sand in present, although in the London basin *Lacerta agilis* has persisted rather better on the greensand heaths than on the Bagshot gravels. This, however, is most probably a coincidental result due to the greater despoilations of the latter heaths. However, there does seem to be some indication of a preference of *Bufo calamita* for greensand heaths. The tertiary sands previously occupied by this species in East Anglia were primarily those of the east Suffolk and Norfolk estuaries, and these may have been partly or even largely derived from wind-blown sea sand of the same quality as that which forms dunes farther north on the coast; in any case, it seems to be different from the large central depositions of the Brecklands. In Surrey and in Dorset, *Bufo calamita* seems to have been much less commonly found on tertiary deposit heaths and this factor could begin to account for the scarcity of the animal in the latter area. Obviously this did not amount to complete incompatibility, and further examination of this point is necessary. As a general rule, tertiary sand heaths tend to occur in large blocks whereas greensand tends to form rather narrower belts of material sandwiched between other strata. The geographical arrangements are such that greensand heaths are frequently well placed to receive substantial freshwater run-off from adjacent richer strata, and tend to harbour productive and permanent freshwater pools of neutral pH in considerably larger numbers than the tertiary sand heaths. The geography of the east Suffolk heaths makes them more similar to the greensand ones in this respect, and it is suggested that this might be the important factor in deciding whether a heath will be able to support natterjacks. Certainly a requirement for these richer pools, rather than the base-poor acid bogs more characteristic of podsol conditions has been established for *Bufo calamita* (Beebee and Griffin, 1977).

The absence of *Lacerta agilis* from East Anglia is difficult to explain in the light of its presence on Merseyside. Summer isotherms and isohels which include Merseyside

Table I. Geology of heathlands

Numbers refer to the approximate percentage of heathland in a particular zone which has developed on a specific substratum, or to the number of records (10 km square sites) of the species from each type (derived from Arnold, 1973). Lower greensand includes Bargate, Sandgate, Folkestone and Hythe beds; tertiary deposits include Bagshot beds and associated sand and gravel mixtures. Other abbreviations as in Fig. 1.

	Cretaceous (Greensand)	Tertiary
East Anglia: %	15	85
BC	5	13
LA	0	0
CA	0	0
London Basin: %	45	55
BC	13	8
LA	9	6
CA	8	8
Dorset/Hants: %	0	100
BC	—	3
LA	—	20
CA	—	18

invariably include East Anglia also (Jackson, 1978). It seems possible that meteorological data used in this was do not adequately reflect the overall climatic situation; thus independent measurements of sunshine hours and shade temperatures may bear little relation to the detailed thermal situation experienced by a reptile at ground level, where such factors as terrain topography, wind speed and frequency, etc., may also need to be considered. East Anglia is renowned for the winds blowing over its relatively flat terrain even in summer, and in this sense is probably a colder place than southern England. At this point it is worthwhile to consider briefly the properties of heathlands in comparison with other habitats in the general way shown in Table II. Heaths and dunes share a number of common features found collectively in no other biotopes in Britain; low-lying, well-drained areas with dense vegetation close to ground level and normally stable over reasonably long time periods. This physical description implies some form of thermal habitat selection for areas allowing maximum insolation combined with adequate vegetation structure for protection from predators and for maintaining adequate invertebrate (food) populations, and if this is true then it follows that temperature is a critical parameter for the rare species in Britain and that any move towards cooler conditions may not be tolerable; thus, even the otherwise suitable heathland habitat may prove thermally inadequate in the more exposed situations of East Anglia.

TABLE II. Characteristics of habitats

	Average height of vegetation (m)	Altitude (m)	Soil state	Stability (average) years
Heath	0.25–0.75	<100	well-drained	10–∞
Dune	0.25–1.00	<100	well-drained	∞
Forest	4.0–30.0	up to 800	often moist	∞
Moorland	0.25–0.50	above 250	moist	10–∞
Arable farm	0.25–2.0	up to 300	variable	1
Pasture	0.25	up to 800	moist	∞

Any attempt to explain the present highly fragmented distribution of the three rare British herpetiles must almost of necessity be inadequate and largely speculative because there can be no way of obtaining definitive evidence on the exact fates of these small vertebrates over millenia. However, it seems of some interest to try and determine possible or probable courses of events since to do so may be of assistance in our understanding of the ecological requirements of the species and our attempts to conserve them. Assuming that *Lacerta agilis* is more restricted than *Bufo calamita* in Britain because of greater temperature sensitivity at some point during the life cycle, then it looks initially as if we must postulate an even greater sensitivity for *Coronella austriaca*. However, observations elsewhere in Europe on distribution suggest that sand lizards and smooth snakes have rather similar northern limits in Sweden though *L. agilis* does attain somewhat more northerly climes in Russia (Curry-Lindahl, 1975). Why should a viviparous snake be the most limited of all the British herpetofauna? A second possibility other than direct thermal limitation could stem from the well-known predatory preference of the species for reptile prey. Being one step higher in the trophic chain than the lizards upon which *Coronella* mainly feeds, it follows that large lizard populations will be needed to support a snake population; thus we would not expect the predator to have a range as extensive as its prey because the latter will inevitably become too scarce as food items (i.e. colonies will become less dense and more isolated) and random fluctuations are likely to become sufficiently serious to prevent the predator ever becoming established. Smooth snakes will of course consume reptiles other than sand lizards, and also small mammals; but in Britain it may well be that only on the heathlands of southern England are reptile populations of any kind (notably the other major prey items *Lacerta vivipara* and *Anguis fragilis*) present at sufficient densities to support viable populations of this snake. The ability of *Coronella* to exist on a diet of small mammals may be the key to deciding between these two possibilities. Suitable mammalian prey is not at all common on open heathland, but species (mainly wood mice, *Apodemus sylvaticus*) do appear in larger numbers as forest conditions encroach. If smooth snakes can manage perfectly well on small mammals there would seem no restriction on a more widespread distribution in England other than a thermal one relating to heathland physiography as discussed above. The evidence available at the present time seems to to me to make reptile prey-dependence by far the most likely cause of the restricted distribution of the smooth snake; the very marked preference of the animal for reptiles observed in captivity together with widespread reports in the European literature support this view and suggest that mammals are taken rather occasionally and probably not at all by many individuals. It is difficult to imagine young smooth snakes consuming mammals, but young common lizards and slow worms are attacked voraciously by new-born *Coronella*. Unlike either *Bufo calamita* or *Lacerta agilis*, both of which offer fairly clear reasons for thermal dependence on heathland structures (larval development in warm, shallow ponds and egg-laying in exposed sand respectively) there is no obvious reason why more far-ranging species such as *Coronella* should be restricted to heath country even if thermal limitations were operative; many other types of terrain in southern England offer sufficient basking facilities for other species such as *Natrix*.

