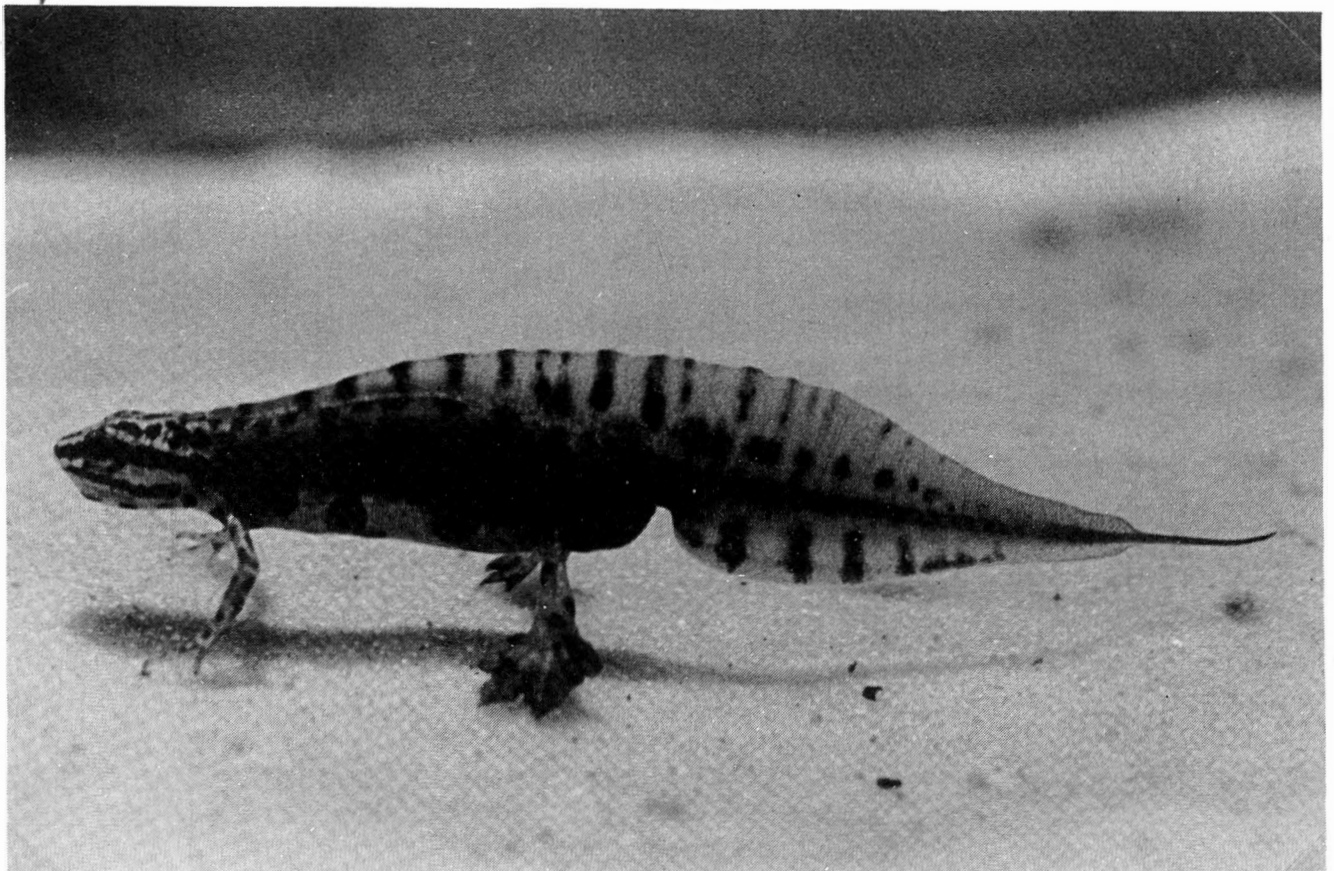


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ANNOUNCEMENTS

Opinions published in the Bulletin of Zoological Nomenclature.

The following Opinions were published on 27 March 1990 in Vol. 47, Part 1 of the *Bulletin of Zoological Nomenclature*.

Opinion 1585 *Ascalabotes gigas* Bocage, 1875 (currently *Tarentola gigas*; Reptilia, Squamata): specific name conserved

The following Opinions were published on 29 June 1990 in Vol. 47, Part 2 of the *Bulletin of Zoological Nomenclature*.

