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AN ALTERNATIVE EXPLANATION OF THE DISTRIBUTIONS OF THE RARE HERPTILES IN BRITAIN

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INTRODUCTION

There are three rare herptiles in Britain, *Bufo calamita, Lacerta agilis* and *Coronella austriaca,* all of which are also restricted in their distribution. In a stimulating review, Beebee (1978) has recently reviewed these distributions, and has very ably gathered information on the ecological requirements of the animals and the ecological characteristics which these areas of distribution provide. In so far as these ecological restrictions explain the patterns of distribution, Beebee (1978) provides an authoritative review with which one can scarcely argue. However, the patterns of distribution also have a historical perspective which seems to be, at best, rather poorly understood by him. There is a considerable body of information on the climatic and vegetational history of the British Isles which has a bearing on this problem.

CLIMATIC HISTORY

It seems clear that between 10 600 and 10 100 years ago, the "Younger Dryas" time, southern Britain had a periglacial climate, with a tundra vegetation and an arctic fauna (*e.g.* Pennington, 1977; Coope, 1977a). While it is possible that some of the present British vertebrate fauna was already established here (arctic species like *Sorex minutus, Lepus timidus* and *Mustela erminea*) it is quite certain that the three essentially southern, heliophilous, rarer herptiles could not have been present. However, there appears to have been, judging from beetle faunas, a very rapid increase in temperature following the end of the Younger Dryas period, so that by about 9500 years ago, southern England had a climate at least as warm as that now experienced (Coope, 1977b; Osborne, 1974). Between about 8000 and 5000 years ago, the period of the climatic optimum, temperatures appear to have been 2–3°C higher in summer than they are now (Lamb, 1966). In historical times, mean July temperatures have fluctuated somewhat between 15–16°C in central England. Independent confirmation of this pattern of climatic change comes from oxygen isotope measurements. For example, at Gotland, Sweden, which has very similar summer temperatures (17°C) now to southern England, Mörner & Wallin (1977) calculated a low summer temperature of about 10°C for the period 10 000 to 9500 years ago, followed by a rapid rise to temperatures of 17°C by 9300 years ago. They too suggest a climatic optimum, with temperatures in summer around 19°C, between around 8000 and 6000 years ago, and then a slight deterioration with fluctuating temperatures between 19°C and 16°C subsequently.

VEGETATION HISTORY

The mass of data now available, from pollen analysis, has been summarized by a number of authors (*e.g.* Godwin, 1975; Pennington, 1969; Rackham, 1976). The general pattern of vegetation history in England which emerges is quite clear, though details vary from site to site. The open, tundra, vegetation of the Younger Dryas, pollen zone III, was replaced first by birch scrub, between 9700 and 8700 years ago (Hibbert *et al.*, 1971). This was an open birch scrub, for the pollen of ericaceous shrubs and grasses was also prominent. This was succeeded by hazel scrub from 8700 to 8100 years ago, by hazel and pine together from 8100 to 7100 years ago, and then by deciduous woodland of oak, elm, alder and hazel which was the dominant vegetation in England from 7100 to 5000 years ago. With this afforestation, the pollen contribution from plants of open country, such as grasses, sedges and heather, declines to negligible proportions, and in general it seems clear that in England, Wales, and southern Scotland the forest cover was virtually complete. Its composition varied somewhat—in south eastern England, lime was an important forest tree, while in northern Scotland pine forest persisted. Only on higher ground, *e.g.* in the Pennines, and in northern Scotland was more open vegetation widely present throughout this period (Tallis, 1964; Rackham, 1976), though there must have been local patches, *e.g.* on the coast, and around human habitation, where herbaceous vegetation survived. Increasingly through this period, however, the affect of man and his livestock on the forests becomes apparent in the pollen record. At first, this is associated with obvious archaeological sites, (though some of these date back to the Mesolithic period, as early perhaps as 8000 years ago) and do not interrupt the general forest cover. At around 5000 years ago, however, there is an abrupt decline in the representation of elm which seems to result directly from the over-exploitation of that species as fodder for livestock. From that time on, the deterioration of the forest cover becomes more and more complete, until

reaching a nadir in the eighteenth century. Reforestation began in Britain around 1750–1800, and is, indeed, detectable in the pollen record (*e.g.* Mitchell, 1965).

THE HISTORY OF THE SITES OF RARER HERPTILES

The botanical evidence is clear, that deciduous forest covered virtually all of southern Britain, including the present ranges of the rarer herptiles, between the period 7000 and 5000 years ago. Equally it is clear that these three animals require open vegetation conditions which allow them to bask or hatch their eggs at temperatures higher than the prevailing shade temperatures. However, certain habitat types would have persisted with open vegetation throughout this forest period. Most obviously, a developing dune system would provide a continual supply of open habitat even if woodland developed on the older dune areas. Unfortunately, this rather specialised type of habitat would be very local; pollen analysis reveals usually the general pattern of vegetation cover rather than such local detail. Only more precise pollen records, for specific sites associated with the animals of interest here, would be of value, and few of these are available. There are, though, a few records of specific value. In north-west Britain, not far inland from the present coastal distribution of *Lacerta agilis* and *Bufo calamita,* the site of Red Moss, near Horwich on the M61 road, shows a persistence of ericaceous pollen throughout the period of afforestation (Hibbert *et al.,* 1971), and implies that the area was not completely covered by closed forest. Moreover, Tooley (1976) has documented a series of alternating peats and clays along the Lancashire coast which suggest at least 10 separate incursions of the sea across the present coastline. His interpretation is controversial, but it seems clear from his results that, at the very least, this was a low coastline, liable to flooding, and unlikely therefore to develop forest cover. In short, open vegetation suitable for the two animals may well have persisted throughout this period.

For the southern heathlands, Dimbleby (1976) has discussed the evidence from pollen analysis. Even as early as 8000 years ago, in the vicinity of Mesolithic camp sites, heather was spreading as the forest was cleared. This strongly suggests that man, or his livestock, may have created small pockets of open vegetation, in which the rare herptiles might have survived, right throughout the period when the general pollen record for the area assures us that forest cover had developed. It is possible, too, that the nearby coast had suitable patches of open country, but in this case we have no direct evidence on the point. Extensive development of open heathland, to the extent that it affects the general pattern of the pollen record, is a later phenomenon, and associated especially with Neolithic and later times. Large-scale clearance of the forests in southern England began around 5000 years ago (Gimingham, 1972), and this marks the start of the spread of the southern heathlands.

DISCUSSION

The arguments above lead clearly to the following hypothesis for the occurrence of the rarer herptiles in Britain.

(1) Between 10 600 and 10 000 years ago, the climate was far too cold for any of these animals to be present in Britain.

(2) Sometime between 10 000 and 9 000 years ago, there was a rapid rise of temperature , which certainly allowed southern, thermophilous beetles to colonise Britain. This rapid improvement is not suggested by the pollen record, but Coope (*e.g.* 1977a, b) has argued cogently that beetles, which are highly mobile, would react more quickly to an improvement in climate than the plants. The vertebrates too would react quickly to this change, and this short period, of improved climate yet open vegetation, would have allowed *Lacerta agilis* and *Bufo calamita* to reach north-west England. It is even possible that *Bufo calamita* also reached Ireland, naturally, at this period, along with the "Lusitanian" plants (see Mitchell & Watts 1970). (Alternatively, it was taken to Ireland by man—Corbet, 1961.)

(3) From around 9500 years ago, increasing forest cover would have progressively restricted these species either to small pockets of natural open vegetation, such as sand dune systems, or to small areas where the (sparse) human population provided similar clearings.

(4) From Neolithic times onwards, with the increasing destruction of the forests, and the expansion, particularly, of the southern heathlands, the rare herptiles could have expanded their ranges to that which Beebee (1978) records, but only if these heathlands were near such focuses of population as had survived the period of forestation.

(5) Within such areas, the occurrence of these animals is limited by habitat considerations, as Beebee (1978) has argued; for example, *Bufo calamita* requires breeding pools of suitable pH and in sunny locations, while *Lacerta agilis* requires open sand patches in which to lay its eggs.

(6) The current vegetation pattern is extremely "open" and would seem to offer little barrier to further spread of these species, but climate, as well as habitat factors, acts as a general restriction. In particular, the daily sunshine contours (isohels) do demarcate in a general way the areas of distribution of these species; the 6 hr, 6.5 hr and 7 hr May isohels circumscribe, respectively, the distributions of *Bufo calamita, Lacerta agilis,* and *Coronella austriaca* (Meteorological Office, 1952), and May sunshine seems to be important for breeding activity of, at least, the first two (cf. Jackson, 1978).

This hypothesis differs from those proposed by Beebee (1978) and Spellerberg (1975) (whom he follows) in several respects. Firstly, they suggest that the period of the climate optimum (7000–5000 years ago) was the time when the rarer herptiles entered Britain, but that they were restricted by the forest cover to the southern coast, perhaps just the south-east corner, of Britian. They imagine that deforestation by man, reaching a peak about 3000 B.P., would have allowed these species to spread north westwards; Spellerberg (1975) suggests that they spread around the

coast, while Beebee (1978) proposes a corridor through the West Midlands to north-west England. This corridor is suggested by the distribution of places with "heath" in the name, and by three doubtful (as Beebee himself says) records of *Bufo calamita* from Shropshire. This general thesis may be criticised on several grounds. Firstly, the period of the climatic optimum also was the period of maximum forest cover, and therefore the least likely period for animals of open habitats to be invading Britain. Secondly, the peak of deforestation was reached not about 3000 B.P. but about A.D. 1700. In particular, early (Neolithic, Iron Age and Romano-British) farming, and therefore forest clearance, was largely confined to the drier, lighter soils, particularly of the downlands; the heavy clay soils of the valley bottoms, which the rare herptiles would have had to cross on the Spellerberg–Beebee hypothesis, remained forested until Anglo-Saxon times (Pennington, 1969; Rackham, 1976). The "heath" place names also derive from the Anglo-Saxons (Gimingham, 1972); while it is possible that they were already open country, but were only bestowed with their modern names by Anglo-Saxon settlers, it seems more likely that they were created as well as named at about that time. Certainly 1300 years ago seems much too late for the rare herptiles to be spreading to the north-west; their recent distribution included both sides of the Dee and Mersey estuaries, while *Bufo calamita* would have had to cross both the Ribble and Lune to reach the Cumbrian coast. This former widespread distribution in the north west seems to argue strongly in favour of the much more ancient colonisation suggested above.

An initial colonisation around 9500 B.P. would also help explain several other points which puzzle Beebee (1978). Most notably, the Breckland of East Anglia had colonies of *Bufo calamita,* but none of *Lacerta agilis* or *Coronella austriaca.* However, the Breckland heaths were created, from formerly forest conditions, by Neolithic farmers (Godwin, 1975); it is quite conceivable that the low coastline of East Anglia provided suitable refuges for the toad, which was later able to spread into the Breckland, but did not provide such refuges for the reptiles. It is, alternatively, possible that the toad (which does extend further north, and is presumably therefore slightly more tolerant) survived the climatic deterioration in East Anglian refuges whereas the reptiles did not. Beebee (1978) also speculates on the absence of rare herptiles from various western dune systems, such as those in Devon, Cornwall, Glamorgan and Anglesey; he points out that it is unlikely that all of these are geologically younger than those in, particularly, N.W. Britain. This is obviously true if one imagines that only the last 3000 years are relevant. However, if a period around 9500 years ago is the crucial one, it seems very likely (given that sea-level had not then reached its present level, and that isostatic recovery of the land, relieved of the weight of ice, was still underway) that *none* of the present dune systems existed. The survival of rare herptiles in any coastal area since then would have been a very chancy affair, requiring not only suitable conditions for initial colonisation but also the somewhat freakish condition that such habitats survived in the vicinity throughout all the subsequent changes in sea level, climate, vegetation and human land use. Over this longer period, "chance" losses of rare herptiles from limited areas of duneland, or failure even to colonise them because the dunes developed too late, seem highly likely explanations.

In summary, there was a short period around 9500 B.P. when the climate had improved so rapidly after the last retreat of the ice that forest cover had not yet spread to Britain. These open conditions would have allowed the rare herptiles to colonise Britain extensively. The subsequent development of forest cover would have restricted them to small refuges of open habitat, perhaps dune systems, cliffs, or around early human settlements. Climatic deterioration might have further restricted their survival in these refugia. With the development of open, heathland, vegetation as a consequence of Neolithic and later farming, a limited extension of range, certainly through the southern heathlands, would have occurred. Even then, persistent forests in the river valleys would have limited the extent of such spreading. There seems no real evidence that the corridor through the West Midlands postulated by Beebee (1978) either existed or was relevant to the distribution of the rare herptiles; and there is a great deal of palaeobotanical and historical evidence that it did not exist.

REFERENCES

Beebee, T. J. C. (1978). An attempt to explain the distributions of the rare herptiles *Bufo calamita, Lacerta agilis* and *Coronella austriaca* in Britain. *British Journal of Herpetology* **5,** 763–770.

Coope, G. R. (1977a). Fossil coleopteran assemblages as sensitive indicators of climate changes during the Devensian (last) cold stage. *Philosophical Transactions of the Royal Society B* **280,** 313–340.

Coope, G. R. (1977b). Quaternary Coleoptera as aids to the interpretation of environmental history, In *British Quaternary Studies: Recent Advances.* Shotton, F. W. (Ed). Oxford: Clarendon Press.

Corbet, G. B. (1961). Origin of the British insular races of small mammals and of the "Lusitanian" fauna. *Nature, London* **191,** 1037–1040.

Dimbleby, G. W. (1976). The history and archaeology of heaths. In *The Southern Heathlands.* Sankey, J. H. P. and Mackworth-Praed, H. W. (Eds). Surrey Naturalists Trust.

Gimingham, C. H. (1972). *Ecology of heathlands.* London: Chapman and Hall.

Godwin, H. E. (1975). *History of the British flora* (2nd ed). London: Cambridge University Press.

Hibbert, F. A. Swiftsur, V. R. & West, R. G. (1971). Radiocarbon dating of Flandrian pollen zones at Red Moss, Lancashire. *Proceedings of the Royal Society of London B.***177,** 161–171.

Jackson, H. C. (1978). Low May sunshine as a possible factor in the decline of the sand lizard (*Lacerta agilis* L.) in North-west England. *Biological Conservation* **13,** 1–12.

Lamb, H. H. (1965). Britain's changing climate. In *The biological significance of climatic changes in Britain.* Johnson, C. G. and Smith, L. P. (Eds). *Symposium of the Institute of Biology* **14,** 3–31.

Meteorological Office (1952). *Climatological atlas of the British Isles.* London: H.M.S.O.

Mörner, N. A., & Wallin, B. (1977). A 10 000-year temperature record from Gotland, Sweden. *Palaeogeography, palaeoclimatology, palaeoecology* **21,** 113–138.