The important possibility which arises from these lines of thought involves current attempts to conserve the rare species and the consideration that the problem may be even more acute than previously believed. It may not be safe to adopt the attitude that since individual populations have been present at a place for thousands of years there is no need to become too concerned over short-term prospects; it may well be that the degree of isolation which we see at present is very recent indeed, and the situation even less stable than widely supposed. The recent very rapid rates of decline of the three species and their habitats confirm the belief that efforts to ameliorate these trends must be pursued with unhesitating urgency. Present land-use precludes any return to greater population fluidity and may well be coming sufficiently intensive to isolate even colonies of common species quite effectively, with ominous overtones for the future.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, pp. 771–773

DOUBLE VOCAL SACS IN THE INDIAN FROG, *RANA CYANOPHLYCTIS*

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INTRODUCTION

Of the secondary sexual characters in anurans, the presence of vocal sacs in the male is the most conspicuous. The sacs are diverticula of the lining of the oral cavity covered by sheets of muscle and skin (Noble, 1954). When the skin is modified such that it balloons out into a large transluscent sac under the chin or into a pair of sacs one on either side of the throat, the sacs are said to be *external.* But if the skin of the throat is not thinned, the whole throat merely assuming a swollen appearance when the frog calls, the sacs are said to be *internal.* Air forced from the lungs through the larynx sets the vocal cords vibrating and the sound is reinforced by the resonating vocal sacs. The air is forced back and forth between the vocal sacs and the lungs; usually very little additional air is taken in through the nostrils. Since vocal sacs usually lie just above the subhyoid muscle, air is forced back into the lungs chiefly by the action of this muscle. Frogs usually have a pair of vocal sacs, as, for example, in *Rana tigrina* where they appear as two wrinkled reddish patches one on either side of the throat. In *R. cyanophlyctis*, however, they show a high degree of specialization.

MATERIALS AND METHODS

Specimens of *Rana cyanophlyctis* (Boulenger) were collected from ponds in and around Lucknow from May to November. The males are no larger than 11 cm from the snout to the tips of their toes; females are larger, reaching 15 cm. These frogs spend much of their time in water, on which they can skip for as many as a dozen jumps before sinking.

THE VOCAL SACS

In the male the vocal sacs are two elongated slits, about 8 mm long, on the sides of the throat, very close to the lower jaw bones, each leading into a pouch. The pouch is better seen by cutting the skin of the throat mid-ventrally and opening out the flaps. The pouch is seen as an oblong (about 5 mm long, 3 mm wide), heavily pigmented, black (hence *pigmented vocal sacs* in Fig. 1), pleated and obliquely wrinkled bag of skin. Internally the sac opens on the floor of the vestibule of the oral cavity by means of a longitudinal slit (about 2 mm). The wall of the pigmented vocal sac has a large number of melanophores along and between the fine blood capillaries. From the structure of these vocal sacs, it appears that they are not outpockets of the lining of the oral cavity, but are formed by the reflection and in-pocketing of the skin, having

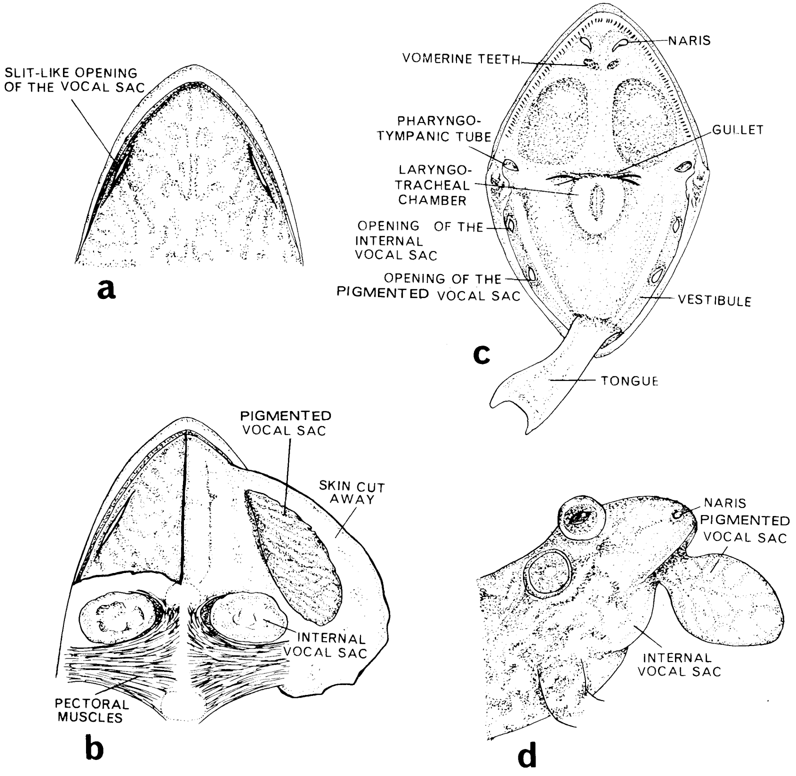

FIG. 1 (a) Throat of *R. cyanophlyctis* showing the openings of the external vocal sacs. (b) Throat opened to show the two internal vocal sacs and the left external vocal sac. (c) Buccal cavity opened to show the relation of the vocal sacs and the large laryngeo-tracheal chamber of the male. (d) Inflated external vocal sac and the internal vocal sac.

gained access to the oral cavity. Both vocal sacs roughly occupy the entire anterior half of the throat.

A second pair of pouches—the internal vocal sacs—is situated just behind the pair of pigmented vocal sacs. They are more or less rounded, colourless and composed of thin skin. When exposed they are seen on the sides of the omosternal muscles and in front of the large pectoral muscles. They open into the oral cavity behind the openings of the pigmented vocal sacs.

Vestiges of the external pigmented vocal sacs are present in the female as two elongated red lines in the same position as in the male, but there are no slits.

DISCUSSION

The frogs were never heard to call during the day. From May to August, after sunset, the males were seen to inflate their throats and produce shrill calls of short duration at intervals of 3–5 min. While calling, the pair of pigmented vocal sacs were not inflated, but at times these were kept inflated before and after the call was emitted. No audible sound was produced when these sacs were inflated or deflated. Therefore, it appears that the pigmented sacs have little or nothing to do with croaking or calling. The presence of a large number of blood capillaries could suggest that when inflated the sacs serve for respiration. But from their small size it would seem unlikely that they need additional respiratory surfaces. What seems more logical is that they may be hydrostatic in function.