Opinion 1604 ICHTHYOPHIIDAE Taylor, 1968 (Amphibia, Gymnophiona): conserved

Opinion 1605 *Thorius pennatulus* Cope, 1869 (Amphibia, Caudata): specific name conserved

Applications published in the Bulletin of Zoological Nomenclature.

The following applications were published on 29 June 1990 in Vol. 47, Part 2 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD.

Case 2693 *Trionyx sinensis* Wiegmann, 1834 (Reptilia, Testudines): proposed conservation of the specific name

Robert G. Webb

*Department of Biological Sciences and Laboratory for Environmental Biology,
University of Texas at El Paso, El Paso, Texas 79968-0519, U.S.A.*

Abstract. The purpose of this application is to conserve the name *Trionyx sinensis* Wiegmann, 1834 for a turtle by the suppression of the senior subjective synonym *Testudo rostrata* Thunberg, 1787.

ADVERTISEMENTS

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REVIEW: A REVIEW OF THE SMOOTH NEWT (*TRITURUS VULGARIS*) SUBSPECIES, INCLUDING AN IDENTIFICATION KEY

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(Accepted 18.8.89)

ABSTRACT

A taxonomic revision of the Smooth Newt, *Triturus vulgaris* leads to the recognition of seven subspecies: *T. v. vulgaris*, *T. v. meridionalis*, *T. v. graecus*, *T. v. lantzi*, *T. v. ampelensis*, *T. v. kosswigi* and *T. v. schmidtlerorum*. *T. v. borealis* and *T. v. tataiensis* are considered to be synonyms of *T. v. vulgaris*. An identification key and updated distribution map is provided. These subspecies are recognised by characters which represent non-independent patterns of racial variation, probably produced as a direct consequence of allopatric divergence in isolated glacial refugia. Based on the biological species concept there can be no justification in raising these taxonomic units to species rank.

INTRODUCTION

The recognition of subspecies has always been considered to be of importance to taxonomists working on European Salamandrids. Many species show clear racial differences between geographical areas, particularly within the genus *Triturus* (see Thorn, 1968). At present there are over 30 described subspecies of European newts, although this will certainly be reduced following a full revision of the group. The Smooth newt *Triturus vulgaris* is exceptional among the *Triturus* species in that the degree of secondary sexual character variation seen between subspecies is far greater than that found in the other 11 species. This has resulted in the description of many *T. vulgaris* subspecies and, in the past, some considerable taxonomic confusion.

The aims of this paper are to review and revise the subspecific taxonomy of the Smooth newt, *Triturus vulgaris*, and discuss the values and applications of the subspecies concept. This taxonomic study represents part of a more detailed comparative investigation of the subspecific evolution of courtship behaviour and secondary sexual characters in the Smooth Newt (Raxworthy, 1989 and in prep.).

A HISTORICAL SUMMARY

The original descriptions of the *T. vulgaris* subspecies were based on museum material which was considered to show significant variation between different geographical populations. Usually material was available to museum taxonomists in only very small samples, and this has sometimes resulted in subspecies having been described based on insignificant variation. Male secondary sexual characters have been used extensively to recognise racial variation, indeed most racial variation is restricted to these characters in *T. vulgaris*. These secondary sexual characters include the crest, tail tip, toe flaps, body cross section, dorso-

lateral folds and pigmentation of the male (Fig. 1). However all these features only fully develop during the breeding season when newts are aquatic. Unless fully developed they are of little taxonomic value. This problem is discussed by Steinitz (1965) in relation to *T. vittatus* taxonomy. He found that only two of the five described subspecies were in fact valid and blamed earlier workers for using small samples and animals which were clearly out of full breeding condition.

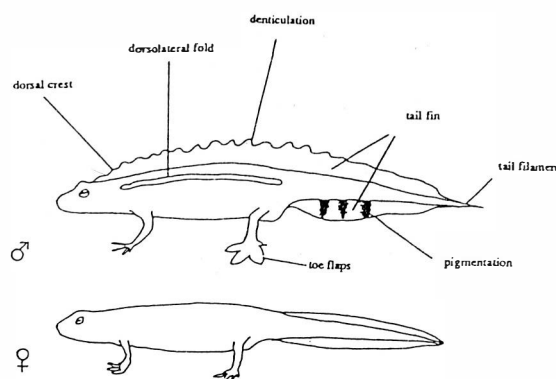


Fig. 1 Some sexually dimorphic characters of *Triturus vulgaris*.