Mitchell, G. F. (1965). Littleton Bog, Tipperary: an Irish vegetational record. In *International studies on the Quaternary* (Geological Society of America, Special Papers) Wright, H. E. and Frey, D. G. (Eds). **84,** 1–16.

Mitchell, G. F. & Watts, W. A. (1970). The history of the Ericaceae in Ireland during the Quaternary Epoch. In *Studies in the vegetational history of the British Isles* 13–21. Walker, D. and West, R. G. (Eds). London: Cambridge University Press.

Osborne, P. J. (1974). An insect assemblage of Early Flandrian age from Lea Marston, Warwickshire and its bearing on the contemporary climate and ecology. *Quaternary Research* **4,** 471–486.

Pennington, W. (1969). *The history of the British vegetation.* London: English Universities Press.

Pennington, W. (1977). The late Devensian flora and vegetation of Britain. *Philosophical Transactions of the Royal Society of London B* **280,** 267–272.

Rackham, O. (1976). *Trees and woodland in the British landscape.* London: Dent.

Spellerberg, I.F. (1975). Conservation and management of Britain's reptiles based on their ecological and behavioural requirements: a progress report. *Biological Conservation* **7,** 289–300.

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GROWTH AND DEVELOPMENT OF TADPOLES OF THE COMMON TOAD *BUFO BUFO* LINNAEUS ON DIFFERENT FOODS

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INTRODUCTION

Savage (1961) considered that all tadpoles are not born equal, and that in the tadpole world, it is the thruster that gets ahead. It is to the tadpole's advantage to grow as fast as possible, and thus minimise the risks of predation (Cooke, 1974), toxic chemicals (Cooke, 1979), desiccation of breeding site or starvation (Savage, 1961). The time required to complete metamorphosis varies enormously, and ambient temperature is an important environmental correlate (Smith, 1973). However, widely different growth rates observed in the field suggest that other factors—perhaps competition for food—also influence development, even though there may be no apparent food shortage (Savage, 1961). Food quality rather than quantity may, therefore, be limiting to the population. For example, Cooke (1977) reported low growth rates of tadpoles despite an abundance of palatable food (filamentous algae). The aim of this study was to examine the effects of different foods, both natural and artificial, on the growth and development of tadpoles of the common toad *Bufo bufo* L.

METHODS

Toad spawn was cultured out-of-doors in 2 plastic tanks (35 × 48 × 50 cm high) filled to a depth of approximately 10 cm with 15 litres of tap water, which had been allowed to stand for 24 hr. After hatching, *Spirogyra* was added to one of the tanks (containing about 100 tadpoles) to serve as food (Group A), but the other group (50 tadpoles) was not fed initially, so that the effects of early food shortage could be observed (Group B). At 20 days after hatching, Group A tadpoles without external gills (stage 24/25, Witschi, 1956) were weighed individually and transferred, in groups of 10, to 8 shallow "Pyrex" dishes (28 × 17 cm) containing 1 litre of aged tap water in the laboratory. The foods used were: (1) *Spirogyra,* washed in distilled water to remove associated debris (3 dishes); (2) a suspension of fresh bakers' yeast in distilled water (2); (3) lightly boiled lettuce leaves (2) and (4) a mixture of each of these potential foods (1). Food was always present in excess and both food and water were changed regularly, at about 2-day intervals. Tadpoles were weighed individually at frequent intervals up to stage 29 (well developed hind limbs), and again at metamorphosis (tail almost completely resorbed, stage 33) (the dishes were raised at one end to facilitate emergence). Observations on feeding behaviour, including the amount of time spent feeding, were made frequently. Group B tadpoles were given an excess of lettuce 37 days after hatching when they were at stage 25. They were weighed individually on 3 occasions, at stages 25, 26 (small hind limb buds) and 29, and again at metamorphosis.

To determine growth rates in the field, samples of 10 tadpoles were collected every two weeks, anaesthetised in MS 222 (Sandoz) and preserved in 5% formalin solution. They were weighed individually in the laboratory and the stage recorded. Later, the gut was dissected out intact, and the contents of a short length (2 mm) was teased out onto a glass slide and examined microscopically to examine recently ingested food. Faecal pellets produced during anaesthetisation were also preserved for comparison.

RESULTS

Tadpoles fed on lettuce (A3) and a mixture of foods (A4) developed more rapidly and grew heavier than those fed on *Spirogyra* (A1) and yeast (A2) (Fig. 1). Average rates of weight gain to stage 29 were 9.3 and 10.7 mg.day^{-1} (A3 and A4) compared with 4.2 and 4.3 mg.day^{-1} (A1 and A2). Mean weights (± S.E.) at stage 29 were 192.9 ± 6.7 (A1), 136.6 ± 7.7 (A2), 240.9 ± 6.7 (A3) and 233.7 ± 7.22 (A4). Mean weights at metamorphosis varied between 47% (A1) and 67% (A3) of the above values for stage 29 (tadpoles stop feeding and lose weight when they metamorphose). The time taken to complete metamorphosis was broadly related to the rate of growth, but tadpoles fed on yeast (A2) suffered an extremely protracted (5 weeks) final phase, and the resulting toadlets were extremely small (78.1 ± 7.4 mg), though perfectly formed.

Group B tadpoles developed normally when feeding was resumed (average growth rate, 6.3 mg.day^{-1}). At stage 26, these tadpoles were as heavy as those collected from the field at the same stage, though the former reached this stage 20 days later (Fig. 2). However, mean weight at stage 29 was only about 65% of the weight of tadpoles collected from the field at the same stage. Mean weight at metamorphosis of Group B tadpoles was 122.5 ± 2.9 mg, 56% of the weight of these tadpoles at stage 29.

Growth rates of tadpoles in the field (10.6 mg.day^{-1}) were similar to those obtained in the mixed foods experiment (10.7 mg.day^{-1}). However, at stage 29,

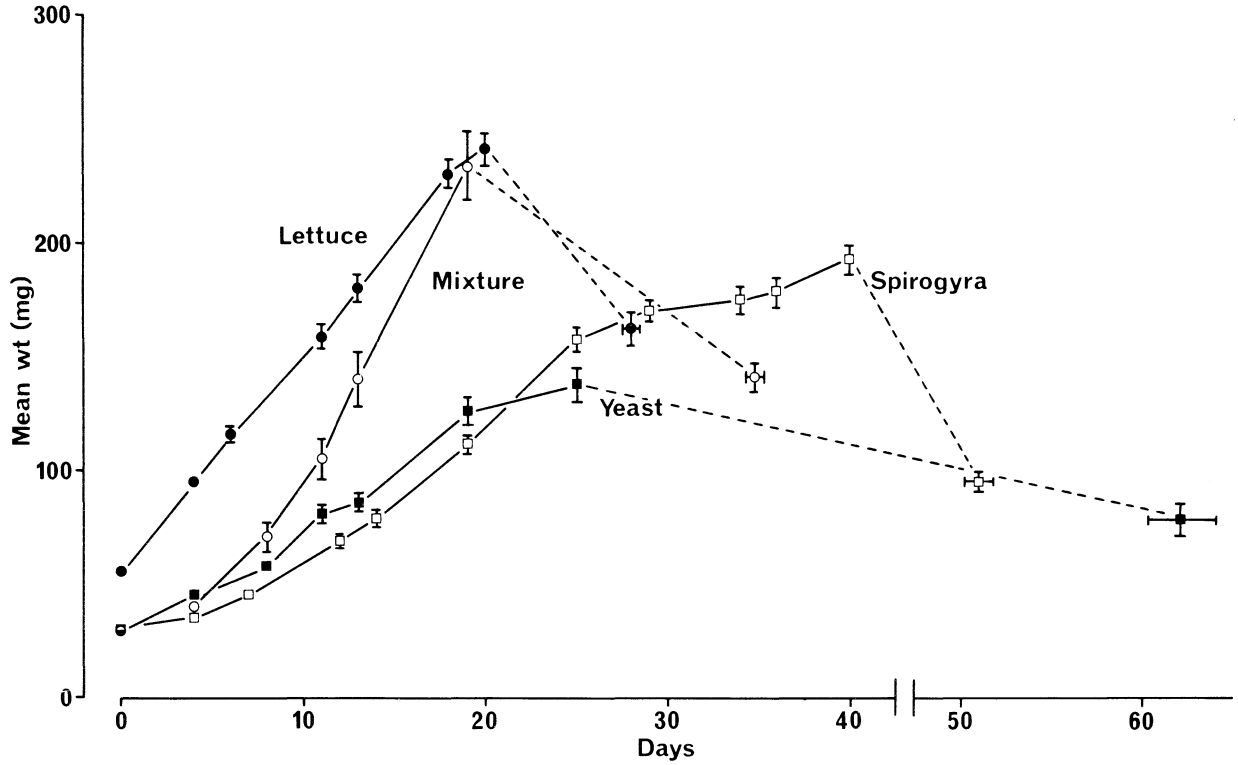

FIG. 1. Growth rates of tadpoles on different foods, including weights at metamorphosis (mean ± S.E.). Mean time (+ S.E.) to metamorphosis is also shown.

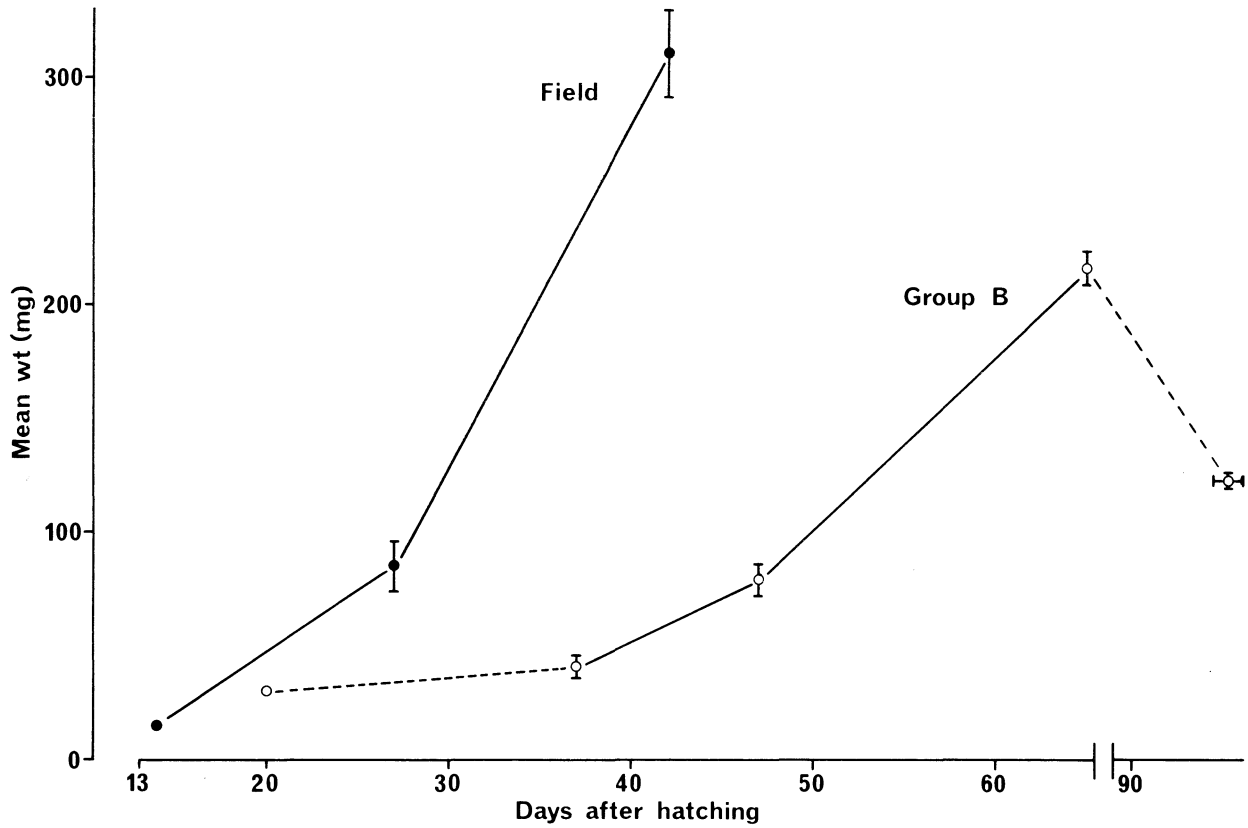

FIG. 2. Growth rates (mean ± S.E.) of tadpoles in the field and in the Group B trial (food added 37 days after hatching). Weight at metamorphosis (mean ± S.E.) and duration of development (to stage 33) is also shown for Group B tadpoles.

field tadpoles were much heavier (311.3 ± 18.9 mg.day^{-1} compared with 233.7 ± 7.2 mg.day^{-1}). Guts of tadpoles collected from the field contained predominantly organic detritus, with varying proportions of inorganic particles, diatoms and other unicellular algae, animal remains, and, particularly in the smaller individuals, filamentous algae. Tadpoles collected on any one day tended to contain the same sorts of food items, in similar proportions, and the composition of the faeces was also similar.

Tadpoles in the lettuce (A3) and food mixture (A4) trials divided their time almost equally between feeding, swimming and resting. Those in the yeast experiment (A2), which produced the slowest rates of growth, rested almost continuously.

DISCUSSION

Tadpoles grew as well in the field (10.6 mg.day^{-1}) as in any of the laboratory tests, and maximum weight (stage 29) was highest (311.3 ± 18.9 mg) in the field group. These values were even better than the results produce by Savage (1952) in 1949 (a "good" year), when growth rate was about 8.8 mg.day^{-1} and maximum weight was about 270 mg. In this case, as in the present study, most of the food material was composed of debris, diatoms and algal spores. Growth rates of tadpoles kept in cages by Cooke (1977) varied between 4.3 mg.day^{-1} (max. wt. 227 ± 10 mg) and 7.1 mg.day^{-1} (316 ± 12). Differences in food availability, resulting from herbicide treatment of the experimental sites were thought responsible in this case.

Early starvation of Group B tadpoles had no obvious effect on subsequent development, apart from delaying the onset of metamorphosis. If such conditions persisted in nature, the animals might suffer because the terrestrial feeding period before hibernation would be much reduced. Also, small tadpoles are very vulnerable to predation. Metamorphosis was reached in all the trials, suggesting that food, particularly when in short supply, is used primarily for development (differentiation), at the expense of increase in size.

Of the foods tested in laboratory experiments, *Spirogyra* was the only one readily available to natural populations of toad tadpoles. Yeast cells do occur naturally in freshwaters, but not as abundantly as in the experiments. It is interesting that growth rates of tadpoles fed *Spirogyra* were lower than in any other treatment. By washing off the associated debris, the alga had presumably lost much of its nutritive value. Analysis of faecal pellets produced by tadpoles in this test, showed the alga to be virtually unchanged after passage through the guts. Tadpoles collected from the field always contained a high proportion of detritus and diatoms as well as filamentous algae. This suggests that normal development is dependent on the presence of bacteria and other microorganisms, which may be more readily assimilated than macroscopic algae. Recent studies have shown that many freshwater invertebrates utilise microorganisms attached to detritus rather than the detritus itself (see Berrie, 1976). Presumably, lightly boiled lettuce is readily digestible and growth on this food is not so dependent on the presence of microorganisms. In the mixed foods trial, lettuce was eaten in preference to the other foods available. Yeast cells alone did not produce good growth, and the rapid and uncontrolled contamination by *Scenedesmus,* a uni-cellular green alga, may have aided development of tadpoles in this trial. Much further work is required before the precise food requirements of tadpoles can be understood, but if a population appears to be suffering from acute food shortage, the addition of some freshly boiled lettuce leaves may temporarily alleviate the problem.