Both lungs of the male and often the right lung of the female appear to be very large in these small frogs (over 30 mm long and occupying about two-thirds of the body cavity). The laryngeo-tracheal chamber of the male was also found to be relatively large when compared with the larger *R. tigrina*. The laryngeo-tracheal chamber is smaller in the female. Large lungs in the male appear to be necessary to operate the two pairs of vocal sacs compared with the one pair in other frogs.

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NOTES ON SOME AMPHIBIANS AND REPTILES FROM SPAIN

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The Spanish herpetofauna has received little attention, despite the considerable number of interesting endemic species.

The present report concerns a first visit by N.D.S. to Zahara de los Atunes, Cadiz Province, from 22 March to 2 April 1975, which was a detailed study of a small area, and another, by C.M., over the eastern half of Spain, from 11 to 29 May 1975. All species observed are reported, with notes on habitat and behaviour in the field and in captivity.

Zahara de los Atunes (36°09′N, 5°50′W), a village on the Atlantic coast in the extreme south-west of Spain, is bounded by salt marshes to the north, and the Sierra de la Plata to the east and south. Many of the species observed were on a low hill (100 m) immediately outside the village. Many sandstone boulders littered this heavily grazed hill; the dominant vegetation was palmetto scrub. Some species were also observed near El Rocio (37°07′N, 6°29′W), on the edge of the Marismas and the Coto Donana Biological Reserve.

Arenas de san Pedro (40°13′N, 5°05′W) is the largest town within the Sierra de Gredos; altitude 524 m. Surrounding slopes are planted mainly with conifers, such as *Pinus* spp.

Nules (39°52′N, 0°10′W) is a small town about 5 km inland, 12 km south of Castellon de la Plana. The area between the town and the sea consists of a wide strip extensively cultivated, reclaimed marshes. Irrigation ditches form a network throughout the area and untended plots have reverted to reed-beds.

Vera de Bidasoa (43°17′N, 1°35′W) is 5 km from the French frontier in the Pyrrenean foothills. The Rio Bidasoa forms a valley of lush, sub-alpine vegetation. Ruined buildings and timber piles provide good cover for a variety of species.

AMPHIBIA

Salamandra salamandra

Larvae found in several pools and roadside fountains on the lower slopes of the Sierra de Gredos. No adults present in any location, which would seem to eliminate the totally aquatic *S. s. almanzoris*. The other subspecies, *S. s. bejarae*, is indicated.

Triturus helveticus

Three adults in a trackside pool near Vera de Bidasoa.

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Triturus marmoratus pygmaeus

Six young adults under a piece of cardboard outside El Rocio, adjacent to the marshes.

Pleurodeles waltl

Ten recently metamorphosed young under same piece of cardboard as previous species.

Alytes obstetricans obstetricans

An adult male and numerous larvae in a roadside cistern near a ruined house, south of Moreela, Valencia Province. Terrain hilly and semi-arid. The large (55–60 mm) larvae, which hung tail-down from the surface, dived rapidly when disturbed. Ten larvae collected for positive identification metamorphosed between 26 June and 11 July.

Pelobates cultripes

An adult brought to N.D.S. by an agricultural worker from fields 2 km north of Zahara. Another disgorged by a *Natrix maura*.

Pelodytes punctatus

Adults and larvae fairly common in fields and rainpools around Zahara.

Bufo bufo

A large dead female and a male found along the Rio Pelayo in the Sierra de Gredos, the female in a small backwater, close to a string of spawn (*B. bufo* type) and the male calling nearby in shallow water at the edge of the stream. Its ventral drab yellow colour extended onto the parotid glands. Appearance and size indicate *B. b. gredosicola*.

Bufo calamita

One adult on the plains about 10 km south of Arenas, beneath a large round boulder. Also several hundred newly metamorphosed toadlets in a dry river bed, north of Almeria. Large numbers of larvae found in a drying pool at the latter site. They formed many small round depressions in the mud on the pool bottom, and in surrounding dry areas. Similar pits of *B. viridis* larvae are described and discussed by Opatrny (1973).

Rana iberica

Three specimens along the Rio Pelayo, near Arenas.

Rana ridibunda perezi

Several adults in pools by roadside, in hills 24 km east of Zahara; altitude 150 m. Extremely common in marshes near El Rocio, calling very loudly at night. Numerous in pools left by the Rio Tietar, near C502 road, and in irrigation ditches and reed-beds near Nules. The frogs basked and called all day during fine weather. Many immature; no larvae found.

REPTILIA

Mauremys caspica leprosa

A young male in a small stream in hills 24 km east Zahara. Carapace 72 mm, plastron 59 mm.

Hemidactylus turcicus

One juvenile (TL 70 mm, SVL 32 mm) in a rock crevice on hill behind Zahara and a tailless adult (SVL 55 mm) beneath a small rock in a dry river bed, north of Almeria.

Tarentola mauritanica

Common on the hill behind Zahara, basking on rocks; retreated into crevices when disturbed. Several seen on walls of an old fort, and on garden walls on the outskirts of Zahara, fronting the beach. Two large adults (largest TL 158 mm, SVL 73 mm) in a crack in a stone bridge, near San Mateo, Castellon Province.

Anguis fragilis

Two adult females, an adult male and three neonates found along a grassy track in the valley of the Rio Bidasoa.

Blanus cinereus cinereus

Common on the hill behind Zahara under large stones. Found usually in late afternoon or evening. Five were juveniles, SVL 79–98 mm. Average adult SVL was 145 mm, tail 18 mm, weight 2.2 g. Aspects of the ecology and behaviour at this site are described by Smith *et al.* (in press). In the Sierra de Gredos, two found under stones at the base of fir trees, and 10 a few km away under large round boulders. Many retreated rapidly down ready-formed burrows. Scorpions, common in the area, frequently found under the same stone as a *Blanus*.

Acanthodactylus erythrurus

Several in stone pine (*Pinus pinea*) on dunes at Los Canos de Meca, 15 km north-west of Zahara. Adult female (TL 150 mm, SVL 57 mm) captured on a dry stone wall near Almeria. Despite many cracks in the wall, this very active lizard was loathe to hide.

Lacerta hispanica vaucheri

Found on dry-stone walls at Facinas, 13 km east of Zahara, on parapet of a bridge in the hills 24 km east of Zahara and among rocks on a hill 4 km south-east of the village. Always seen on rocks or concrete surfaces. Very similar in habits to *L. muralis*.