Secondary sexual characters such as the crest, toe flaps and tail filament may all regress over a matter of days if animals are kept under stressful conditions or starved. Also, these characters are not fully developed at the very start and end of the aquatic breeding period (Verrell, Halliday and Griffiths, 1986; Griffiths and Mylotte, 1989).

T. vulgaris was originally described by Linnaeus in 1758 which he placed in the genus *Lacerta* with the European lizards. His form became the first nominal subspecies upon the discovery more than one hundred and twenty years later of the next subspecies, *T. v. meridionalis* which was described by Boulenger (1882). At around the turn of the century many more

SUBSPECIES	ORIGINAL NAME AND SYNONYMS
<i>Triturus vulgaris vulgaris</i>	<i>Lacerta vulgaris</i> (Linnaeus 1758) <i>Triton vulgaris</i> subsp. <i>typica</i> forma <i>Kammereri</i> (Wolterstorff 1907) <i>Triton vulgaris</i> forma <i>Schreiberi</i> (Wolterstorff 1914) <i>Triturus vulgaris borealis</i> Kauri 1959 <i>Triturus vulgaris tataiensis</i> Dely 1967
<i>Triturus vulgaris meridionalis</i>	<i>Molge vulgaris</i> subsp. <i>meridionalis</i> (Boulenger 1882) <i>Molge vulgaris</i> subsp. <i>kapelana</i> (Méhely 1905) <i>Molge vulgaris Boulengeri</i> (Dunn 1918)
<i>Triturus vulgaris graecus</i>	<i>Triton vulgaris</i> subsp. <i>graeca</i> (Wolterstorff 1905) <i>Triton vulgaris</i> subsp. <i>graeca</i> forma <i>corcyrensis</i> (Wolterstorff 1908) <i>Triton vulgaris</i> subsp. <i>graeca</i> forma <i>Tomasinii</i> (Wolterstorff 1908)
Hybrid <i>T. v. vulgaris</i> x <i>T. v. graecus</i>	<i>Triton vulgaris</i> subsp. <i>dalmatica</i> (Kolombatovic 1907) <i>Triton vulgaris</i> subsp. <i>intermedia</i> (Kolombatovic 1907)
<i>Triturus vulgaris lantzi</i>	<i>Triturus vulgaris</i> subsp. <i>typica</i> forma <i>Lantzi</i> (Wolterstorff 1914)
<i>Triturus vulgaris ampelensis</i>	<i>Triturus vulgaris ampelensis</i> Fuhn 1951 <i>Triturus vulgaris vulgaris</i> (ampelensis-Form) Fuhn and Freytag 1952
<i>Triturus vulgaris kosswigi</i>	<i>Triturus vulgaris kosswigi</i> Freytag 1955
<i>Triturus vulgaris schmidtlerorum</i>	<i>Triturus vulgaris schmidtleri</i> Raxworthy 1988

TABLE 1: Original subspecific names and post-1882 synonyms of *T. vulgaris*.

subspecies were described. The most prolific taxonomist of this time was Wolterstorff who described in all a total of five forms, although only two are still recognised. The post-1882 synonyms are given on Table 1 for all recognised subspecies. All earlier synonyms refer to the nominate form and are given by Mertens and Wermuth (1960). A brief summary of recent taxonomic changes since then is given below:

Mertens and Wermuth (1960) included *T. italicus* as a subspecies of *T. vulgaris*, despite the detailed and well illustrated description given by Peracca (1898a,b) who rightly considered this to be a good species. Mertens and Wermuth's taxonomic view was followed by Steward (1969) in his review of the European Urodeles. However Mancino (1961) provided strong evidence that *T. italicus* was a good species based upon his hybridisation experiments between *T. italicus* and *T. vulgaris*. This was supported by Thorn (1968) who gave *T. italicus* species rank in his review of *Triturus* and this has been followed by all more recent studies.

Thorn (1968) recognised all the presently subspecies with the exception of *T. v. schmidtlerorum* (which had not been described then) and also *T. v. tataiensis* (which had only just been described by Dely in 1967). He also included three other subspecies: *T. v. schreiberi*, *T. v. dalmaticus* and *T. v. borealis*.