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REFERENCES

Berrie, A. D. (1976). Detritus, micro-organisms and animals in fresh water. In *The role of terrestrial and aquatic organisms in decomposition processes.* Anderson, J. M. and Macfadyen, A. (Eds) Oxford: Blackwell.

Cooke, A. S. (1974). Differential predation by newts on anuran tadpoles. *British Journal of Herpetology* **5**, 386–390.

Cooke, A. S. (1977). Effects of field applications of the herbicides diquat and dichlobenil on amphibians. *Environmental Pollution* **12**, 43–50.

Cooke, A. S. (1979). The influence of rearing density on the subsequent response to DDT dosing for tadpoles of the frog *Rana temporaria. Bulletin of Environmental Contamination and Toxicology* **21**, 837–841.

Savage, R. M. (1952). Ecological, physiological and anatomical observations on some species of anuran tadpoles. *Proceedings of the Zoological Society of London* **122**, 467–514.

Savage, R. M. (1961). *The ecology and life history of the common frog.* London: Pitman.

Smith, M. A. (1973). *The British amphibians and reptiles* (5th edition). London: Collins.

Witschi, E. (1956). *Development of vertebrates.* Philadelphia: Saunders.

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AN ASSESSMENT OF CHANGES IN POPULATIONS OF THE WARTY NEWT (*TRITURUS CRISTATUS*) AND SMOOTH NEWT (*T. VULGARIS*) IN TWENTY PONDS IN WOODWALTON FEN NATIONAL NATURE RESERVE, 1974–1979

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INTRODUCTION

The warty newt (*Triturus cristatus*) apparently suffered population declines in Britain during the 1960s and early 1970s (Beebee, 1975). Loss of suitable habitat was probably the main cause of these declines. Beebee (1975) drew attention to the need for "data collection, surveying and ecological research relating to this species". The smooth newt (*T. vulgaris*) has fared much better in Britain, although some local declines in population may have occurred (see Beebee, 1973, 1975; Prestt, Cooke & Corbett, 1974). The main problem in assessing changes in population levels of British Amphibia, and of newts in particular, is a general lack of quantitative data.

Some figures are, however, available since 1972 for the warty and smooth newt populations living in 20 experimental ponds on Woodwalton Fen National Nature Reserve in Cambridgeshire. In 1972, four ponds were treated with herbicide and four others were studied as controls (Cooke, 1977). Herbicide treatment resulted in a reduction in aquatic macrophytes, and numbers of larval smooth newts were relatively low in the treated ponds. By 1974, the warty newt was no longer found in one of the treated ponds which had few macrophytes but a dense algal mat on most of the surface (Cooke, 1977). An investigation into factors affecting the distribution of newts in Britain showed that warty newts prefer breeding sites with plenty of open water (Cooke & Frazer, 1976). As part of that investigation, all 20 ponds were netted for warty and smooth newts in 1974 (Cooke & Frazer, 1976). In 1979. the ponds were netted again. During the intervening five years there has been virtually no human disturbance to the ponds. However, all 20 ponds dried out completely during the drought in the summer of 1976.

The results of netting in 1979 are reported in this paper. The aim was to determine whether populations of either species had changed markedly since 1974.

SITE AND METHODS

The 20 ponds were dug in 1961 by the Nature Conservancy on a five-by-four grid (see Table I). Each pond is approximately 5 m in diameter and the distance between adjacent ponds is approximately 25 m. Water depth varies up to about 2 m. Smooth newts started to colonise the ponds in 1964 and warty newts were first observed in 1968 (Cooke & Frazer, 1976). Within the reserve, newts are virtually confined to the pond system during the breeding season (M. Palmer, pers. comm.), while in ditches on the arable farmland surrounding the reserve, newts are now extremely rare (unpublished observations). At the present time, the populations utilising the ponds tend to be isolated and significant emigration or immigration is unlikely to occur.

Field methods were as described by Cooke & Frazer (1976). In early May, each pond was netted (with pond nets of 400 μm mesh) for 15 min and catches were recorded. The two species can be readily distinguished in the field, so any newts which were seen but not caught were also noted. Because warty newts are relatively easier to see than to catch, sight records are especially useful for this species (see Cooke & Frazer, 1976; Frazer, 1978). In early June, ponds that had previously failed to produce both smooth and warty newts were netted again. Maximum depth and percentage plant cover were recorded for each pond.

TABLE I. Ponds in which newts were found during the netting programmes in 1974 and 1979. S = smooth newt (*T. vulgaris*), W = warty newt (*T. cristatus*)

Pond no.	1974				1979			
1–4	SW	S	SW	SW	S	SW	SW	SW
5–8	SW	SW	S	S	SW	SW	SW	SW
9–12	SW	SW	W	S	SW	SW	SW	SW
13–16	SW		SW	S	SW	SW	SW	SW
17–20	S	S	S	S	SW	S	SW	S

TABLE II. Numbers of newts caught during the netting programmes in 1974 and 1979.[c]

	No. of ponds	Males	Females	Immatures	Larvae[a]	Mean numbers caught/pond: Arithmetic mean (range)	Mean numbers caught/pond: Geometric mean[b] (GM ± SE)
Smooth newt (*T. vulgaris*)							
1974	31	25	44	6	13	2.8 (0–19)	1.4 (1.0–1.8)
1979	31	12	28	4	7	1.6 (0–7)	0.9 (0.7–1.1)
Warty newt (*T. cristatus*)							
1974	31	2	3	4	0	0.3 (0–2)	0.18 (0.15–0.21)
1979	31	1	8	26	0	1.1 (0–6)	0.42 (0.32–0.55)

[a] Those that had overwintered.
[b] Zero catch taken as 0.1 in calculation.
[c] Newts seen but not caught are excluded from this Table.

RESULTS AND DISCUSSION

When this netting technique was used in 1974, species composition of the catches was the same in virtually every pond in the second catch as in the initial operation (Cooke & Frazer, 1976). In 1979, however, out of the 11 ponds for which the netting operation needed to be repeated, at least one of the species was recorded for the first time for the year in nine ponds. The weather was generally cold and wet in 1979 and the breeding season of the newts was unusually protracted. In June, many of the female smooth newts captured were still gravid, although newly-hatched larvae were present in most of the ponds by this time. Plant cover at the surface was general lower in 1979, probably because of slow growth during this particular year. Maximum water depth ranged from 1.15 to 1.65 m in 1979.

In 1979, smooth newts were present in every pond, whereas in 1974 smooth newts had not been found in two ponds (numbers 11 and 14; see Table I). During the netting programme in 1979, warty newts were found in 17 ponds (all, except numbers 1, 18 and 20, but this species was recorded in pond 1 later in 1979). In 1974, warty newts were detected in only 10 ponds. The increase in 1979 was statistically significant (chi-squared = 5.58, $P < 0.05$).

All four of the ponds which had been treated with herbicide in 1972 (numbers 5, 6, 7 and 13) contained both species of newt in 1979. Plant growth in each of these ponds in 1979 did not differ markedly from that in the other ponds.

There were evidently no long-term detrimental effects of the drought of 1976. On the contrary, it may have been beneficial by eliminating predatory fish. In 1974, two ponds (numbers 14 and 17) held large numbers of ten-spined sticklebacks (*Pungitius pungitius*); at that time, no newts were found in pond 14 (the only pond to be devoid of newts) and only smooth newts were found in pond 17. In 1979, no fish were caught in any of the 20 ponds, and ponds 14 and 17 held both species of newt.

Numbers of newts caught in the two years can only be compared with caution. Eleven ponds had to be netted again in both 1974 and 1979. Catches for each year, based on a total of 31 ponds (i.e. 20 + 11), are summarised in Table II. There was a tendency for fewer smooth newts and more warty newts to be caught (per pond) in 1979, but these trends were not statistically significant. The appreciable increase in immature warty newts presumably reflects good recruitment in most recent years. Smith (1969) stated that warty newts usually become sexually mature at three years of age, but Hagström (1975) demonstrated that both smooth and warty newts tend to mature at about five years old in the Gothenburg area of Sweden.

Adult female newts outnumbered adult males for both species in both years (Table II). This may have been the result of a tendency to net the well-vegetated edges of the ponds where eggs were laid (see Frazer, 1978) rather than being an indication of a real preponderance of females.

Thus, to conclude, the smooth newt was found in every pond in 1979, although the total catch was rather lower than that for 1974. The warty newt was found in all but three of the 20 ponds, with many immatures being caught. Neither the herbicide treatment in 1972 nor the drought of 1976 had any long-term detrimental effect on the newt populations.

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REFERENCES

Beebee, T. J. C. (1973). Observations concerning the decline of the British Amphibia. *Biological Conservation* **5**, 20–24

Beebee, T. J. C. (1975). Changes in status of the great crested newt *Triturus cristatus* in the British Isles. *British Journal of Herpetology* **5**, 481–490.

Cooke, A. S. (1977). Effects of field applications of the herbicides diquat and dichlobenil on amphibians *Environmental Pollution* **12**, 43–50.

Cooke, A. S. & Frazer, J. F. D. (1976). Characteristics of newt breeding sites. *Journal of Zoology* **178**, 223–236.

Frazer, J. F. D. (1978). Newts in the New Forest. *British Journal of Herpetology* **5,** 695–699.

Hagström, T. (1975). Notes on growth and age distribution of adult *Triturus vulgaris* L. and *T. cristatus* Laurenti (Urodela, Salamandridae) in SW Sweden. *Bulletin de la société Zoologique de France* **100,** 680.

Prestt, I., Cooke, A. S. & Corbett, K. (1974). British amphibians and reptiles. In *The changing flora and fauna of Britain,* 229–254. Hawksworth, D. L. (Ed). London and New York: Academic Press.

Smith, M. (1969). *The British amphibians and reptiles* (4th edition) London: Collins.

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GENETIC VARIATION AND DIFFERENTIATION OF THREE COMMON EUROPEAN NEWTS (*TRITURUS*) IN YUGOSLAVIA

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SUMMARY

The present study was undertaken to assess levels of genetic variation within and between certain Yugoslavian populations of *Triturus vulgaris, Triturus alpestris* and *Triturus cristatus,* as well as the amount of genetic differentiation among these species. A starch gel electrophoretic survey for genetic variation in eight population samples reveals differences among taxa in amounts of intrapopulational variability. Average heterozygosities range from 13.5% in *T. alpestris*, through 8.7% in *T. vulgaris*, to 5.2% in *T. cristatus*. Average numbers of alleles per locus and proportions of loci polymorphic per population follow similar trends. We tentatively propose that this heterogeneity in amount of genetic variability corresponds to differences in the degree of habitat variation experienced by these taxa.

In order to estimate the amount of genetic divergence among the taxa studied, Nei's statistics of genetic identity (*I*) and genetic distance (*D*), as well as the proportion of diagnostic loci, were calculated from allele frequencies. These statistics show that the species and subspecies examined are very well separated in comparison to the amount of divergence among North American salamanders. Genetic similarities among the three species of *Triturus* suggest that *T. vulgaris* and *T. alpestris* are more closely related to each other than either is to *T. cristatus*. This electrophoretic survey also reinforces the findings of earlier cytological studies that two subspecies of *T. cristatus, T. c. karelinii* and *T. c. dobrogicus,* are probably reproductively isolated species.

INTRODUCTION

European newts, genus *Triturus,* comprise almost one-third of the world's living Salamandrid species and subspecies (Brame, 1967). Of nine *Triturus* species three (*T. alpestris, T. vulgaris* and *T. cristatus*) have extensive ranges being essentially pan-European. Thus, *T. cristatus* covers most of Europe (but not Ireland, S. and S.W. France, Iberia, S. Greece and Mediterranean islands), the Caucasus and Central Asia. *T. vulgaris* is distributed over most of Europe (S. France, Iberia, S. Italy and most of Mediterranean islands are exceptions) and in West Asia too. *T. alpestris* is restricted to Europe where it has, however, as fairly extensive range, from W. Russia to N. and E. France and from S. Denmark to N. Italy and Central Greece (Arnold & Burton, 1978).

The Balkan region and, in particular, Yugoslavia, with as many as nine endemic taxa, is an important centre of evolutionary radiation of *Triturus* salamanders, especially of the species *T. vulgaris* and *T. alpestris*. We report here an electrophoretic survey of biochemical genetic variation within and between certain Yugoslavian populations of *T. alpestris, T. vulgaris* and *T. cristatus*. As in the related North American genus *Taricha* (Hedgecock, 1976) we find the species of *Triturus* to be heterogeneous in amount of intrapopulational gene diversity. We tentatively propose that this heterogeneity corresponds to differences in the degree of habit variation experienced by the various taxa.

In comparison with the amount of evolutionary divergence among North American salamandrids (Hedgecock, 1974, 1976) or even to the differentiation of North American and European genera (Hedgecock & Kalezić, in preparation), the species and subspecies of *Triturus* we examined are surprisingly well separated.

MATERIALS AND METHODS

Triturus vulgaris—samples of three natural populations of the nominal subspecies were collected from the following localities: Beograd, Srbija (22 adults), Fruška Gora, Vojvodina (48 larvae) and Sisevac, Srbija (35 adults).

Triturus alpestris—assayed populations belong to the nominal subspecies and were collected from Mount Komovi, Crna Gora (72 larvae and 30 adults) and from Mount Mokra Gora, Srbija (29 adults).

Triturus cristatus—two subspecies were the subject of this study: the lowland form *T. c. dobrogicus* which is confined to the Danube basin (50 adults were collected from Ečka, Vojvodina, and 32 adults from Obedska bara, Vojvodina) and the highland form *T. c. karelinii* which inhabits the hilly and mountainous areas of the Caucasus reaching the south parts of Yugoslavia (28 adults specimens were collected near the town of Berovo, Makedonija).

Collection localities for all *Triturus* samples are mapped in Fig. 1.