Lacerta lepida

Adults and juveniles seen in a variety of habitats around Zahara and El Rocio, i.e., sand dunes and stone-pine wood (Barbate and Los Canos de Meca), hillside and beachfront (Zahara), flat scrub-land (El Rocio). An adult living on the beachfront at Zahara in a pile of stones had two regenerated tails about 10–12 cm long. A complete skull found on the hill at Zahara was of exceptional size, 69 mm long by 43 mm wide, indicating a TL in life of 800 mm, SVL 280 mm. The average SVL of seven previous year juveniles was 61 mm. One (TL 174 mm, SVL 62 mm) grew to TL 298 mm, SVL

98 mm in 5 months captivity. In a field north of Avila an adult male captured under a large boulder. A juvenile found under a stone by a stream in foothills near Jaen. Adult disturbed on a rocky mountainside on the lower slopes of the Sierra Nevada, altitude 1200 m. A dead, tailless and partly eaten adult dropped on to the road by a bird of prey near Almeria.

Lacerta muralis muralis

Abundant around ruined houses and piles of timber by the roadside near Vera de Bidasoa. Many gravid females.

Lacerta schreiberi

Fairly common in a large field north of Avila, occurring singly at intervals along a stone wall bordering a stream, or on rock outcrops. They were extremely wary, few seen for any length of time, but several heard retreating into undergrowth.

Psammodromus algirus

Fairly common on the hill behind Zahara and in *Opuntia* hedge along beachfront, also common at Facinas, Los Canos de Meca, El Rocio, in a variety of habitats. One adult female caught at Zahara with the apical cap of a tail regenerate just forming. Maintained in captivity on a light-dark cycle of 14:10 hours, a daily minimum temperature of 25°C, and a diet of mealworms, locusts and cockroaches fed *ad libitum*. Additional heat provided during the light period. For the first 5 weeks the tail regenerated at 2.4 mm per day. Between 5 and 10 weeks the rate gradually decreased to 0.1 mm per day. The regenerate reached 95 mm after 19 weeks. This initial high rate of regeneration is similar to, or higher than, that of other warm-temperate lacertids, such as *Lacerta dugesii* (Bryant & Bellairs, 1967). Several colonies in the field near Avila, among rock outcrops. Others seen near Candeleda, in the Sierra de Gredos, and in this area a *Coronella girondica* disgorged an adult.

Psammodromus hispanicus

Around Zahara, found in the same habitats as *P. algirus*, but not as common. It is much smaller than the latter species; adults averaged about 45 mm SVL. One specimen had a large tick in the front axilla, another had an incompletely autotomised tail which failed to regenerate, and the third laid two eggs on 22 May 1975, which did not hatch (8.5 × 5.1 mm, 0.09 g and 7.9 × 5.2 mm, 0.08 g). Species also seen in many areas of central and southern Spain, but in especially large numbers in the field near Avila, where *P. algirus* also found. Both species of *Psammodromus* squeaked when handled, perhaps caused by rubbing together the strongly keeled dorso-lateral scales (see also Arnold, 1973).

Chalcides bedriagae

One adult (TL 133 mm, SVL 64 mm) buried in sand in dunes 2 km west of Barbate. One specimen under a stone on a shrubby hillside near the village of Hornillo (TL 130 mm, SVL 65 mm), and two others basking among bracken in a conifer forest north of Arenas.

Chalcides chalcides striatus

A single adult under a stone on a hill 4 km south-east of Zahara.

Coronella girondica

One adult extracted from a stone wall after its cast skin was found nearby. Disgorged adult *P. algirus* 2 days after capture.

Elaphe scalaris

Four specimens found on the lower slopes of the Sierra de Gredos, consisting of an adult male (TL 750 mm, SVL 633 mm), a sub-adult (TL 470 mm, SVL 395 mm) and two juveniles (TL 320 mm, SVL 275 mm and TL 350 mm, SVL 295 mm). One juvenile found under a small rock by an exposed roadside, north of Arenas, and the other three under flat rocks along a track east of the town. Predominant vegetation here of sparse conifers, with fairly heavy undergrowth of bramble and grass. The three smallest specimens had the striking juvenile "ladder" markings (Fig. 1); the adult little trace of the transverse blotches, but retained the longitudinal stripes. All four, especially the adult, bit and hissed vigorously. The adult voided faeces containing some black fur and in captivity all fed readily on mice. The day-light hours spent in a retreat, becoming active towards dusk and frequently emerging at night.

Macroprotodon cucullatus

Six under stones on the hill behind Zahara, one at Facinas and one 2 km north of Barbate, under a log. Generally similar to *Coronella girondica*, but more grey in colour. Recognised by the dark mark on the neck—the "cowl"—the sixth supralabial touching the parietal and the lower number of subcaudals. Shape of cowl fairly constant but it and dark dorsal spots vary in colour from brown to nearly black. Readily bites when handled, no toxic effects noted.

Coluber hippocrepis

Three on beachfront at Zahara, in *Opuntia* hedge. Very nervous and aggressive. Dark blotches reduced, compared with published illustrations (e.g., Steward, 1971) (Fig. 2).

FIG. 1. *Elaphe scalaris*, juvenile, from Arenas de San Pedro.

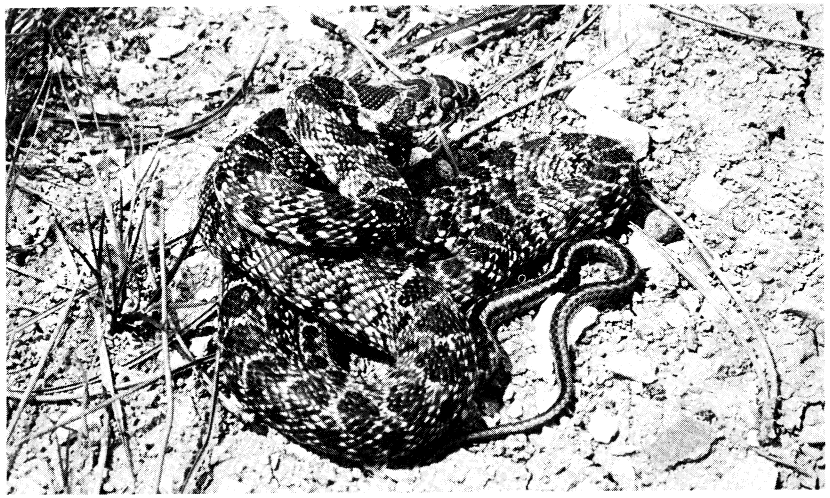

FIG. 2. *Coluber hippocrepis*, adult, from Zahara.