The situation regarding the Dalmatian coast *T. vulgaris* subspecies remained confusing with five subspecies having been described from this region of Yugoslavia. This is especially evident when referring to the descriptions given by Steward (1969) for *T. v. dalmaticus*, *T. v. graecus* and *T. v. schreiberi*. The differences he gives (based on the original descriptions) are strikingly unconvincing. Schmidtler and Schmidtler (1983) finally resolved the taxonomic status of these

forms by making a detailed survey of the Adriatic region. They considered *T. v. schreiberi* to be a synonym of *T. v. vulgaris*, which they found established in the type locality area. *T. v. dalmaticus* and *T. v. intermedia* are considered to be forms collected in the intergradation zone between *T. v. vulgaris* and *T. v. graecus*, while *T. v. tomasinii* is a synonym of *T. v. graecus* (Schmidtler and Schmidtler 1983).

The latest subspecies to be described is *T. v. schmidtlerorum* collected from Turkey (Raxworthy, 1988). It had been suspected earlier to deserve subspecific status by both Eiselt (1966) and Schmidtler and Schmidtler (1967), although this view was not supported by Özeti (1964). The subspecific name of this subspecies has been changed from *Triturus vulgaris schmidtleri* to *Triturus vulgaris schmidtlerorum*, because this subspecies was named after two people: J. J. Schmidtler and J. F. Schmidtler and therefore the original subspecific name was grammatically incorrect (Raxworthy, 1989).

A population of *T. vulgaris* discovered in the Sava Valley, north Yugoslavia, resembles the nominate form but may deserve subspecific status (Schmidtler and Schmidtler 1983) following further studies. There is also a possibility that specimens from the Danube basin may also represent another new subspecies (Schmidtler, pers. com.).

PROPOSED REVISION

Triturus vulgaris borealis Kauri 1959

T. v. borealis was recognised by its low crest, smaller body spots, general marked 'longitudinal ridges' on the back and in some specimens a thread like appendage (Gilsén and Kauri 1959). The description

was based on 11 males caught in Northern Sweden. I have examined six specimens of *T. v. borealis* kindly loaned to me by J. Elmberg which were collected from Stokärret (Skeleftea), Alnön (Medelpad), Vindelgransele (Lykselle) and Strigtjärn (Sabrå). There is no evidence of true dorso-lateral folds or a tail filament (as defined by Raxworthy, 1988) and body pigmentation does not differ significantly from the nominate form. The crest however is slightly lower (mean = 1.4mm, $n = 6$) than that seen in good breeding condition males from England (mean = 2.5mm, $n = 19$), although the small sample size does not allow a firm conclusion to be made on this. Kauri found that this northern race is subject to a poor diet and has a shorter period of activity than populations further South. Crest development is known to be dependent upon food availability (Halliday, 1977) and therefore the slightly lower crest seen in *T. v. borealis* might be due to local environmental factors. Translocation experiments would readily support or reject this hypothesis. However based on the material examined I conclude that these specimens belong to the nominate subspecies.

Triturus vulgaris tataiensis Dely 1967

Dely (1967) described a paedomorphic subspecies *T. v. tataiensis* from Tata, Hungary. The adults had external gills and the males had poorly developed secondary sexual characters. This paedomorphic condition, which is seen in *T. vulgaris* is most suitably be described as facultative partial neoteny (Raxworthy, 1989, in prep.). From the description of *T. v. tataiensis* it is clear that it is separated from the nominate form by paedomorphic features only. Paedomorphic specimens examined during this study from Smilic, Yugoslavia, show similar features, although they belong to the nominate subspecies.

The paedomorphic and metamorphic condition represent the two states of a polymorphism. The phenotypic expression of the paedomorphic condition is known to be affected by environmental conditions (e.g. Gabrion, Sentein and Gabrion, 1977), since paedomorphs usually undergo metamorphosis when subject to laboratory conditions. The unstable nature of the paedomorphic condition and the fact that it only represents a different morph within a population invalidate the use of this character being used in taxonomic studies regarding the description of subspecies. The paedomorphic *T. v. vulgaris* described by Dely (1967) as *T. v. tataiensis* should therefore be rejected unless other evidence can be produced which demonstrated clear differences between this form and the nominate subspecies.