The collected specimens were frozen at −25°C after

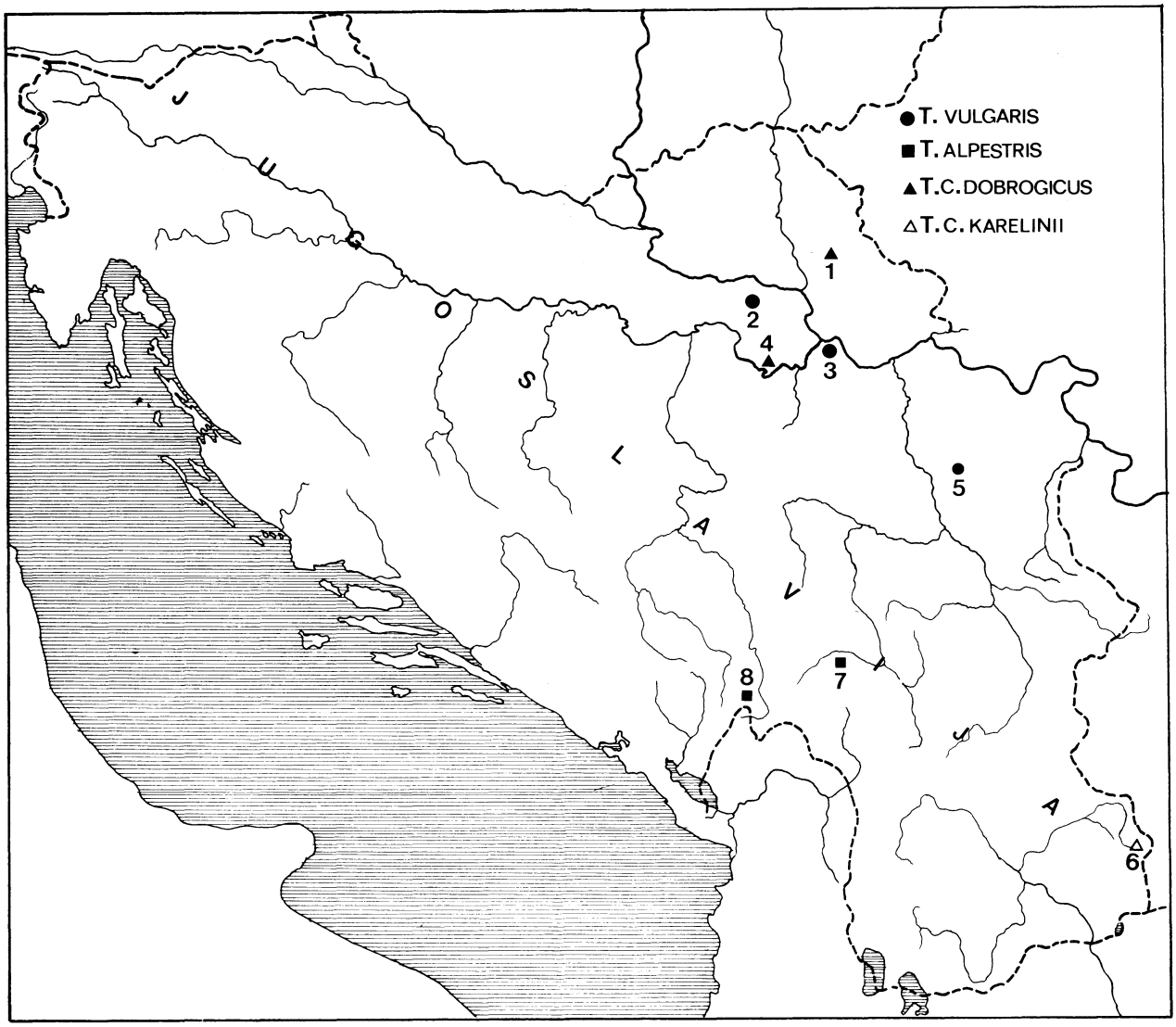

FIG. 1. Map showing localities of eight population samples of *Triturus*. Localities are: (1) Ečka, (2) Fruška Gora, (3) Beograd, (4) Obedska bara, (5) Sisevac, (6) Berovo, (7) Mokra Gora and (8) Komovi.

transportation to the laboratory. Larvae and small adults were wholly homogenised in 2–3 volumes of grinding buffer (0.05 M Tris-HCl, pH = 7.1) while only livers were removed from large adults and homogenised in the same buffer. After centrifugation (30 min at 2000 r.p.m. under 5°C refrigeration) the supernatant was stored at −25°C until subjected to electrophoresis.

Techniques of electrophoresis and protein staining were the same as those described in detail by Hedgecock (1976).

RESULTS

We studied the variability of 21 different enzymes and one group of general proteins (Table I). Thirty-five discrete zones of band phenotypes can be distinguished in gels assayed for these enzymes and proteins; each zone is presumed to be encoded by a single gene locus that is symbolised by an abbreviation of the enzyme name. Multiple zones on complex zymograms are denoted by the addition of hyphenated integers to the gene-enzyme symbol, −1 corresponding to the least anodally migrating isozyme.

Nine enzymes, presumably encoded by a maximum of 12 loci (see Table I), show no variability in each of the assayed taxa: ACPH, CK, GDH, G-3-PDH, HBDH, IDH, LDH, PROT and SDH. In some variable zones of other enzymes presumptive heterozygotes appear either as double-banded phenotypes, indicative of monomeric structure (EST and PGM), or as three-banded phenotypes indicative of dimeric structure (FUM, GOT, α-GPDH, MDH, PGI and 6-PGDH). Heterozygotes of G-6-PDH, ME, ODH and TPI enzymes appear as blurred regions intermediate between the two homozygous phenotypes. In the case of the second zone of tetrazolium oxidase activity (coded by the *To-2* gene) all individuals display multibanded phenotypes, presumptive homozygotes having a pattern in which the least migrating band is most prominent and heterozygotes having the additive pattern of three homozygous phenotypes.

Zymograms of the above-mentioned enzymes are very similar to those described for the related North American genus *Taricha* by Hedgecock & Ayala

TABLE I. Enzymes and proteins assayed in three species of *Triturus*, their symbols and number of loci scored

Enzyme	Abbreviation	Number of loci scored
Acid phosphatase	ACPH	2
Creatine kinase	CK	1
Esterase	EST	5
Fumarase	FUM	1
Glutamate dehydrogenase	GDH	1
Glutamate-oxaloacetate transaminase	GOT	2
Glyceraldehyde-3-phosphate dehydrogenase	G-3-PDH	1
α-Glycerophosphate dehydrogenase	α-GPDH	1
Glucose-6-phosphate dehydrogenase	G-6-PDH	1
β-Hydroxybutyrate dehydrogenase	HBDH	1
Isocitrate dehydrogenase	IDH	2
Lactate dehydrogenase	LDH	2
Malate dehydrogenase	MDH	2
Malic enzyme	ME	1
Octanol dehydrogenase	ODH	2
Phosphoglucose isomerase	PGI	2
6-Phosphogluconic dehydrogenase	6-PGDH	1
Phosphoglucomutase	PGM	2
Protein	PROT	1
Sorbitol dehydrogenase	SDH	1
Triosophosphate isomerase	TPI	1
Tetrazolium oxidase	TO	2

(1974). Lactate dehydrogenase isozyme patterns, however, differ greatly having, instead of four-banded homozygote phenotypes, only one somewhat broad band. The most probable interpretation of these is similar mobility of subunits which obscures the well known tetrameric pattern of this enzyme. Only in the case of *T. alpestris* individuals is it possible to recognise the *Ldh-2* homotetramer which migrates only 1 mm more than the *Ldh-1* homotetramer.

For each gene-enzyme system, the allele corresponding to the band found most commonly in *T. v. vulgaris* specimens is arbitrarily designated as "100"; other allelic variants are represented by numerals obtained by adding or subtracting from 100 the number of millimeters separating the variants from the 100 band under standard electrophoretic conditions.

The goodness of fit between observed phenotypic distributions and those expected by Levene's formula for small samples (Levene, 1949) was tested by chi-square test. The absence of significant differences between these values indicates general conformity to expected Hardy–Weinberg equilibria for the populations assayed. Nevertheless, as pointed out below, a deficiency of heterozygotes is evident in the sums over all loci within each population.

We use three measures of genetic variability: proportion of polymorphic loci, average number of alleles detected per locus, and heterozygosity averaged over loci. In most cases the number of genes sampled per locus is less than 100 so a locus is considered polymorphic whenever two or more alleles are detected in a sample.

The results of our survey of genic variation in the genus *Triturus* are summarised in Table II. These allelic frequencies are the actual frequencies of protein variants in pooled samples of the taxa *T. vulgaris*, *T. alpestris* and *T. c. dobrogicus*. Allelic frequencies of the two subspecies of *T. cristatus* are listed separately because of considerable genetic differentiation between them.

Inspection of the Table II reveals that loci differ greatly in levels of variability. Some of them are monomorphic, or nearly so, within each taxon (*Est-1*, *Gdh*, *G-3-pdh*, *Idh-1*, *Ldh-1*, *Prot-4* and *Tpi*). Others are monomorphic in some taxa but polymorphic, sometimes to a great extent, in other taxa (*Est-3*, *Est-4*, *Est-5*, *Fum*, *α-Gpdh*, *G-6-pdh*, *Pgi-1*, *6-pgdh*). Only in the case of *Got-2*, *Odh-2*, *Pgi-2* and *Pgm-1* does polymorphism appear consistently at least for the taxa assayed.

The number of alleles ranges from one at loci monomorphic for the same allele throughout the genus to six for *α-Gpdh*; however, no more than three alleles are distinguished at a single locus in any one taxon.

Locus *Pgi-2* appears to be the most polymorphic locus in the *T. vulgaris* populations; 33% of *vulgaris* individuals are heterozygous at this locus. The most polymorphic locus in any population studied is *Est-4* in *T. alpestris* ($H = 54.5\%$). Besides this locus, the highly polymorphic loci, $H > 35\%$, in *alpestris* are: *Est-3*, *Fum*, *6-pgdh*, *Pgm-2*. Locus *Est-3* appears to be the most polymorphic in *T. c. karelinii* ($H = 25\%$), while *Fum* has the highest value in *T. c. dobrogicus* populations ($H = 31.6\%$).

Samples of three natural populations of *T. vulgaris* have been assayed for genetic variation. The results are summarised in Table III. On the average, 34.9% of the assayed loci are polymorphic in populations of this taxon. Average number of alleles detected per locus ranges from 1.37 in the Fruška Gora sample to 1.53 in the Beograd sample with the mean value for all populations of 1.44 alleles per locus. The observed percentage of heterozygous individuals average over all loci assayed in a given sample ranges from 6.7% in the Sisevac sample to 11% in the Fruška Gora sample, with the mean value for all samples of 8.7%.

Samples of two populations of *T. alpestris* have been assayed for genetic variation at 13 loci in Mokra Gora and 23 in the Komovi sample (Table IV). This discrepancy in the number of loci studied most likely caused discrepancies in estimates of genetic variation; namely, some of the polymorphic loci were unscorable in the Mokra Gora sample. Thus, average number of alleles detected per locus is 1.70 in the Komovi sample while this statistic has the value of 1.54 in the Mokra Gora sample. The same occurs with the proportion of polymorphic loci per population; 52.2% of loci assayed in the Komovi sample are segregating for more than one allele as against the Mokra Gora sample where 46.2% of the loci are polymorphic. Discrepancies in average proportions of heterozygous individuals per locus are more conspicuous, 16.7% versus 10.2%, respectively. Despite obvious downward bias introduced by the Mokra Gora sample, the average proportion of loci heterozygous in *T. alpestris* individuals (13%) is substantially higher than any other taxon studied.

TABLE II. Genetic variation in assayed taxa of the genus *Triturus*. N is the number of individuals studied and H is the observed proportion of heterozygotes in the pooled samples (omitted when 0.0 in all taxa)

Gene	Alleles	*T. vulgaris*	*T. alpestris*	*T. cristatus dobrogicus*	*T. cristatus karelinii*
Acph-1	N	22	—	—	—
	100	1.000	—	—	—
Acph-2	N	5	—	—	—
	100	1.000	—	—	—
Ck-1	N	20	—	—	—
	100	1.000	—	—	—
Est-1	N	74	102	14	16
	92	—	—	—	1.000
	98	—	1.000	—	—
	100	1.000	—	—	—
	103	—	—	1.000	—
Est-2	N	—	—	45	—
	100	—	—	1.000	—
Est-3	N	—	28	23	28
	98	—	0.179	—	0.232
	100	—	0.821	1.000	0.768
	H	—	0.357	0.000	0.250
Est-4	N	—	99	50	21
	97	—	—	0.100	—
	98	—	0.465	0.900	1.000
	100	—	0.449	—	—
	102	—	0.086	—	—
	H	—	0.545	0.120	0.000
Est-5	N	—	71	32	21
	98	—	0.183	—	—
	100	—	0.817	1.000	1.000
	H	—	0.197	0.000	0.000
Fum	N	57	104	76	28
	95	—	—	0.684	1.000
	98	—	—	0.316	—
	100	1.000	—	—	—
	102	—	0.624	—	—
	106	—	0.376	—	—
	H	0.000	0.352	0.316	0.000
Gdh	N	89	131	79	28
	98	—	—	1.000	1.000
	100	1.000	1.000	—	—
Got-1	N	46	22	—	—
	98	—	1.000	—	—
	100	1.000	—	—	—
Got-2	N	49	55	29	—
	88	—	—	0.241	—
	93	—	—	0.759	—
	95	0.081	0.036	—	—
	100	0.887	0.936	—	—
	105	0.032	0.027	—	—
	H	0.180	0.127	0.345	—
G-3-pdh	N	22	37	32	—
	100	1.000	1.000	1.000	—
α-Gpdh	N	35	56	57	27
	90	—	0.089	—	—
	95	—	0.911	—	—
	97	—	—	—	0.167
	98	—	—	1.000	0.833
	100	0.986	—	—	—
	104	0.014	—	—	—
	H	0.029	0.143	0.000	0.185
Hbdh	N	22	—	—	—
	100	1.000	—	—	—
G-6-pdh	N	73	47	82	28
	97	—	0.479	—	—
	100	1.000	0.521	0.018	0.107
	102	—	—	0.982	0.893
	H	0.000	0.319	0.037	0.214

TABLE II (*continued*)