Natrix maura

Three males and two females in rain pools on rough ground about 200 m from the sea, 4 km north-west of Zahara. A large female (TL 670 mm) disgorged an adult *P. cultripes*. A male disgorged several earth-worms. The dorsal pattern, though variable, rather viper-like, but with a pale yellow line on either side of the vertebral zig-zag, and a series of pale centred markings laterally. Also common on edge of marshes at El Rocio. An adult and sub-adult on the bank of the Rio Tietar, Avila Province had a distinct vertebral zig-zag on an olive ground colour. At Nules, many basked and swam in an extensive semi-cultivated area of rectangular, surrounded by irrigation ditches of varying sizes. Varous markings were displayed by all sizes from adults to previous year's young, including Steward's (1971) "viperine", "tessellated" and "striped" phases, as well as intermediates. Two individuals were bright red ventrally; another had a ground colour of pale orange. The latter (TL 550 mm, SVL 450 mm) layed five eggs, typically 35 × 14 mm, on 27 July 1975. On 28 August one contained a fully formed, unpigmented embryo with a large yolk-sack. Three hatched on 18 September, the other a day later. Total lengths of hatchlings were 146 to 150 mm. All sloughed within 8 days of hatching.

Natrix natrix astreptophora

Juvenile found in Pyrennean foothills near Vera de Bidasoa, (TL 205 mm, SVL 175 mm), under a piece of slate by roadside, in light rain.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 5, 783–788

THE EFFECT OF TEMPERATURE AND STAGE OF DEVELOPMENT ON THE DURATION OF IMMOBILITY IN SELECTED ANURANS

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INTRODUCTION

Although immobility has often been noted in anurans, most records are of casual observations involving few individuals. Indeed, the value of immobility to frogs has been questioned by authors such as Mangold and Eckstein (1919), Noble (1931), and Bragg (1945) who doubted its selective advantage. Dickerson (1906), however, implied that toads avoided predation by becoming immobile because of predator association of movement with life. Recent studies involving other groups of animals (see Dodd and Brodie, 1976; Ratner, 1967; Culver, 1973; Sargeant and Eberhardt, 1975; Fitzsimons, 1973) suggest immobility is widespread and probably of high selective value.

While the effects of temperature on the behaviour of many groups of ectotherms, particularly reptiles, is reasonably well known, little is known about temperature effects on the behaviour of amphibians. Dodd and Brodie (1976) reported that the duration of immobility in some species of neotropical salamanders was affected by both temperature and size, and therefore age.

Many anurans breed in shallow temporary pools or shallow areas in larger bodies of water. Because tadpoles approaching metamorphosis may be exposed to eurythermal conditions, this study was undertaken to obtain preliminary data on the effects of temperature and stage of development on immobility, a potentially important defensive mechanism.

METHODS

Tadpoles approaching metamorphosis and adults of *Bufo americanus*, *Pseudacris triseriata*, and *Scaphiopus holbrooki* were collected from various localities within a 22 km radius of Clemson, South Carolina, during May and June, 1973.

The frogs were acclimated in temperature-controlled refrigerators to within ±1°C at temperatures of 10, 20, and 30°C. Adult *S. holbrooki* (56–72 mm snout-vent length) were acclimated a minimum of 7 days. Tadpoles of all species were acclimated a minimum of 4 days at 20 and 30°C; 5 days was the minimum acclimation time at 10°C (Cupp, 1974). Tadpoles were staged according to Gosner (1960).

All observations were made in the laboratory on damp paper towels under dim fluorescent lighting. Testing was conducted at room temperature (21–23°C).

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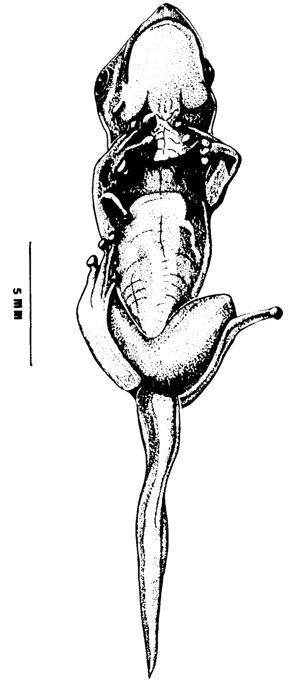

FIG. 1. Immobility posture of metamorphosing *Pseudacris triseriata*.

The tadpole was considered immobile when, after brief prodding, it assumed a rigid unmoving posture. The developing hind limbs were often kept clasped to the body (Fig. 1) or they were held rigid out from the body. The same postures were observed in all species tested. The immobile posture of adult *S. holbrooki* consists of holding the body slightly rounded with the eyes closed and the extremities drawn tightly to the body. Immobility times were recorded with a stopwatch and an arbitrary time limit was set at 180 s.

Differences between means were tested by Least Significant Difference (Sokal and Rohlf, 1969). Differences were considered significant if $P < 0.05$.

RESULTS

The results of these observations are presented in Table I and Fig. 2. At 20°C acclimation temperature, stage 46 (newly metamorphosed) *B. americanus* remained immobile for significantly shorter periods of time than earlier stages ($F = 6.45$, $P < 0.01$) whereas there were no significant differences among the stages of *P. triseriata*. At 30°C, adult *S. holbrooki* remained immobile for a significantly shorter period of time ($F = 4.15$, $P < 0.05$) than at the other acclimation temperatures; there were no significant differences for stage 46 animals among the various acclimation temperatures although there appears to be an inverse relationship between acclimation temperature and duration of immobility.

TABLE I. Duration of immobility of frogs at various experimental temperatures and stages of development

Species	Acclimation temperature (°C)	Stage of development	Immobility in seconds	
			N	$\bar{x}$ (range)
Bufo americanus	20	43	12	18.33 (2.5–41)
		44	12	25.63 (3–54.5)
		46	12	6.67 (1–37)
Pseudacris triseriata	20	41	10	45.25 (11–84.5)
		42	10	60.95 (18–180)
		45	10	35.55 (10–72)
		46	10	30.20 (4–90)
Scaphiopus holbrooki	10	46	12	25.70 (11–76.5)
	20		12	21.88 (5–76)
	30		12	11.96 (3–29)
Scaphiopus holbrooki	10	Adult	10	53.15 (3.5–156.5)
	20		10	80.50 (3.5–180)
	30		10	10.10 (2–52.5)

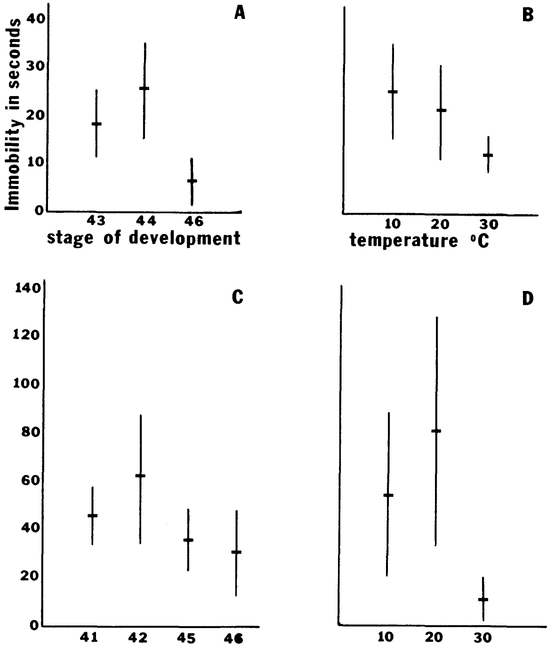

FIG. 2. Means and confidence intervals of means (±2 × standard error of the mean) of immobility times in selected anurans at various acclimation temperatures and stages of development. (A) *Bufo americanus* at 20°C acclimation temperature. (B) *Scaphiopus holbrooki* at Stage 46. (C) *Pseudacris triseriata* at 20°C acclimation temperature. (D) *Scaphiopus holbrooki* adults.