Gislén and Kauri (1959) for similar reasons questioned on what basis Radovanovic (1951a) distinguished his new paedomorphic subspecies of *T. alpestris*. They presumed it was because these animals were permanently paedomorphic, although in fact Radovanovic (1951b) himself reports that some captive animals did undergo partial metamorphosis before they died. Rocek (1974), Gabrion *et al* (1977) and Breuil and Thuot (1983) all have considered paedomorphosis to be an unreliable indicator of subspecific status for *Triturus* newts, and Breuil and

Guillaume (1984) have found the electrophoretic studies were unable to separate the metamorphic form from the paedomorphic form.

THE *TRITURUS VULGARIS* SUBSPECIES

A total of seven subspecies are recognised in this study. These are:

Triturus vulgaris vulgaris (Linnaeus 1758)

Triturus vulgaris meridionalis (Boulenger 1882)

Triturus vulgaris graecus (Wolterstorff 1905)

Triturus vulgaris lantzi (Wolterstorff 1914)

Triturus vulgaris ampelenis Fuhn 1951

Triturus vulgaris kosswigi Freytag 1955

Triturus vulgaris schmidtlerorum Raxworthy 1988

A brief description of the seven recognised subspecies is presented below. Because fully developed male secondary sexual characters are used to distinguish subspecies, only these features are considered here. Body size is not a diagnostic feature of subspecies (Raxworthy, 1988). Because of the well known differences in body size between populations of newts (Bell, 1966, Tucic and Kalezic, 1984, Clifford, 1986) body size is considered to be largely influenced by local environmental factors.

Triturus vulgaris vulgaris (Linnaeus 1758)

Common Smooth newt

The dorsal crest is high along the body (>1.0mm at mid-body) and deeply notched by rounded denticulations. There is no tail filament, the tail usually tapers to a blunt end. There are no dorso-lateral folds. The body cross section is rounded. The toe flaps are moderately or poorly developed. Fig. 2 and Fig. 8.

Triturus vulgaris meridionalis (Boulenger 1882)

Southern Smooth newt

The dorsal crest is low and smooth edged (<1.5mm at mid-body). The tail tapers to a fine point but there is no tail filament. Weak dorso-lateral folds are present. The body cross section is square-shaped dorsally. The toe flaps are strongly developed. Fig. 3.

Triturus vulgaris graecus (Wolterstorff)

Balkan Smooth newt

The dorsal crest is low (<1.0mm at mid-body) and smooth edged. The tail ends in a long filament. The dorso-lateral folds are strongly developed and the body cross section square-shaped dorsally. The toe flaps are strongly developed. The lower margin of the tail fin is usually unspotted. The belly has many small spots. Fig. 4.

Triturus vulgaris lantzi (Wolterstorff 1914)

Lantz's Smooth newt

The dorsal crest is of medium height (>1.0mm at mid-body) and denticulated by almost spine shaped serrations. The tail gradually tapers to a long fine thread (but there is no tail filament as defined by Raxworthy, 1988). No dorso-lateral folds. The body cross section is slightly square-shaped dorsally. The toe flaps are moderately well-developed. Fig. 5.