Gene	Alleles	*T. vulgaris*	*T. alpestris*	*T. cristatus dobrogicus*	*T. cristatus karelinii*
Idh-1	N	12	39	27	9
	95	—	—	1.000	1.000
	100	1.000	1.000	—	—
Idh-2	N	—	—	—	19
	100	—	—	—	1.000
Ldh-1	N	88	131	81	28
	91	—	1.000	1.000	—
	95	—	—	—	1.000
	100	1.000	—	—	—
Ldh-2	N	—	131	—	—
	92	—	1.000	—	—
Mdh-1	N	70	131	82	28
	93	0.150	—	—	—
	100	0.850	1.000	1.000	1.000
	H	0.214	0.000	0.000	0.000
Mdh-2	N	100	—	—	—
	100	0.490	—	—	—
	107	0.505	—	—	—
	112	0.005	—	—	—
	H	0.480	—	—	—
Me	N	54	—	—	—
	98	0.094	—	—	—
	100	0.811	—	—	—
	102	0.094	—	—	—
	H	0.245	—	—	—
Odh-1	N	51	55	—	28
	100	1.000	0.945	—	1.000
	102	—	0.055	—	—
	H	0.000	0.073	—	0.000
Odh-2	N	—	55	41	22
	95	—	0.143	—	—
	100	—	0.857	—	—
	105	—	—	0.841	0.864
	108	—	—	0.159	0.136
	H	—	0.179	0.171	0.182
Pgi-1	N	103	130	82	28
	95	0.005	—	—	—
	100	0.985	0.169	0.976	1.000
	105	0.010	0.827	0.024	—
	110	—	0.004	—	—
	H	0.029	0.277	0.006	0.000
Pgi-2	N	15	—	—	25
	98	0.367	—	—	—
	100	0.633	—	—	0.060
	103	—	—	—	0.940
	H	0.333	—	—	0.120
6-pgdh	N	105	121	82	28
	97	—	0.632	—	—
	98	0.029	—	—	—
	100	0.967	0.368	1.000	—
	102	—	—	—	1.000
	108	0.004	—	—	—
	H	0.067	0.471	0.000	0.000
Pgm-1	N	90	128	—	—
	98	0.268	—	—	—
	100	0.732	0.003	—	—
	101	—	0.977	—	—
	103	—	0.020	—	—
	H	0.326	0.047	—	—
Pgm-2	N	—	26	73	28
	94	—	0.250	—	—
	98	—	0.211	—	—
	100	—	0.539	—	—
	105	—	—	0.753	1.000
	110	—	—	0.247	—
	H	—	0.472	0.137	0.000

TABLE II (*continued*)

Gene	Alleles	*T. vulgaris*	*T. alpestris*	*T. cristatus dobrogicus*	*T. cristatus karelinii*
Prot-4	N	22	24	32	28
	100	1.000	1.000	1.000	1.000
Sdh	N	22	—	24	—
	100	1.000	—	—	—
	110	—	—	1.000	—
Tpi	N	89	49	80	28
	98	—	—	0.013	—
	100	1.000	1.000	0.987	—
	102	—	—	—	1.000
	H	0.000	0.000	0.025	0.000
To-1	N	—	30	—	—
	100	—	1.000	—	—
To-2	N	—	30	42	28
	100	—	0.866	1.000	1.000
	106	—	0.134	—	—
	H	—	0.267	0.000	0.000

TABLE III. Summary of genetic variation in samples from three populations of *T. v. vulgaris*

	Beograd	Fruška Gora	Sisevac	Average
Number of loci studied	19	16	14	16.3
Average number of genes sampled per locus	40 ± 2	66 ± 7	60 ± 4	55 ± 4
Average number of alleles detected per locus	1.53 ± 0.19	1.37 ± 0.12	1.43 ± 0.17	1.44
Proportion of polymorphic loci per population	0.316	0.375	0.357	0.349
Averages over loci of the proportions of heterozygotes				
—observed	0.085 ± 0.035	0.110 ± 0.048	0.067 ± 0.018	0.087
—expected	0.090 ± 0.037	0.115 ± 0.050	0.083 ± 0.043	0.096

TABLE IV. Summary of genetic variation in samples from two populations of *T. a. alpestris*

	Komovi	Mokra Gora	Average
Number of loci studied	23	13	18
Average number of genes sampled per locus	120 ± 14	55 ± 2	87.5
Average number of alleles detected per locus	1.70 ± 0.16	1.54 ± 0.14	1.62
Proportion of polymorphic loci per population	0.522	0.462	0.492
Averages over loci of the proportions of heterozygotes			
—observed	0.167 ± 0.043	0.102 ± 0.039	0.135
—expected	0.184 ± 0.047	0.124 ± 0.043	0.154

TABLE V. Summary of genetic variation in samples from three populations *T. cristatus*

	T. c. dobrogicus		*T. c. karelinii*	
	Ečka	Obedska bara	Berovo	Average
Number of loci studied	16	18	21	18.3
Average number of genes sampled per locus	82 ± 6	55 ± 2	50 ± 2	62.3
Average number of alleles detected per locus	1.37 ± 0.12	1.22 ± 0.10	1.24 ± 0.10	1.28
Proportion of polymorphic loci per population	0.373	0.222	0.238	0.278
Averages over loci of the proportions of heterozygotes				
—observed	0.056 ± 0.026	0.055 ± 0.030	0.045 ± 0.019	0.052
—expected	0.070 ± 0.034	0.077 ± 0.040	0.056 ± 0.024	0.068

We studied genetic variation in two of four recognised subspecies of *T. cristatus*: ssp. *dobrogicus* and ssp. *karelinii*. Two populations of *dobrogicus* (Ečka and Obedska bara) and one of *karelinii* (Berovo) were sampled. Average number of alleles ranges from 1.22 in the Obedska bara sample to 1.35 in the Ečka sample with the average of 1.28 over these three populations (Table V). The population sample from Obedska bara has the lowest proportion of polymorphic loci (22.2%), the sample from Berovo slightly more (23.8%), while the sample from Ečka has a somewhat higher proportion of polymorphic loci (37.5%). Averaged over loci, individuals from Ečka and Obedska bara have practically the same mean heterozygosity, 5.6% and 5.5% respectively. In the case of the *karelinii* sample this statistic has somewhat lower value, 4.5%.

In all *Triturus* populations sampled, observed mean heterozygosities are less than expected means such that the difference between these two statistics over all eight samples is significantly different than zero ($d = -0.014 \pm 0.0009$, $t_7 = 5.75$, $P \ll 0.001$). A similar deficiency of observed heterozygosity in *Taricha* populations was attributed to Wahlund effect (Hedgecock, 1978) and that would appear to be the most likely explanation in this case as well.

As can be seen from Table II, taxa assayed in this

TABLE VI. Percentage of diagnostic loci among assayed taxa of *Triturus*. A locus is considered diagnostic if the probability of correct classification is 0.99 or greater

	T. a. alpestris	*T. c. dobrogicus*	*T. c. karelinii*
T. v. vulgaris	29.4%	60.0%	66.7%
T. a. alpestris		45.0%	47.4%
T. c. dobrogicus			22.2%

TABLE VII. Average genetic similarity (above diagonal) and distance (below diagonal) between the assayed taxa of the genus *Triturus*

	T. v. vulgaris	*T. a. alpestris*	*T. c. dobrogicus*	*T. c. karelinii*
T. v. vulgaris		0.504 ± 0.039	0.435 ± 0.019	0.268 ± 0.018
T. a. alpestris	0.702 ± 0.081		0.359 ± 0.020	0.347 ± 0.042
T. c. dobrogicus	0.838 ± 0.044	1.030 ± 0.058		0.707
T. c. karelinii	1.321 ± 0.070	1.194	0.347	

study are fixed for the same allele at only two loci, *G-3-pdh* and *Prot-4*. At some loci taxa share alleles but the frequencies of alleles are different (*Pgi-1*, *Est-4*). Most numerous are loci at which taxa have different alleles or even different sets of alleles showing complete genetic differentiation. At the *Est-1* locus, for example, each of the assayed taxa are fixed for different alleles: *T. vulgaris* allele 100, *T. alpestris* allele 98, *T. c. dobrogicus* allele 103 and *T. c. karelinii* allele 92. Because each of these taxa possesses a unique allele, this locus may be used to assign a given individual to its species or subspecies (Ayala and Powell, 1972). A locus may, by convention, be considered diagnostic whenever the probability of correct classification exceeds 0.99. The proportion of diagnostic loci in all pairwise comparisons of assayed taxa has been calculated from the allele frequency data of Table II and is shown in Table VI. These proportions range from 22.2% between the two subspecies of *T. cristatus* to 66.7% between *T. vulgaris* and *T. c. karelinii*. It is worth pointing out that the proportion of diagnostic loci between *T. alpestris* and *T. vulgaris* is significantly exceeded by the proportions of both the *T. vulgaris* × *T. cristatus* or *T. alpestris* × *T. cristatus* comparisons. At the same time, the proportion of diagnostic loci between *T. vulgaris* and *T. cristatus* is much higher than the proportion between *T. alpestris* and *T. cristatus*. The mean proportion of loci diagnostic of the three species of *Triturus* is 46.3% which emphasises the significance of allozymes in delimiting taxa of this genus (Kalezić, 1978).

Nei's statistics of genetic identity (I) and genetic distance (D) were estimated for each pairwise comparisons of eight population samples studied; a total of 28 pairwise comparisons were obtained. Among these comparisons 5 are between samples of consubspecific populations, 2 are between samples of subspecific populations and 21 are interspecific comparisons. Mean values of genetic similarity and genetic distance for these three levels of comparison are:

$I_{\text{consubspecific}} = 0.970 \pm 0.016$
$I_{\text{subspecific}} = 0.707$
$I_{\text{specific}} = 0.404 \pm 0.024$

$D_{\text{consubspecific}} = 0.031 \pm 0.017$
$D_{\text{subspecific}} = 0.347$
$D_{\text{specific}} = 0.906 \pm 0.058$

In order to estimate the amount of genetic differentiation among taxa we averaged genetic similarity and genetic distance statistics over appropriate inter-taxa population comparisons (Table VII).

DISCUSSION

Genetic variation in Triturus

The results of our survey of genetic variation among three species of the genus *Triturus* are summarised in Table VIII. It is obvious that *T. alpestris* is the most variable species having the highest values on all three measures. These data suggest that the level of polymorphism in *alpestris* is one of the highest reported for an Amphibian species. A higher level of genetic polymorphism was estimated only for some toads of the genus *Bufo* (Matthew, 1975; Nevo, 1976). Species *T. vulgaris* is less variable than *T. alpestris* but apparently more variable than *T. cristatus*. Up to now, genetic variation in the Salamandridae has been studied only in the North American genus *Taricha* (Hedgecock and Ayala, 1974; Hedgecock, 1976; Hedgecock, 1978). The highest level of heterozygosity was observed in *T. granulosa* (9.6%) followed by the values for *T.*

TABLE VIII. Summary of genetic variation in the three species of genus *Triturus*

	T. cristatus	*T. vulgaris*	*T. alpestris*
Number of populations assayed	3	3	2
Average number of loci studied	18.3	16.3	18
Average number of genes sampled per locus	62.3	55.4	87.5
Average number of alleles detected per locus	1.28	1.44	1.62
Proportion of polymorphic loci per population	0.28	0.35	0.49
Averages over loci of the proportions of heterozygotes	0.052	0.087	0.135

torosa sierrae (7.2%), *T. rivularis* (6.4%) and *T. torosa torosa* (3.3%).

Genetic variability in natural populations is primarily affected by breeding system, by population size, by various modes of natural selection and by recent history. Thus, it seems beyond question that for satisfactory explanation of different levels of genetic variability among species of *Triturus* we need to develop deeper understanding of the ecology, population biology and evolutionary history of these newts. Nevertheless, Levin's theory (1968) provides a basis for speculation about the possible relationship between levels of heterozygosity in *Triturus* species and environmental heterogeneity.

A general expectation from this theory is that species in more stable environments will have lower levels of genetic variability while those in more unstable environments will have greater genetic variability.

The crested newt, *T. cristatus,* is basically a lowland species being rarely found above 900 m and generally at much lower levels. It is most often found associated with deciduous woods; local distribution of this newt is, more than anything else, affected by the occurrence of waters suitable for breeding. Crested newts prefer fairly deep, weedy pools, spending daytime on the bottom and foraging more actively at night. *T. cristatus* is believed to hibernate in water more often than the other European newts.

The largest populations of the alpine newt, *T. alpestris,* are mostly found in hilly or mountainous districts although sizeable colonies are also met in some lowland areas almost at sea level. Moreover, the alpine newt in many respects appears to be more adaptable than other newts. It is apparently more resistant to desiccation since individuals can often be found far from water. It is certainly able to withstand considerable cold, being active at quite low temperatures and able to survive at least short periods below freezing. It may be found too in very small shallow pools where summer temperatures can rise to 25°C.

The smooth newt, *T. vulgaris*, is in many respects ecologically similar to the alpine newt. It occupies many different types of habitats, almost any kind of standing water from temporary pools to the margins of lakes. Although it is generally considered a lowland species, it can be found living in sympatry with the alpine newt at elevations of 1250 m, particularly in the southern parts of its range. It is a very active species and often the first to colonise newly formed bodies of water.

Although meaningful measures of environmental variation are not available, it can be presumed that the crested newt has the lowest level of environmental heterogeneity and thus, according to Levin's theory, it should have the lowest level of genetic variation. This appears to be the case in the present study. Similar results have been obtained by Nevo (1976) who found among some anuran species that heterozygosity was positively correlated with environmental heterogeneity and unpredictability. In a survey of 54 decapod crustaceans, however, measures of environmental heterogeneity correlated positively only with Group I (central metabolic enzymes, see Gillespie & Kojima, 1968) but negatively with Group II enzymes heterozygoties (Nelson & Hedgecock, 1979). Clearly, further study will be required to establish any causal relationship between genetic and environmental variation for salamanders.

Genetic differentiation among assayed taxa of Triturus

Populations belonging to different species studied in this work invariably show considerable genetic difference (Tables VI and VII). As pointed out earlier, not only polymorphic, but also monomorphic loci contribute to observed genetic distance since species are frequently monomorphic for different alleles (Table II). The estimated average genetic distance between populations belonging to different species ($D = 0.906$) is significantly greater than that found among species of the genus *Taricha* ($D = 0.296$; Hedgecock, 1974). These two genera are closely related to each other; actually they belong to the same group of genera in the family Salamandridae (Wake & Özeti, 1969). Interestingly, genetic distance among *Triturus* species is nearly as large as the distance between the two North American salamandrids, *Taricha* and *Notophthalmus* (see data in Ayala, 1975), or distance between European and North American salamandrids (Hedgecock & Kalezić, in preparation). Thus the magnitude of genetic differentiation among the species of *Triturus* may reflect taxonomic and evolutionary rank higher than the species level. Indeed, according to Bolkay (1928), the species studied here belong to different subgenera of *Triturus*; his division, based on the osteology of the skull, recognises three subgenera: *Paleotriton*, *Mesotriton* and *Neotriton*, *T. vulgaris* is the type species of *Paleotriton*, *T. alpestris* is the type species of *Mesotriton*, *T. cristatus* is the type species of *Neotriton*. Furthermore, postmating isolating mechanisms are not well developed among species within subgenera. Thus, naturally occurring hybrids of newts are known from crossmatings of *T. helveticus* and *T. vulgaris* (*Paleotriton*; Benazzi, 1957) and of *T. cristatus* and *T. marmoratus* (*Neotriton*; Lantz, 1947). In F_1 hybrids from these crosses the heterogametic sex (male) is commonly sterile. Hybrids between species belonging to different subgenera have been obtained, but, only by artificial crosses (Porter, 1972).