Comparisons of stage 46 *B. americanus*, *P. triseriata*, and *S. holbrooki* at 20°C showed that *B. americanus* remained immobile for significantly less time than the other species ($F = 3.83$, $P < 0.05$).

Finally, comparison of duration of immobility of adult versus stage 46 *S. holbrooki* showed that only at 20°C was there a significant difference; stage 46 animals remained immobile for shorter periods of time than adults ($F = 6.67$, $P < 0.05$).

DISCUSSION

Studies on the effects of ecological variables, including temperature, on the duration of immobility have been confined mainly to invertebrates and there has been scant speculation as to the significance of the varied results. Holmes (1906) and Fabre (1900?) reported that the duration of immobility in the water scorpion, *Ranatra* sp., and the wood borer, *Capnodis tenebrionis*, increased with a reduction in temperature. Severin and Severin (1911) showed that duration of immobility decreased with increasing temperature in the water scorpion, *Nepa* sp., whereas the giant water bug, *Belostoma* sp., showed a decrease in duration of immobility at both high and low temperatures. The isopod, *Cylisticus convexus* was reported by Crozier and Federighi (1923) to decrease the duration of immobility with increasing temperature.

Only two studies have examined the effects of temperature on the duration of immobility in vertebrates. Hoagland (1927, 1928a, b) reported greater duration of immobility in the lizard *Anolis carolinensis* with increasing temperature as a function of the Arrhenius equation. Dodd and Brodie (1976), studying three species of high elevation neotropical salamanders, found that *Bolitoglossa subpalmata* generally had a decreased duration of immobility with increasing temperature whereas *Chiropterotriton multidentatus* and *C. dimidiatus* had longer immobility at both high and low temperatures. They attributed the differences to different adaptive strategies in the defensive mechanisms of brightly coloured and highly noxious salamanders (such as *B. subpalmata*) versus drab and relatively non-noxious salamanders (such as the *Chiropterotriton*). Both *P. triseriata* and *B. americanus* exhibit a general trend toward decreasing the duration of immobility as metamorphosis is approached. Although the reason for this trend is not apparent, Cupp (1974) noted that the Critical Thermal Maxima (CTM) of these species also decreased as they approached metamorphosis, except that the CTM of stage 46 *P. triseriata* returned to a point not significantly different from premetamorphic tadpoles. Since metamorphosis occurs during the late spring and summer months when temperatures around the pools may be quite high, it may be that it would be disadvantageous for a metamorphosing froglet to become immobile and thus risk overheating at a time when its physiological mechanisms are least able to handle long exposure to warm temperatures. Also, other factors may interact with temperature to affect the duration of immobility, such as humidity and tolerance to desiccation. It may then be more of a selective advantage to rely on other defensive mechanisms, such as quick movements to a place of refuge, to avoid predators. More work is needed to ascertain why *B. americanus* should have a significantly less tendency to become immobile than either of the other two species at Stage 46.

There would also appear to be little reason for adult *S. holbrooki* adults to differ significantly in the duration of immobility compared with Stage 46 animals at 20°C. Cupp (1974) found that at 30°C, adults and young differed significantly in their CTM whereas at 20°C, there were no significant differences. Therefore, an explanation based solely on temperature tolerance does not seem sufficient.

Adult *S. holbrooki*, however, are known to possess noxious skin secretions which may be effective in deterring predators (Dodd and Brodie, unpublished data). It would seem unlikely that the poison glands of recently metamorphosed *S. holbrooki* would be sufficiently developed to produce enough secretion to ward off predators. Licht (1967) showed that the parotoid glands of toads are not well developed at metamorphosis and Dodd (1977) felt that juvenile toads were less likely to become immobile when approached because these glands are not capable of producing secretion to deter predators. It may be that the longer duration of immobility of adult *S. holbrooki* at 20°C (near the temperature at which nocturnal foraging often occurs) allows them to rely on their noxious secretions for defence whereas it would be more advantageous for recently metamorphosed animals to try to escape. Since *S. holbrooki* is nocturnal and fossorial, it may be that 30°C is above the thermal preferendum for metamorphosed young and adults of this species.

This study indicates that the tadpoles of some anuran species do exhibit immobility at least as early as developmental stage 41 and through metamorphosis, and that temperature may have a significant effect on the duration of this behavioural pattern. More extensive studies are needed on the immobility behaviour of tadpoles and metamorphosing froglets.

ACKNOWLEDGEMENTS

We would like to thank James R. Holman of the Experimental Statistics Department of Clemson University for running the statistical analysis. Bart Kavruck (U.S. National Museum) provided the illustration for Fig. 1.

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WINTER AGGREGATION OF *LEIOLOPISMA GUICHENOTI*

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Winter aggregations occur in a variety of reptilian species. The most conspicuous are the denning aggregations of snakes although, on occasions, smaller aggregations of lizards have been noted (Neill, 1948; McCoy, 1974). The present paper reports on winter aggregations in the small scincid lizard, *Leiolopisma guichenoti*, near Armidale, N.S.W., Australia. This species ranges throughout coastal southeastern Australia and inland into the Great Dividing Range (Cogger, 1975). It undergoes variable periods of inactivity throughout the winter months. However, during unseasonably warm periods at any time of winter, individuals may become active on the surface of the ground. For example, on the austral shortest day (22 June) of 1969, a number of *L. guichenoti* were found active in sunny spots on the leaf litter at mid-day near Armidale; a dissected male had motile sperm in the vas deferens (Heatwole, 1976). Thus, these lizards may not undergo brumation in the strict sense of the term even though there may be periods of weeks or even months (depending on locality and weather) during which they cannot be found active on the surface of the ground.

On 14 August 1976 a section of sawn log 23 cm long and 40 cm diameter was split for firewood. A central cavity and smaller crevices collectively contained 18 individuals of *L. guichenoti*. The animals were capable of sluggish movement; crevice temperature (11.40 hours) was 7.6°C as measured by a Comark Electronic thermometer. Air temperature was 4–10°C depending on whether or not there were clouds obscuring the sun. Soil under the chunk of wood was 5.8°C. A light snow had been present on the ground that morning but had melted by the time the present observations were made.