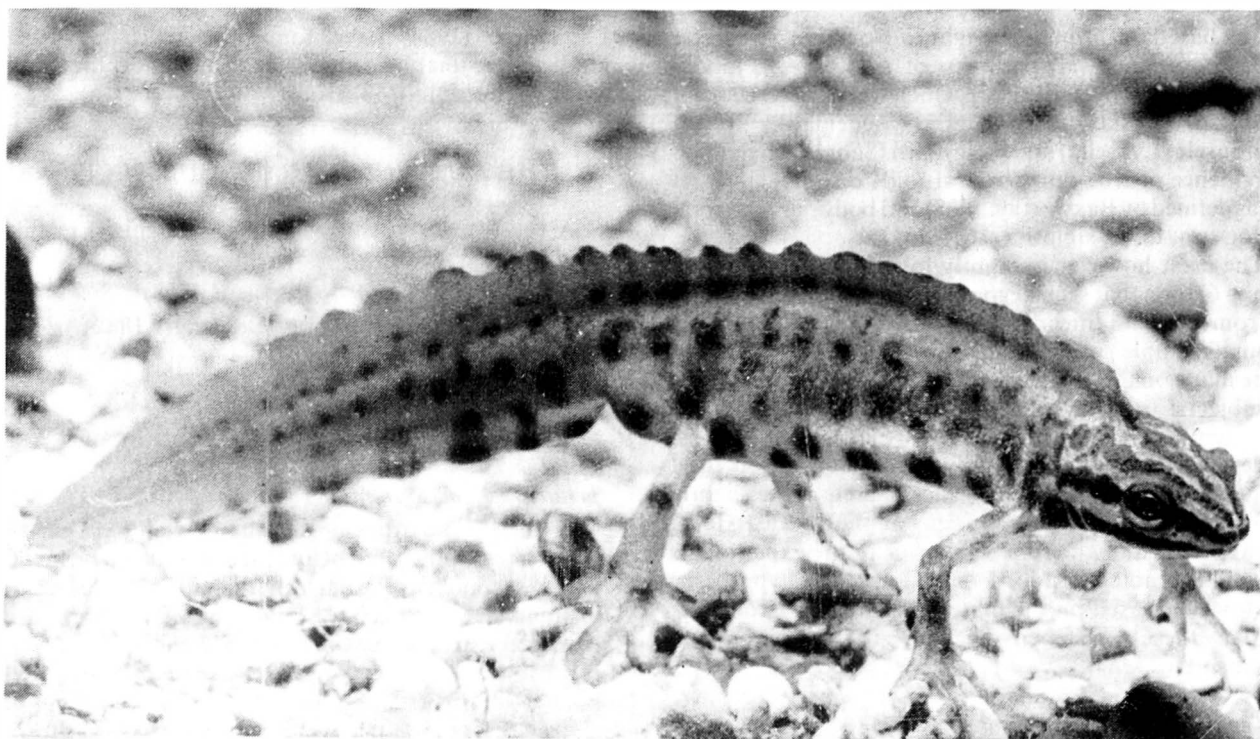


Fig. 2 *T. v. vulgaris*, Oxford, England. (T. R. Halliday).