Genetic similarities among three species of *Triturus* (Table VII) suggest that *T. vulgaris* and *T. alpestris* are closer to each other than either is to *T. cristatus*. *T. cristatus* is easily distinguished from the other two species by unique alleles or sets of alleles at several loci (*Got-2*, *Gdh*, *Idh-1*). Overall morphological behavioural and electrophoretic resemblance as well as patterns of geographic distributions leave the impression that *T. cristatus* is more derived from the ancestral group than either *T. alpestris* or *T. vulgaris*. This notion requires additional evidence, however, both from more extensive field work and from electrophoretic comparisons of more of the 18 taxa remaining in the genus.

Considerable genetic divergence separates the two subspecies of *T. cristatus, karelinii* and *dobrogicus*. Nei's genetic distance suggests that since these taxa shared a common ancestor about 35 electrophoretically detectable codon substitutions have accumu-

lated per 100 loci. About one out of five loci are monomorphic or nearly so for different alleles. The most striking difference in the mobility of allozymes at such diagnostic loci occurs at the *Ldh-1* locus (Kalezić, 1978). The overall genetic distance between *karelinii* and *dobrogicus* (Table VII) is in the range of distance estimated for different species of *Taricha*. This may indicate that *karelinii* and *dobrogicus* represent an advance stage in the process of divergence approaching the species level. Other evidence supports this viewpoint. Callan & Lloyd (1960) have shown characteristic differences in the lampbrush chromosomes especially in the centromeric region. Subspecies *dobrogicus*, *cristatus* and *carnifex* have spheric chromomeres at the centromere position, while *karelinii* has thick blocks of heterochromatin flanking the centromeric chromomere. Moreover, in *karelinii* oocyte nuclei homologous centromere regions are frequently fused together, a condition not observed in other subspecies of *T. cristatus* (White, 1973). Callan & Spurway (1951) made an intraspecific study of *cristatus* and found considerable disturbance of meiotic paring in hybrids between the various subspecies. Although the F_1 hybrids are vigorous, F_2 and backcross hybrids have high larval and metamorphic mortality. All these data indicate that *karelinii* and *dobrogicus* have perhaps diverged beyond the level of subspecies.

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REFERENCES

Arnold, E. N. & Burton, J. A. (1978). *A field guide to the reptiles and amphibians of Britain and Europe.* London: Collins.

Ayala, F. J. & Powell, J. P. (1972). Allozymes as diagnostic characters of sibling species of *Drosophila. Proceedings of the National Academy of Sciences U.S.A.* **69,** 1094–1096.

Ayala, F. J. (1975). Genetic differentiation during the speciation process. In *Evolutionary biology,* vol. 8, Dobzhansky, Th., Hecht, M. K. and Steere, W. C. (Eds). pp. 1–78. New York: Plenum Press.

Benazzi, M. (1957). Sulla ibridazione fra *Triturus helveticus* e *T. vulgaris. Bollettino di Zoologia* **24,** 235–242.

Bolkay, S. J. (1928). Die schädel der salamandrinen, mit besonderer rücksicht auf ihre systematische bedeutung. *Zeitschrift für anatomie und entwicklungsgeschichte* (München, Berlin) **86,** 259–319.

Brame, A. H. (1967). A list of the world's recent and fossil salamanders. *Herpeton, Journal of the Southwestern Herpetologists Society* **2,** 1–26.

Callan, H. G. & Lloyd, L. (1960). Lampbrush chromosomes of crested newt *Triturus cristatus* (Laurenti). *Philosophical Transaction of the Royal Society of London,* **B, 243,** 135–219.

Callan, H. G. & Spurway, H. (1951). A study of meiosis in interracial hybrids of the newt *Triturus cristatus. Journal of Genetics* **50,** 235–249.

Gillespie, J. H. & Kojima, K. (1968). The degree of polymorphisms in enzymes involved in energy production compared to that in two *Drosophila ananassae* populations. *Proceedings of the National Academy of Sciences U.S.A.* **61,** 582–585.

Hedgecock, D. (1974). Protein variation and evolution in the genus *Taricha* (Salamandridae). Ph.D. dissertation, University of California, Davis.

Hedgecock, D. (1976). Genetic variation in two widespread species of salamanders, *Taricha granulosa* and *Taricha torosa. Biochemical Genetics* **14,** 561–576.

Hedgecock, D. (1978). Population subdivision and genetic divergence in the red-bellied newt, *Taricha rivularis. Evolution* **32,** 271–286.

Hedgecock, D. & Ayala, F. J. (1974). Evolutionary divergence in the genus *Taricha* (Salamandridae). *Copeia* (3), 738–747.

Kalezić, M. L. (1978). The significance of allozymes in differentiating some taxa of the genus *Triturus* (Urodela, Salamandridae). *Genetika (Beograd)* **10,** 173–184.

Lantz, L. A. (1947). Hybrids between *Triturus cristatus* Laur. and *Triturus marmoratus* Latr. *Proceedings of Zoological Society of London* **117,** 247–258.

Levene, H. (1949). On a matching problem arising in genetics. *Annals of Mathematical Statistics* **20,** 91–94.

Levins, R. (1968). *Evolution in changing environments.* Princeton New Jersey: Princeton University Press.

Matthews, T. C. (1975). Biochemical polymorphism in populations of the Argentine toad, *Bufo arenarum. Copeia* (3) 454–465.

Nei, M. (1972). Genetic distance between populations. *The American Naturalist* **106,** 283–292.

Nevo, E. (1976). Adaptive strategies of genetic systems in constant and varying environments. In *Population genetics and ecology.* Karlin, E. and Nevo, E. (Eds). pp. 141–158. New York: Academic Press.

Nelson, K. & Hedgecock, D. (1979). Enzyme polymorphism and adaptive strategy in the decapod crustacea. *The American Naturalist,* in press.

Porter, K. R. (1972). *Herpetology.* London: W. B. Saunders.

Wake, D. B. & Özeti, N. (1969). Evolutionary relationship in the family Salamandridae. *Copeia* (1) 124–137.

White, M. J. D. (1973). *Animal cytology and evolution.* London: Cambridge University Press.

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BELLY COLOUR AND FOOT-WEBBING IN NEWTS OF THE GENUS *TRITURUS*

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INTRODUCTION

Of the many aspects of newt biology which have as yet received scant attention, two features seem particularly curious and to warrant consideration with regard to their function. These are: (i) the variable but often brilliant coloration of the lower body surface, and (ii) the extent to which the digits of the hind feet are webbed. Of the eight species of *Triturus* indigenous to Europe I shall be mainly concerned with but four, *T. vulgaris, T. helveticus, T. alpestris* and *T. cristatus* though I believe that the proposals made can readily be extrapolated to the other types.

OBSERVATIONS

Belly colour

One of the most well known features of several species of European newts is the bright colour patterning found on the ventral surface of the trunk; yet the significance of this character in evolutionary terms is not immediately obvious and has attracted little or no comment in standard texts. Belly colours usually seem to be of similar intensity in both sexes of any particular species and are therefore unlikely to be a secondary sexual characteristic such as, for example, are the crests, spots and lateral tail colorations of many male newts. Indeed, courtship stances adopted by males tend to obscure rather than promote observation of the belly area by the female (Smith, 1951). This and the ubiquity of similar belly colours in European newts also suggest that the feature is unlikely to be of importance in promoting correct interspecific recognition.

Another possible function of bright coloration, on the basis of many well-worked precedents, is to provide a warning to potential predators that the animal is either distasteful or capable of effective defence. The immediate problem here, of course, is that the colours are restricted in newts to a part of the body which is rarely visible to other animals. Both on land, where most newts spend the majority of their time, and even in the water it is unusual to obtain a clear view of a newt belly unless the creature is actually seized. Thus there is a contrast between newts and other European amphibians which display warning colours as *Salamandra salamandra* where the bright spots are clearly visible on the dorsal surface and *Bombina* species where the colours are restricted to the belly but behavioural mechanisms have evolved for displaying them to predators.

However, there are times in the lives of adult newts when belly colours could be of considerable defence value; these times occur during the regular journeyings to the surface of ponds which are necessary for respiration during the breeding season. Newts are forced to make these trips very frequently; detailed studies have been made with *T. cristatus* (Spurway & Haldane, 1953) and *T. vulgaris* (Halliday & Sweatman, 1976). Although there is considerable variation between individuals and a dependence upon levels of dissolved oxygen and water temperature, Halliday & Sweatman (1976) observed an average of one trip to the surface every 176 sec by male *T. vulgaris* in captivity. During this time any reliance upon dorsal camouflage colours or cautious, slow movements as defence mechanisms against detection by predators are sacrificed and for a few seconds the newt often becomes dramatically conspicuous. I suggest that it is only during this dangerous activity that the belly colours become clearly visible to other animals beneath the water (though still not to potential predators such as herons stationed above the surface) and that they have evolved to counter serious risk during these transient but frequent times of greatly increased vulnerability.

What types of predators might be influenced by such coloration? The most obvious and perhaps the only likely candidates would seem to be fish. Few other freshwater animals are capable of devouring adult newts, and fish are known to recognise bright coloration (most famously in the case of the three-spined stickleback *Gasterosteus aculeatus*). If belly colours have indeed developed as a defence against predatory fish, we would expect to find: (i) that newts live and breed in ponds containing fish: (ii) that there is some correlation between the use of fishponds by different species and the brightness of belly colour. We might also anticipate that the colours could warn of real effects in some species but represent only mimicry in others.

All of these predictions seem to be supported by the available facts, though verification certainly requires many more observations. Thus, *T. vulgaris* is widespread in garden ponds including those containing fish, although the newt populations were higher in those without fish (Mathias, 1974–5; Beebee, 1979). *T. cristatus* and *T. alpestris*, the two species with the most brightly coloured bellies, are also the two species which

frequent the deepest ponds (Steward, 1969). It seems likely that such ponds are more likely than shallow ones to be permanent and to support fish populations. Also, of course, trips to the surface by newts will be longer and exposure time greater. On the other hand, *T. helveticus* and *T. marmoratus* have much less striking belly colours and are often associated with shallow base-poor ponds in marginal habitats such as heaths and (in the case of the former species) highlands (Smith, 1951; Steward, 1969); they are perhaps the least likely to be faced with the problem of fish predation.

On what basis could the colour patterns deter predators? *T. cristatus* is well known for secreting distasteful toxins from warty protuberances on its skin (Smith, 1951); *T. alpestris* also has a markedly verrucose epidermis which may serve a similar function. More enigmatic is the situation regarding *T. vulgaris*. This species has a smooth skin and is predated by many animals, and it seems possible that in this instance we are looking at an example of mimicry in the newts. Both the European distributions and the preferred habitat types of *T. cristatus* and *T. vulgaris* are remarkably coincidental (Arnold, Burton & Ovenden, 1978); perhaps the latter has benefited from the distastefulness of the former.

Foot-webbing

Another interesting variable among European newts is the extent to which the hindlimb digits are webbed. Specifically, no webbing occurs in females of any species, and the males vary between *T. helveticus* (complete webbing) through *T. vulgaris* (fringe-webbing) to others such as *T. alpestris* and *T. cristatus* (no webbing). What is the use of this feature? It appears to play no part in courtship nor is it used in swimming since propulsion is provided almost entirely by rhythmic flexing of the tail.

Once again it is of interest to consider the behaviour of newts rising to the surface of a pond to breathe. As mentioned by Halliday & Sweatman (1976), two strategies are commonly observed in clear water: the animal may swim rapidly up to the surface and down again in a power-dive with vigorous tail-lashing; or it may adopt a more leisurely approach in which the descent is made under gravity. The latter method seems to be common in the absence of obvious danger, perhaps because it requires less energy and attracts less attention. In this instance the newt descends slowly with feet splayed out to give a parachute effect; it is during this period that I believe webbing of the hindfeet may be advantageous, the extent of the benefit depending upon the relative body proportions of the newt. Tritons have a potential problem with balance; the presence of a tail displaces the centre of gravity towards the posterior end of the trunk, and the anterior situation of the lungs leads to a gradation of buoyant densities along the length of the animal (accentuated after taking in air) such that the rear end tends to sinks faster in the water than the front. Anyone who has watched newts in ponds or aquaria cannot fail to have noticed this simple phenomenon. The tendency to divert from a horizontal stance during the descent could be a serious disadvantage, if only by restricting visibility of the forthcoming landing area and of potential predators lurking beneath.

Table I presents some measurements made on the relative proportions of four species of European newts. From the data, and in particular the ratio of body volume : tail area, it is clear that the contribution of the tail to the total bulk of the animal is much greater in *T. helveticus* and *T. vulgaris* males than in females of the same species and greater than in either sex of *T. cristatus* and *T. alpestris*. Various simplifying assumptions were made in the calculations; the widths of the tails were ignored, and the contributions of the crests of males to body volumes were not accounted. The latter, if done accurately, would undoubtedly emphasise the tail imbalance in *T. helveticus* since this species has virtually no crest on the body whereas *T. vulgaris* and *T. cristatus* have large dorsal protuberances. Thus, those individuals with the greatest tail imbalances (male smooth and palmate newts) are also those which have some degree of webbing on the hind feet and it is suggested that the latter feature has evolved to allow a more controlled descent after rising to the surface to breathe.

TABLE I. Measurements of newt body and tail dimensions. Three adult specimens of each sex from each of the four species were measured (*i.e.* 24 individuals) during the breeding season. Body volume was calculated from snout-vent length (l) and mid-body diameter (d) by approximating to a cylinder (i.e. using $\pi\left(\frac{d}{2}\right)^2 l$). Tail area was calculated from vent-tail tip length l_t and maximum height h by approximating to a triangle (females of all species and male *T. vulgaris*) or a rhombus (male *T. helveticus, T. alpestris* and *T. cristatus*); in both instances, tail area $= \frac{h}{2} l_t$. Measurements were in mm

Species	Sex	Body l (av.†)	Body d (av.)	Body Vol. (mm³)	Tail l_t (av.)	Tail h (av.)	Tail Area (mm²)	Body vol. / Tail area
T. alpestris	M	40.2	8.8	2445	39.0	7.7	150	16.2
	F	46.7	12.2	5459	43.2	6.0	130	42.0
T. helveticus	M	35.0	8.0	1759	39.0	9.5	185	9.5
	F	38.0	10.0	2984	40.0	5.0	100	29.8
T. vulgaris	M	46.5	8.5	2638	45.0	14.0	315	8.3
	F	45.0	11.0	4276	45.0	6.0	135	31.7
T. cristatus	M	66.4	14.0	10 221	58.9	15.0	441	23.2
	F	74.2	18.5	19 945	62.3	8.2	225	78.2

† average.

DISCUSSION

Many simple and well-known features of amphibians and reptiles still await attempts to explain their function. This paper represents an approach to two characteristics of European newts which have been conserved by selection throughout the ranges of the individual species and which must have some survival advantages. There are many other things which would repay investigation (*e.g.* the distinctly coloured vertebral stripe seen on many anurans and urodeles). Halliday (1975) has recently discussed the roles of dorsolateral ridges and webbed hindfeet in *T. vulgaris* and *T. helveticus* as well as the tail filament in males of the latter species. He sought to confirm webbing as a secondary sexual characteristic in the way originally proposed by Darwin (1871) on the basis that male smooth and palmate newts are more active during courtship than their counterparts in *T. alpestris* and *T. cristatus*. I reject this argument because simple observation denies a significant contribution to swimming by the hindlimbs of any of these species and suggest that the disproportionate weight distribution is a more likely cause. More experimental information may clarify the truths of these propositions.