The woodpile from which the log was taken had been on the ground for 2 years, during which time wood was periodically split for firewood; no lizards had been previously found. The log containing the lizards was characterised by (i) lying on the ground with the cut end in contact with the soil, rather than on its side, and (ii) it had longitudinal crevices and a central cavity, the openings of which were in contact with the soil beneath the log. Following the discovery of the lizards, the woodpile was taken apart and one more log with that combination of characteristics found. It was split and 16 lizards found to be present. Cavity temperatures were 3.5 to 5.0°C (11.50 hours). Four other logs not with the above characteristics were taken from the same woodpile and split but none contained lizards. It would appear that access to crevices from the undersurface of the wood is important in determining suitability of a log as a winter refuge.

The size structure of the groups in the two logs was different (Fig. 1). One log contained primarily large individuals, mostly in individual small crevices. The other contained mostly juveniles, all together in the central cavity. It would appear that there

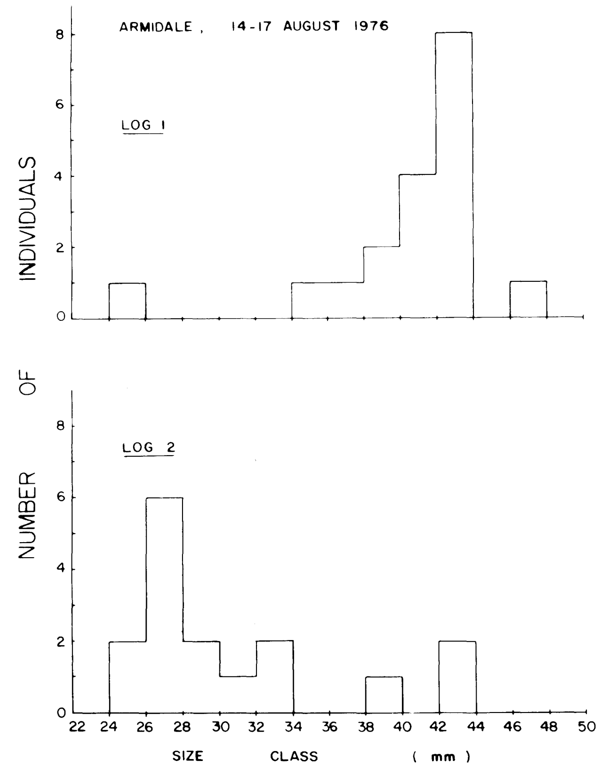

FIG. 1. Size structure of two winter aggregations of *Leiolopisma guichenoti*.

is a tendency for juveniles and adults to seek separate winter refuges. There was no segregation by sexes as the sex ratios in the two logs were 9 males : 9 females and 7 : 9 respectively. Of the 12 mature males, all contained motile sperm.

The present observations do not permit assessment as to whether winter aggregation was in response to other individuals and hence a social phenomenon, or whether it resulted from a common response of many individuals to the same few suitable winter sites. Whatever the immediate stimulus, the resulting behaviour was markedly different from that occurring in summer. Over the past 9 years, John Veron and we have collected approximately 150 individuals of this species for use in studies of reproductive cycles; usually only one or two animals were found associated with a given log and rarely three or four but never in the numbers described above for winter.

Interspecific aggregation may occur. On 20 September 1976, two individuals were found coiled together under a log in a woodland habitat at Armidale, N.S.W. They were cold and slow-moving. One individual was a female *L. guichenoti* and the other a male *Leiolopisma delicata*.

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BOOK REVIEWS

BIOLOGY OF THE REPTILIA, volume 7, Ecology and Behaviour A. Edited by C. Gans and D. W. Tinkle (1977). 720 pp. London, New York: Academic Press. £31.80.

This volume is the first dealing with ecology and behaviour in the series and it maintains the high standards. There are seven chapters, of varying length and scope. "Competition and the niche" (T. W. Schoener) is essentially an essay: stimulating, lucid and concise, but certainly not bedside reading—perhaps I can best indicate the approach by noting that there is a two-page appendix of the mathematical symbols which are used to develop the argument. Other chapters are masterly discussions of the literature relevant to their titles; those on population dynamics (F. B. Turner) and learning processes (G. M. Burghardt) are particularly thorough, and include German and Russian work which has tended to be neglected by English-speaking herpetologists. J. A. Stamps surveys "social behaviour and spacing patterns in lizards", family by family; this is useful because it demonstrates how unevenly the different groups have been studied. There is little to say, for example, about geckoes, agamids or anguids such as the slow-worm.

Shorter chapters by E. R. Pianka on species diversity and H. Heatwole on habitat selection also highlight our ignorance. Pianka is constrained to deal almost exclusively with deserts, and Heatwole treats his subject from a descriptive and theoretical standpoint, because there are so few relevant experimental studies. Finally, in "Variation and evolution of stereotyped behaviour", C. C. Carpenter and G. W. Ferguson classify a prodigious amount of data—it comes as a surprise to discover how much has been written on the subject. They refer to no less than 158 kinds of behavioural acts, and give taxonomic lists showing which ones have been observed in each species. Compilation must have been a mammoth task; it would be easy to criticise this chapter as mere fact-grubbing, but it will continue to be an invaluable source of reference for many years to come.

On the other hand, much of this volume will soon be out of date. Therefore the book does not represent such a good investment as the volumes of morphology. It is the fattest and most expensive book in the series; future volumes must revert to a slimmer format or *Biology of the Reptilia* will become beyond the means of even the best-endowed libraries.

R. A. AVERY

NARKOSE DER REPTILIEN, AMPHIBIEN UND FISCHE. By K. Bonath (1977). 159 pp. Berlin: Paul Parey. DM 49.

This book is the fourth in a series on laboratory animals and, like the previous volumes, is written in German. It is in paper-back and there are 30 photographs and 30 tables.

The reviewer is not qualified linguistically to comment in detail on the German text. Nevertheless, the book appears to be comprehensive and each part is further divided into sections on the application of anaesthetics, the agents used and their action. There is also a short section on euthanasia and a list of references. The photographs of manipulation and injection techniques are valuable and, while not every herpetologist will approve of the handling methods depicted, there is no doubt that they will prove useful to the veterinary surgeon or research worker. The tables of anaesthetic agents are a particularly welcome feature and permit rapid reference to drugs and their reported uses in a wide range of species.