An understanding of such details should benefit our overall comprehension of the biology of the animals in question. For example, if the evolution of belly colour in newts has been related to deriving protection from fish then it follows that at least in some circumstances newts should be able to breed successfully in fishponds. Cooke (1975) has suggested that goldfish in garden ponds may be incompatible with frogs due to heavy predation of the anuran larvae, but in a recent study both frogs *Rana temporaria* and newts *Triturus vulgaris* were found commonly with fish although the population sizes of newts and fish seemed to be inversely proportional (Beebee, 1979). It may be that the balance between these two classes of vertebrates in freshwaters is a delicate but not impossible one.

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I thank J.R. Griffin (Xenopus Ltd) for the supply of alpine newts *Triturus alpestris*.

REFERENCES

Arnold, E. N., Burton, J. A. & Ovenden, D. W. (1978). *A field guide to the reptiles and amphibians of Britain and Europe*. London: Collins.

Beebee, T. J. C. (1979). Habitats of the British amphibians (2): Suburban Parks and gardens. *Biological Conservation* **15,** 241–257.

Cooke, A. S. (1975). Spawn site selection and colony size of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *Journal of Zoology (London)* **175,** 29–38.

Darwin, C. (1981). *The descent of Man*. London: Murray.

Halliday, T. R. (1975). On the biological significance of certain morphological characters in males of the smooth newt *Triturus vulgaris* and of the palmate newt *Triturus helveticus* (Urodela: salamandridae). *Zoological Journal of the Linnean Society* **56,** 291–300.

Halliday, T. R. & Sweatman, H. P. A. (1976). To breathe or not to breathe; the newt's problem. *Animal Behaviour* **24,** 551–561.

Mathias, J. H. (1974–5). A survey of amphibians in Leicestershire gardens. *Transactions of the Leicestershire Literary and Philosophical Society* **69,** 28–41.

Smith, M. A. (1951). *The British amphibians and reptiles*. London: Collins.

Spurway, H. & Haldane, J. B. S. (1953). The comparative ethology of vertebrate breathing. I. Breathing in newts, with a general survey. *Behaviour* **6,** 8–34.

Steward, J. W. (1969). *The tailed amphibians of Europe*. Newton Abbot: David and Charles.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 63–64

MATERNAL CARE IN THE GHARIAL, *GAVIALIS GANGETICUS* (GMELIN)

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INTRODUCTION

For many years there have been unsubstantiated reports of varying degrees of parental care by crocodiles often reputedly as a result of first hand observation by native peoples. However, with the exception of nest-guarding, known in *Crocodylus niloticus* since the time of Aristotle and Pliny, scientific observations have almost all been made within the last few years.

Cott (1971) provided an outstanding historical review, with special reference to *C. niloticus*, documenting maternal care during incubation, defence of the clutch against predators, parental care at hatching time, including maternal reaction to vocalisation by the young, exhumation of eggs and release of young from the nest. Recent studies provided additional detail and often photographic corroborating evidence (see del Toro, 1969; Hadley, 1969; Pooley, 1969, 1974; Hunt, 1973, 1974; Singleton & Ogden, 1973; Lang, 1974; Pooley & Gans, 1976).

Cott (1961), in the section entitled "Parental Care", listed: "Nest-guarding, Release of the Young, and Care of the Young". He summarised the last-mentioned as follows: "While these stories may not be entirely reliable, there is good modern evidence for some after care". Recent work has provided the required documentation. Cott (1971) discussed transit of the young from nest to nursery and maternal defence of the young, the latter witnessed personally by Cott "on many occasions". At the inaugural meeting of the IUCN Crocodile Specialist Group in New York in March 1971, Dr Cott showed photographs detailing maternal care of the young *C. niloticus* in special nurseries.

Del Toro (1969) observed a captive male specimen of *Caiman crocodilus* to open the nest. Hunt (1973, 1975) observed captive *C. moreletii* to open the nest, take hatchlings in the mouth, and wash them free of eggshell and other debris. Singleton & Ogden (1973) using infra-red photography, published photographs showing a wild specimen of *C. acutus* opening its nest and carrying hatchlings to the water in its mouth, and Pooley (1974a, b) recorded photographically, in captivity, the release of hatchling *C. niloticus* from the nest and egg, and transport of the brood in the mother's gular pouch to the water.

There are few data on the American alligator (see Neill, 1971). Neill stated that apart from defence of the nest no maternal behaviour has been reported in the alligator by a reputable observer. However, Joanen (1969) noted that females returned to 9 out of 11 nests around hatching time and in 1970 he stated that two females freed the young but the actual process was not observed. A female in a breeding population of captive alligators was observed apparently opening a nest (Hertzog, 1975). Thirteen eggs were intact and there were remains of 6 which had hatched. Two intact eggs hatched within one hour of collection suggesting that the female was at the nest to liberate the young. A captive female returned hatchlings to the water after they had been removed (Kushlan, 1973).

Singh & Bustard (1977) described nest-guarding in the gharial. Most of the above cases deal with captive crocodiles.

It is suggested that there are four "categories" of parental care: (a) nest-guarding, (b) nest opening, (c) removal of young to the water, and (d) subsequent (prolonged) protection of the brood. The evidence presented for the Indian gharial refers to the last-mentioned, highest, category.

OBSERVATIONS

In mid-July 1974, in the North Indian State of Rajasthan, a female gharial was observed with her brood of 34 hatchlings in the wild state on 5 occasions. The female's length was approximately 4 m and the young 37–45 cm.

When first observed the young were lined up on the bank facing the water and basking in the sun. The female was resting in the shallows facing the young with her elongated jaws beside the bank. One juvenile rested on the female's head, another on her back just below the neck region, which was exposed from the water, and several others were swimming in close proximity. The sex of the adult was apparent from the absence of the "ghara", the nasal swelling which is a male secondary sexual character.

On my approach to about 10 m the female sank backwards into the water and the young jumped into the water. All juveniles dived, to reappear in the middle of the stream where they quickly "shoaled" like a group of fish orienting themselves to face up the small stream. The instinct to aggregate was well pronounced, the few stragglers soon joining the group. After several minutes the female surfaced beside them.

The female and young were in an ideal nursery area—Padajhor, a small *nulla* (side stream) leading into the Chambal River near Rawat Bhata, below a series of dams on the Chambal and above the barrage at Kotah. This stretch of the main river is known as Ranapratapsagar.

The nest was located on the opposite bank of the nulla scarcely 50 m from where the group was sighted. In contrast to normal nesting conditions (on steep sandbanks) the nest was in the mud of the nulla bank 1 m above the water level. As a result of damming the main river, the water level no longer recedes so much as formerly during the long, dry summer, so that sandbank islands in the middle of the Chambal River, once only inundated during high monsoonal floods, now remain submerged throughout the year. The female gharial had apparently adapted to the loss of these sandbanks, formerly used for nesting, by nesting in the mud of the nulla bank.

I was advised by Officers of the Rajasthan State Forest Service that the female guarded the nest from nearby in the nulla throughout the incubation period and that young had hatched some 4 to 6 weeks previously (information corroborated by noting hatching time in 1976).

The same female laid eggs in a closely adjacent area of the same nulla in 1973, guarded the nest and young until they were swept away by the artificially rapid rate of water rise in the nulla, resulting from sudden simultaneous opening of all, or most, of the dam gates. In 1975 the female did not nest. She nested again in 1976 in the same locality, guarded the nest and then "disappeared" with the young after they had hatched (information received from the Rajasthan State Forest Service).

DISCUSSION

The described female gharial guarded her nest in 1973, 1974 and 1976 and a lengthy period of post-natal care was a feature of her behaviour during 1974 and I am informed also during 1973 and 1976.

There was a close relationship between the mother and young, the young quickly aggregating to the female when she surfaced, and a closely synchronised behaviour exhibited by the hatchling group.

The survival advantages of maternal care of hatchlings by adult crocodilians are obvious, especially where hatchling size is tiny compared to the adult (difference in mass more than one thousand-fold). This is particularly so with virtually defenceless gharial hatchlings, compared to hatchling *Crocodylus*, which readily threaten potential aggressors.

It is suggested that maternal behaviour similar to that of *Gavialis* will be found in other species of crocodilians. However, the degree of maternal care may be expected to show considerable inter- and intra-specific variation.

REFERENCES

Cott, H. B. (1961). Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* **29,** 211–357.

Cott, H. B. (1971). Parental care in the Crocodylia, with special reference to *Crocodylus niloticus*. *IUCN Publs. N.S. Suppl. Pap.* **32,** 166–180.

F.A.O. (1974). *India: A preliminary survey of the prospects of Crocodile Farming.* UNDP/FAO. FO:IND/71/033. October 1974. Rome (based on the work of Dr H. R. Bustard).

Hadley, D. (1969). Breeding of crocodiles in Livingstone Game Park. *Puku: Occasional Papers of the Department of Wildlife and Fisheries, National Parks of Zambia* **5,** 226–228.

Herzog, H. A. (1975). An observation of nest opening by an American alligator *Alligator mississippiensis*. *Herpetologica* **31,** 446–447.

Hunt, R. H. (1973). Breeding Morelet's crocodile *Crocodylus moreletii* at Atlanta Zoo. *International Zoo Yearbook.* **13,** 103–105.

Hunt, R. H. (1975). Maternal behaviour in the Morelet's crocodile *Crocodylus moreletii*. *Copeia* 1975, 763–764.

Joanen, T. (1969). Nesting ecology of alligators in Louisiana. *Proc. Southeast Assoc. Game Fish Comm.* **23,** 141–151.

Joanen, T. (1970). A telemetric study of nesting female alligators on Rockefeller Refuge, Louisiana. *Proc. Southeast Game Fish Comm.* **24,** 175–193.

Kushlan, J. A. (1973). Observations on maternal behavior in the American Alligator, *Alligator mississippiensis*. *Herpetologica* **29,** 256–257.

Lang, J. W. (1974). Ecological studies of crocodilians in Florida. *Progress Rept. to NYZS* (July 1973–June 1974).

Neill, W. T. (1971). *The Last of the Ruling Reptiles.* Columbia Univ. Press, N.Y.

Pooley, A. C. (1969). Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus* in Zululand. *Lammergeyer.* **3,** 22–24.

Pooley, A. C. (1974a). Parental care in the Nile crocodile: a preliminary report on behaviour of a captive female. *The Lammergeyer* **21,** 43–45.

Pooley, A. C. (1974b). How does a baby crocodile get to water? *African Wildlife.* **28,** 8–11.

Pooley, A. C. & Gans, C. (1976). The Nile crocodile. *Scientific American* **234,** 114–124.

Singh, L. A. K. & Bustard, H. R. (1977). Studies on the Indian gharial (*Gavialis gangeticus* (Gmelin)). (Reptilia, Crocodilia) V: Preliminary observations on maternal behaviour, *Indian Forester* **103,** 671–678.

Singleton, C. & Ogden, J. (1973). Nights of the crocodile. *Audubon.* **75,** 32–37.

del Toro, A. (1969). Breeding of the spectacled caiman (*Caiman crocodylus*) at Tuxtla Gutierrez Zoo. *International Zoo Yearbook.* **9,** 35–36.

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PHARYNGEAL RESPIRATION IN AN AUSTRALIAN CHELID TORTOISE

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Cogger, (1967) wrote that virtually nothing is known concerning the biology of Australian freshwater tortoises (family Chelidae). Observations on *Chelodina expansa* Gray, the subject of the present note, indicate that it rarely leaves the water to bask in the sun. Even in waters where the snouts of tortoises are readily observed protruding from the water, the snout of *C. expansa* is seldom seen compared to that of other sympatric species (Goode, 1967).

Two adult females were observed in aquaria. A constant stream of water was seen to enter their nostrils and the floor of the mouth slowly dilated. Periodically the water was expelled by opening the mouth and contracting the hyoid muscles. Under resting conditions the tortoises were rarely seen to breathe air although they were able to do this by extending their necks even when resting on the bottom of the aquarium.

In order to confirm that oxygen was being extracted from the water, that is that pharyngeal respiration was occurring, measurements were made of dissolved oxygen tension in the aquarium using the Winkler method. The surface of the water was then covered by a layer of liquid paraffin and further measurements were made after noted time intervals. During this work the tortoises were confined below water in metal boxes with gauze covered ends and circulatory currents were maintained in the aquarium so that water samples would be characteristic of the aquarium as a whole. In all cases the dissolved oxygen tension fell indicating that the tortoise was extracting oxygen from the water. The following result for a 5 kg individual at 20°C is typical: initial oxygen tension 1.532 mgm, oxygen tension after 90 min 1.516 mgm (this is equivalent to an extraction of 4.7 ml of dissolved oxygen from the aquarium). It must be remembered that this figure is for the animal during diving when presumably bradycardia and oxygen saving are in operation (Andersen, 1961).

The respiratory movements differ greatly from that shown by soft-shells (*e.g. Trionyx* and *Amyda*, personal observations), which take *in* a continual current of water through the mouth and *expel* it from the snout. Not only is the water current reversed in *C. expansa* but it processes a much smaller volume of water. Water was expelled from the mouth about every 30 sec in *C. expansa* at 20°C whereas the mouth movements of soft-shells tend to be virtually continuous at this temperature like those of fish. It seems probable, therefore, that the mechanism is less efficient than in soft-shells. However, in view of the sluggish habits of *C. expansa* (see below) it is likely to be adequate. The continual slow stream of water entering the nostrils is sucked in by gradually relaxing the hyoid muscles thereby reducing the pressure in the buccal cavity.

Chelodina expansa is the largest Australian freshwater tortoise. Specimens reach a shell length in excess of 40 cm and a weight of 5–6 kg. The animals appear to be bottom dwellers and not efficient swimmers. The shell is heavy and shows little stream-lining. The creeks inhabited by *C. expansa* are often 10 to 12 ft deep and regular surfacing for air would involve considerable expenditure of energy. Furthermore, during the journey to and from the surface, and while at the surface, they are much more liable to predation hazard than while hiding on the bottom.

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I thank Peter Wilson for technical assistance and Jim Russel for providing the tortoises.

REFERENCES

Andersen, H. T. (1961). Physiological adjustments to prolonged diving in the American alligator (*Alligator mississippiensis*). *Acta physiol. scand.* **53,** 23–45.

Cogger, H. G. (1967). *Australian reptiles in colour.* Sydney: Reed.

Goode, J. (1967). *Freshwater tortoises of Australia and New Guinea.* Melbourne: Lansdowne Press.