There has long been a need for a detailed publication on the anaesthesia of the lower vertebrates and in many respects this book fills the niche. However, there are many errors and omissions in the references and this is likely to prove a drawback to those wishing to use the book in practical or academic studies. It is hoped that a second edition, appropriately corrected and updated, will be translated into English in order to make the wealth of data which it contains more accessible to the British and North American reader.

J. E. Cooper

Venoms: Chemistry and Molecular Biology. By Anthony T. Tu (1977). 560 pp. New York; John Wiley and Sons. £25.90.

Any zoologist concerned with scorpions or the venomous types of spiders, insects and snakes will find plenty to interest him in this book but it will probably hold the greatest appeal for those who find such creatures to be useful sources of experimental reagents. For anyone working in the acetylcholine-receptor field, for instance, the book is a valuable source of information and there is much of relevance to enzymologists, haematologists and immunologists.

Occasionally, the experimental findings are presented as something of a catalogue and it is left to the reader to recognise interrelationships and implications. Although the book could be criticised on these grounds it is unrealistic to expect the author to make a pertinent comment on every item in the wealth of data he has amassed. The reference list includes classical as well as more modern papers and citations of the latter are commendably up to date.

A particularly pleasing feature of the book is the inclusion of fold-out tables. Publishers are generally reluctant to provide these but they are much easier to study than are tables that continue over several pages. Less pleasing are the illustrations. The electronmicrographs are not well reproduced and labelling is often inadequate or even non-existent. Where structures are labelled, the abbreviations have not always been included in the legend.

Despite this shortcoming, the author and publishers are to be congratulated on producing such a comprehensive work, and one which may well become a classic in its field.

Ann Silver

Bestimmen von Krokodilen und Ihrer Häute. By H Wermuth and K. Fuchs (1978). 100 pp. Stuttgart: Gustav Fischer. DM 29.

This is a most useful and important booklet on the taxonomy of crocodilian skins. Useful because even the herpetologist may not know that there are 38 different species of crocodilian he might be called upon to identify; important because customs officials have now got to enforce the Washington Convention for the preservation of animals threatened with extinction, 14 of which are crocodilians. It is most gratifying to note that a leading engineer in the tanning industry has collaborated with a zoologist in writing this book, which should make it easier for anybody, not herpetologically trained, to determine the exact nature of any crocodile skin dealers may want to import. Since English-speaking customs officers would benefit from having it on their shelves, it is hoped that a publisher for an English translation will be found without delay.

E. Elkan

Dietary Adaptations in Animals. By J. L. Cloudsley-Thompson (1976). 70 pp.
The Size of Animals. By J. L. Cloudsley-Thompson (1977). 58 pp.
The Tuatara. By J. Robb (1977). 64 pp.
Patterns in Progress (Zoology). Shildon, Co. Durham: Meadowfield Press.

I am not sure why these paperbacks have been published. The information is readily available in standard textbooks and I cannot see at what level the books are aimed; they are certainly too elementary as university texts, and seem poor value at £2.80 for 58–70 not very well printed pages. For the herpetologist, the monograph on the tuatara seems the most useful but again the information is well known, and it falls between what is expected of an interesting, elementary account and a technical monograph.

M. Peaker

Handbuch der Palaeoherpetologie, Part 13 (1976). Edited by O. Kuhn. Stuttgart and New York: Gustav Fischer Verlag.

This part of this important handbook contains articles in German on the Thecodontia by A. J. Charig and H.-D. Sues, B. Krebs and F. Westphal.

A. D'A. Bellairs

International Zoo Yearbook, volume 17, edited by P. J. S. Olney (1977). 392 pp. London: The Zoological Society of London.

Herpetological topics covered in this issue include breeding amphibians, Galapagos tortoises, *Clemmys muhlenbergii, Crocodylus johnsoni, Epicrates fordii, Liasis* spp., *Ophiophagus hannah* and *Bitis gabonica*; ulcerative shell disease in chelonians; an artificial diet for snakes, and determination of sex in *Varanus komodoensis*. The latter is particularly important for it paves the way for distinguishing males from females on the basis of steroid hormone measurements. Section 1 is the proceedings of the Second World Conference on Breeding Endangered Species held in July 1976; it is essential reading.

M. Peaker

HANDBUCH DER PALAEOHERPETOLOGIE, Part 18 *Pterosauria*. By P. Wellnhofer (1978). 82 pp. Stuttgart: Gustav Fischer Verlag. DM 84.

This volume deals with the first, perhaps homeothermic, vertebrates which took to the air. Their classification as an Order within the Reptilia is still under dispute. Remains attributed to this group have been found in Germany, England, North America, Africa, Mongolia, Brazil and Jordan. The volume ends with an extensive list of references covering the literature on this difficult subject which should yet be fascinating to every herpetologist.

E. ELKAN

BRITISH AMPHIBIANS, REPTILES AND POND DWELLERS. By Maxwell Knight (1977). 136 pp. Hornchurch, Essex: Ian Henry Publications Ltd. £4.25.

This book is a reprint of that originally published in 1956 and written by the distinguished late amateur naturalist. Why the present publisher should wish to reprint it without revision is beyond my comprehension, and it would be quite unfair to comment on the text 22 years after its first appearance, except to say that anybody following the advice on the care of natterjacks, sand lizards and smooth snakes in captivity is likely to find themselves on the wrong side of the law. It is intended for young people but the price for 136 pages of dated information is ridiculous, especially when more recent accounts are available and the original is still in public and school libraries. Let sleeping books, unless absolute classics, lie.

M. PEAKER

ANNOUNCEMENTS

A NEW CHECKLIST

Annotated Checklist with Keys to the Chelonians of Hong Kong. By J. D. Romer. *Memoirs of the Hong Kong Natural History Society*, No. 12, 1978.

Copies of this publication may be obtained on application to: The Hong Kong Natural History Society, c/o Department of Zoology, University of Hong Kong, Hong Kong. A crossed postal order for £1.20 should be enclosed to cover the cost of a single copy sent by surface mail.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinion published in *Bulletin of Zoological Nomenclature*, 34 (4), 1978—Opinion No. 1104 (p. 222). Relative precedence of *Cornufer* Tschudi, 1838, and *Platymantis* Gunther, 1858 (Amphibia, Salientia).

The required 6 months' notice is given of the possible use of plenary powers by the International Commission on Zoological Nomenclature in connection with the following name (see *Bulletin of Zoological Nomenclature*, 35 (1), 1978).

2162 (*Trionyx*) *steindachneri* Siebenrock, 1906: proposed validation (Reptilia, Testudines).

Comments should be sent in duplicate (if possible within 6 months of the date of publication in the *Bulletin*), citing case number to: R. V. Melville, The Secretary, International Commission on Zoological Nomenclature, c/o British Museum (Natural History), Cromwell Road, London, SW7 5BD.