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LETTERS TO THE EDITOR

ALBINO MALE *RANA TEMPORARIA* WITH BLACK NUPTIAL PADS

In March 1979, Colvin Osborn, a pupil at Portsmouth Grammar School, discovered an albino adult male common frog *Rana temporaria* in his garden. The specimen was captured on 20 March 1979 and proved to be a typical albino, with pale gold dorsal surface and speckled white ventral surface. The pupils of the eyes were pink and there were pink blotches on the fore limbs. A feature of special interest was the presence of distinct black nuptial pads.

The enclosed photographs were taken a few days later by Mr M. Baggs. The original colour slides show that the nuptial pads include numerous small black excrescences from the skin.

The site of capture of the frog was a pond in a private garden adjacent to farm land on the southern slopes of Portsdown Hill above Porchester, Hants., SU 618068. Several rather pale coloured *Rana temporaria* have been observed there but no other albinos. Some newly-emerged froglets were observed during July 1979 which were also unusually pale compared with other froglets in this population.

When placed with a gravid female in the laboratory, the albino male readily entered amplexus which was maintained for four days but unfortunately no eggs were laid.

On 30 March 1979 the black skin of the nuptial pads was shed. The weight of the male was found to be 24.8 g and its length from snout to cloaca was 64 mm.

The male albino frog was transferred to a vivarium at Cumberland House Museum, Eastern Parade, Southsea where it has been maintained in excellent condition by the curator Mr P. Sewell and his staff. It is hoped that the frog may breed in captivity during the 1980 season with females from the same natural population. Mr Sewell has made interesting observations of the inefficiency of this albino frog in catching its prey compared with normal frogs in the same vivarium and he suggests that this may be attributable to poor visual ability.

I understand that the occurrence of black nuptial pads has been recorded in albino *Xenopus laevis* but I have been unable to find definite records of this

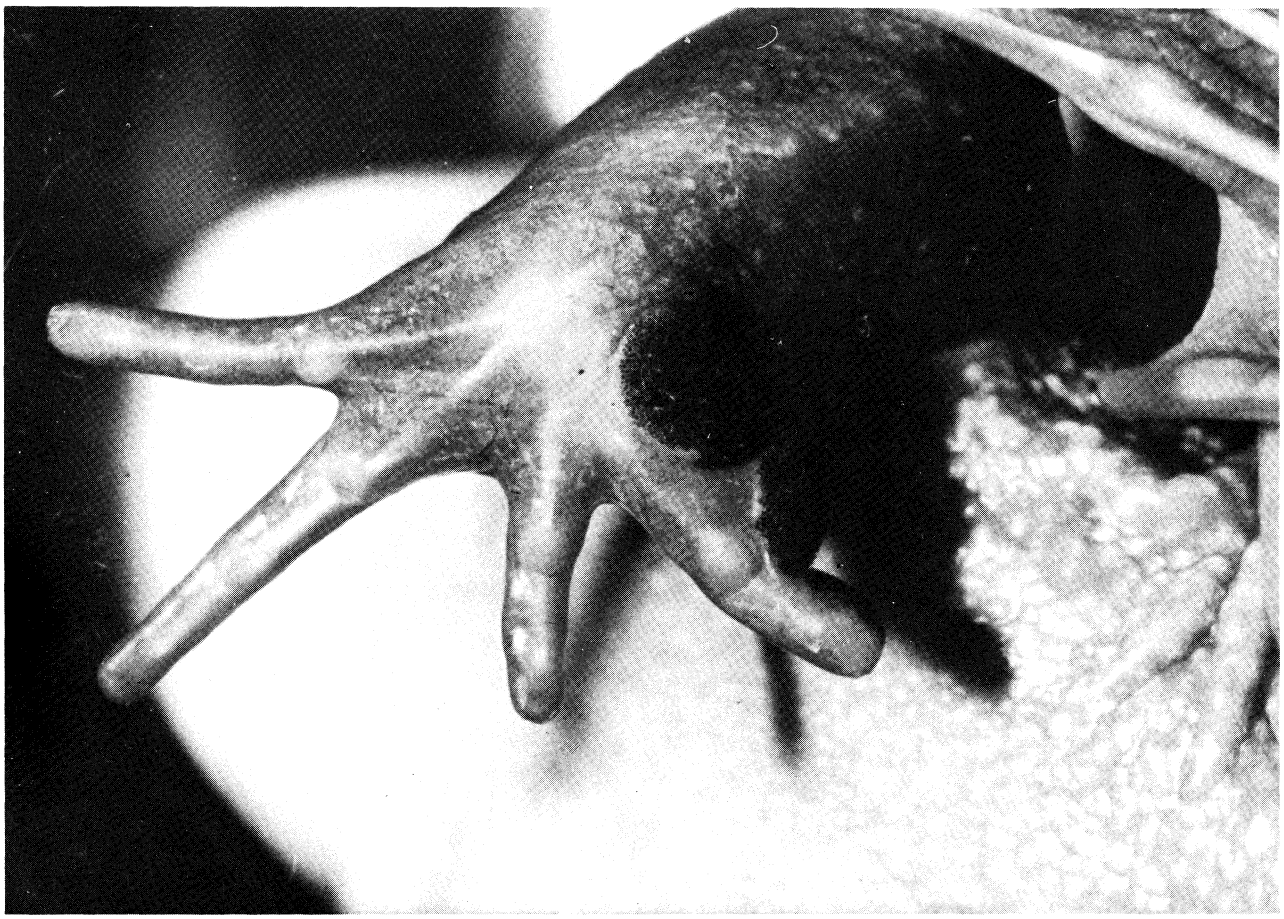

FIG. 1. *Rana temporaria*, albino male, general view.

phenomenon in *Rana temporaria*. I would be grateful if readers can supply any further information. I am particularly interested in the genetic basis of the appearance of the black colouration in an otherwise albino specimen.

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EXTINCTION OF THE GHARIAL (*GAVIALIS GANGETICUS*) IN BHUTAN

The gharial formerly occurred in the portion of the Manas River which flows through the Kingdom of Bhutan, northern Bangladesh and Assam, and in the adjacent stretch of the river within India. Adults were last seen there during the 1960s. Recent field work (H. R. Bustard, 1979, *Bhutan: crocodile conservation and commercial farming*. Project Working Document FO:DP/BHU/78/003, Food and Agriculture Organisation of the United Nations: Rome) indicated that the gharial no longer occurs there today, and the animal can be regarded as extinct within Bhutan. Measures to re-establish the gharial in this region, which affords an ideal habitat for the species, are strongly recommended.

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BOOK REVIEWS

BIOLOGY OF THE REPTILIA, Volume 8, *Physiology* B. Edited by C. Gans and K. A. Gans (1979). London and New York: Academic Press, £35.00.

In the Preface to this, the latest volume in an admirable series, Dr. Gans refers to the "information explosion" that is occurring in connection with venoms. A continuous and rapid growth of knowledge, such as this, creates great difficulties for anyone attempting to summarise the literature. Those who are acquainted with the qualities of previous *Biology of the Reptilia* volumes will not be surprised by the superlative skill with which the challenge is tackled.

Following an introductory chapter by the series editor entitled "Reptilian venoms: some evolutionary considerations", there are sections by various authors on oral glands, chemistry, immunology and pharmacology of reptilian venoms, commercial production of anti-snake bite serum and the physiology of the digestive tract. While each chapter is impressive, Dr Elliott's one on the chemical and immunological aspects, which contains many helpful tables and cites over 1100 references, must rate as a *tour de force.* Special mention must also be made of the chapter on the digestive tract by Dr Skoczylas both for its originality of approach (in emphasising the influence of temperature on the digestive process) and also for its clear exposure of the gaps in our knowledge of the physiology of this system in reptiles.

I have detected a few anomalies and a small number of typographical errors, some of the more potentially misleading ones being in the list of members of poisonous snake families compiled by Dr Gans where the same species (*loriae*) is listed under both *Apistocalamus* and *Toxicocalamus*. *Apistocalamus* was in fact relegated to a subgenus of *Toxicocalamus* by McDowell in 1969. *Elaps* is used instead of *Homoroselaps* for the species *dorsalis* and *lacteus* although Smith and Smith 1976 proposed the shift of the name *Elaps* to the synonymy of *Micrurus*. On page 356 mention is made of erabutoxins *a* and *b* of *Laticauda laticaudata* but these toxins are only found in *L. semifasciata* (as is made clear in Table XII in the same chapter). These blemishes, however, scarcely detract from the excellence and usefulness of the work.

I have no hesitation in recommending the volume notwithstanding the fact that at least two other books have very recently been published on venoms namely Tu (1977) *Venoms: Chemistry and Molecular Biology* (John Wiley and Sons) and Chen-Yuan Lee (ed.) (1979) *Snake Venoms* (Handbook of Experimental Physiology, Volume 52). The information available in Tu (1977) overlaps to a large extent that appearing in the chemical and pharmacological sections of *Biology of the Reptilia* **8**, but other topics covered extensively by this volume, including immunology, are treated briefly or not at all by Dr Tu. I have, unfortunately, not seen Chen-Yuan Lee (1979) in its entirety and am therefore not able to make a comparison.

The price of the work may seem prohibitive but it is a superb treatment of one of today's most active areas of herpetological research and therefore adds further to the importance of an already classic serial publication.

C. MCCARTHY

EARLY HERPETOLOGICAL STUDIES AND SURVEYS IN THE EASTERN UNITED STATES. One volume, $40.00. HERPETOLOGICAL EXPLORATIONS OF THE GREAT AMERICAN WEST. Two volumes $75.00. Edited by K. Adler (1978). New York: Arno Press.

Although these three volumes are related they do not represent a simple division of early American Herpetology into two regions in the manner of field guides. Development and exploitation of the Eastern Seaboard pre-dated the opening of the West by a century and the earliest reports date from the great Naturalist Period of 1725 to the 1800's. Consequently, the content of the first book varies from the descriptive, with legendary overtones, to the meticulously detailed cataloguing and precise engravings that represent some of the finest work of the museum pioneers. The perseverance and dedication of these early explorers verged on the fanatical, many undergoing great discomfort and personal suffering in pursuance of their studies. Their names are now revered and preserved in the language of taxonomy; some are legendary. What extraordinary people they were.

The first meeting between Audubon and the spectacularly colourful Constantine Rafinesque (alias Schmaltz) terminated with the latter leaping in wild frenzy, and stark naked, around his host's log cabin in pursuit of a bat, Rafinesque chose Audubon's valuable violin as a Bat-swat and demolished the instrument in the excitement of the chase.

The work of Mark Catesby, who first arrived in America in 1712, serves as an example of the dedication and industry of these early pioneers. His classic work *Natural History of Carolina, Florida and the Bahama Islands*, took twenty years to produce, whilst the author maintained himself as a nurseryman. His meagre income forbade him from employing a professional engraver so he was forced to learn the art of engraving himself and then to hand-colour the large plates. The magnitude of this task is matched only by the exquisite artistry he applied to the task; each set consists of 220 plates and he produced 156 sets, a total of 34 320 separate plates.

The volumes dealing with the West span the nineteenth century and the self-supporting amateur is replaced by the Government Employee engaged on Military/Geographical Surveys. Inevitably, lists and diagnoses are prominent in many of the papers which lack the excitement of the first volume. However, compensation is provided by the numerous line drawings which accompanied the original papers.

My only criticism of the entire work concerns the quality of production. Why, when the books clearly make a set, was it deemed necessary to make the Eastern volume on a smaller format, and why, when dealing with a potential classic, use such shoddy paper that reduces some of the drawings to little more than dark smudges?

The content and scope of the complete works cannot be faulted and to the serious student of American Herpetology these three volumes present a unique opportunity to acquire a collection of many of the classics of historical literature. Each volume is preceded by a masterly, but far too brief, introduction by the editor and the list of authors includes, amongst others, Audubon, Holbrook, Say, Yarrow, Rafinesque, Dekay and Baird.

D. BLATCHFORD

COMMON INDIAN SNAKES, A FIELD GUIDE. By Romulus Whitaker (1978). 154 pp. Macmillan Co. of India Ltd. £3.50.

There is a great imbalance in herpetological literature, and hence general awareness, between the Western and Eastern Hemispheres. So many books now exist on the fauna of North America, Europe and to a lesser extent Australasia, that the would-be purchaser has the luxury of choice. The East, and its herpetofauna, is still very much the Mysterious Orient so anything that will shed light into this gloom of ignorance is welcome. Whitaker's slender, but modestly priced, book is, even if a rather sombre volume, truly excellent. It succeeds because of its size and scope; only thirty species are covered in detail but extensive tables list two hundred and thirty species by Latin and English names and location.

Each of the detailed descriptions is accompanied by a dull, but always adequate, monochrome plate and follows the format; Distinctive Features, Length, Description, Distribution, Habitat, Habits, Young, Food, Status and Venom. Apart from the Checklist other tables list the vernacular names (in five languages) and rainfall in the principal districts. There is a key, a useful bibliography plus chapters on natural history: the book is designed for the layman who might encounter the snakes in the wild. Apart from the horrific advice on first aid for snake bite this book is essential reading for anyone with an interest in snakes.

D. BLATCHFORD

RARE AND ENDANGERED BIOTA OF FLORIDA—AMPHIBIANS AND REPTILES. Volume 3. Edited by R. W. McDiarmid (1979). 74 pp. University Presses of Florida. $5.50.

The Florida Committee on the Rare and Endangered Plants and Animals have produced four volumes in a series of seven that eventually will encompass the flora and fauna of that State; volume 3 is concerned with the amphibians and reptiles.

This is an unusual book in many respects, not the least being the dimensions (it measures 195 × 270 × 5 cm thick). It is written by a group of experts and edited by R. W. McDiarmid of the University of Florida. The species described are grouped into one of five categories, Endangered, Threatened, Rare, Species of special concern and Status Undetermined, and apart from a division into amphibians and reptiles the book is laid out according to these headings. Thus the Endangered Reptile section consists of 1 Crocodilian followed by Chelonians and then 2 Snakes; initially this intermixing of Orders is somewhat confusing. However, this does not detract from the thoroughness of each description nor the overall excellence of the book.

Although designed for the specialist there is much here to appeal to anyone with a general interest in American Herpetofauna principally because so much emphasis is placed on descriptions of habitat. One brief chapter is concerned exclusively with the major habitat types found in Florida.

Each animal is shown in monochrome together with a precise distribution map. The text follows the pattern; Description, Range, Habitat, Life History, Ecology, Unique characteristics, Basis of Status Classification and recommendations for protection. In addition a short list of selected references accompanies each description.

This book represents an immense effort by a large number of people who are to be congratulated on the excellence of their achievement. They have created a work that speaks eloquently of their authority.

D. BLATCHFORD

ANNOTATED CHECK-LIST WITH KEYS TO THE ADULT AMPHIBIANS OF HONG KONG. By J. D. Romer (1979). 14 pp. *Mem. Hong Kong nat. Hist. Soc.* No. 15.

Copies of this publication are available from: The Hong Kong Natural History Society, c/o Department of Zoology, University of Hong Kong, Hong Kong. HK$10 or £1.00 per copy plus postage. Remittances from U.K. by British Postal Order, please.