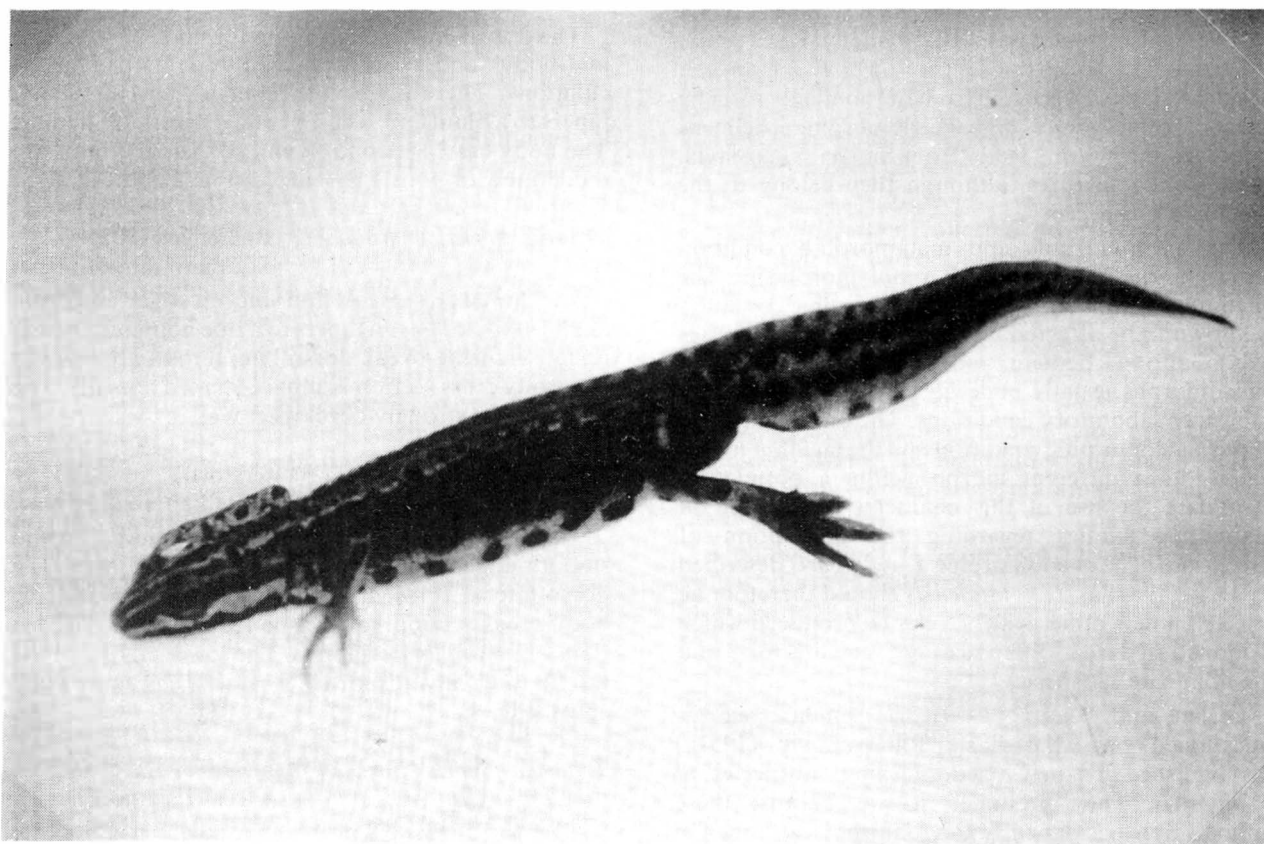


Fig. 3 *T. v. meridionalis*, Torino, Italy. (C. J. Raxworthy).

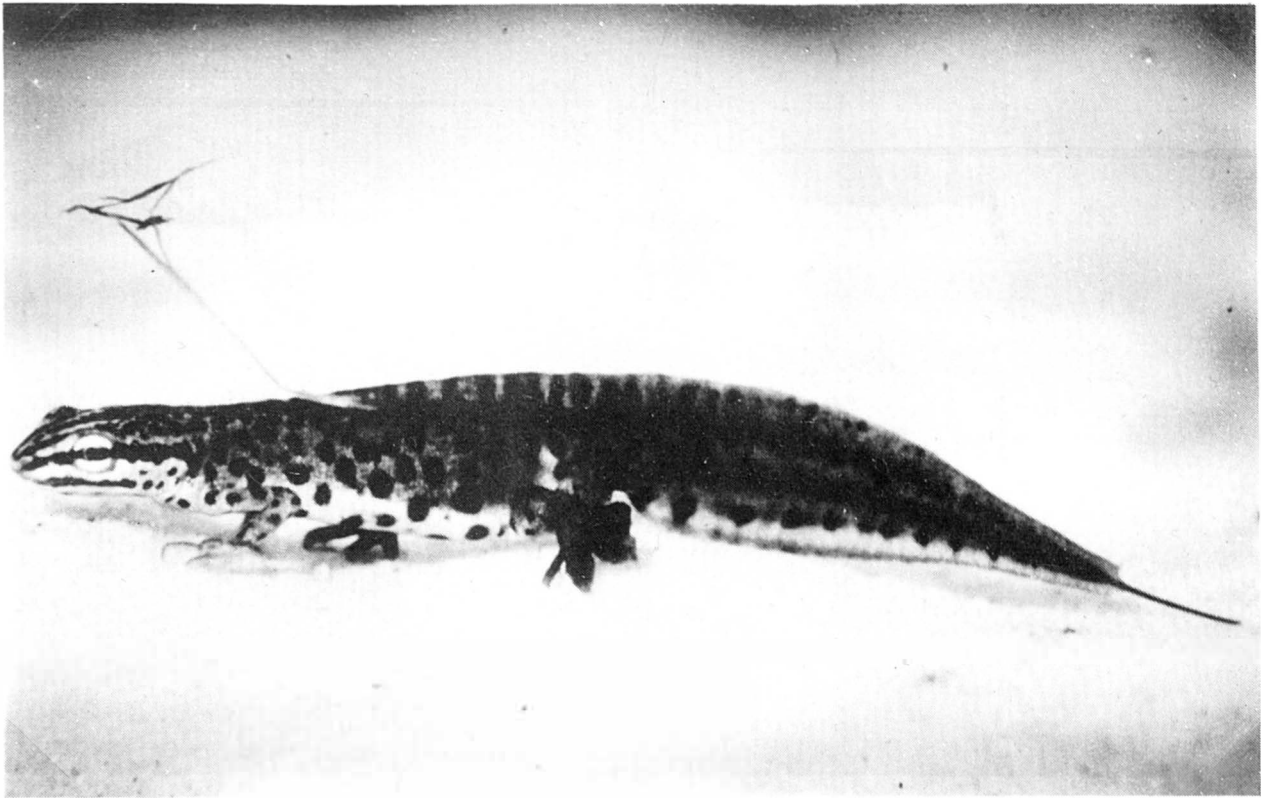


Fig. 4 *T. v. graccus*, Vilusi, Yugoslavia. (C. J. Raxworthy).

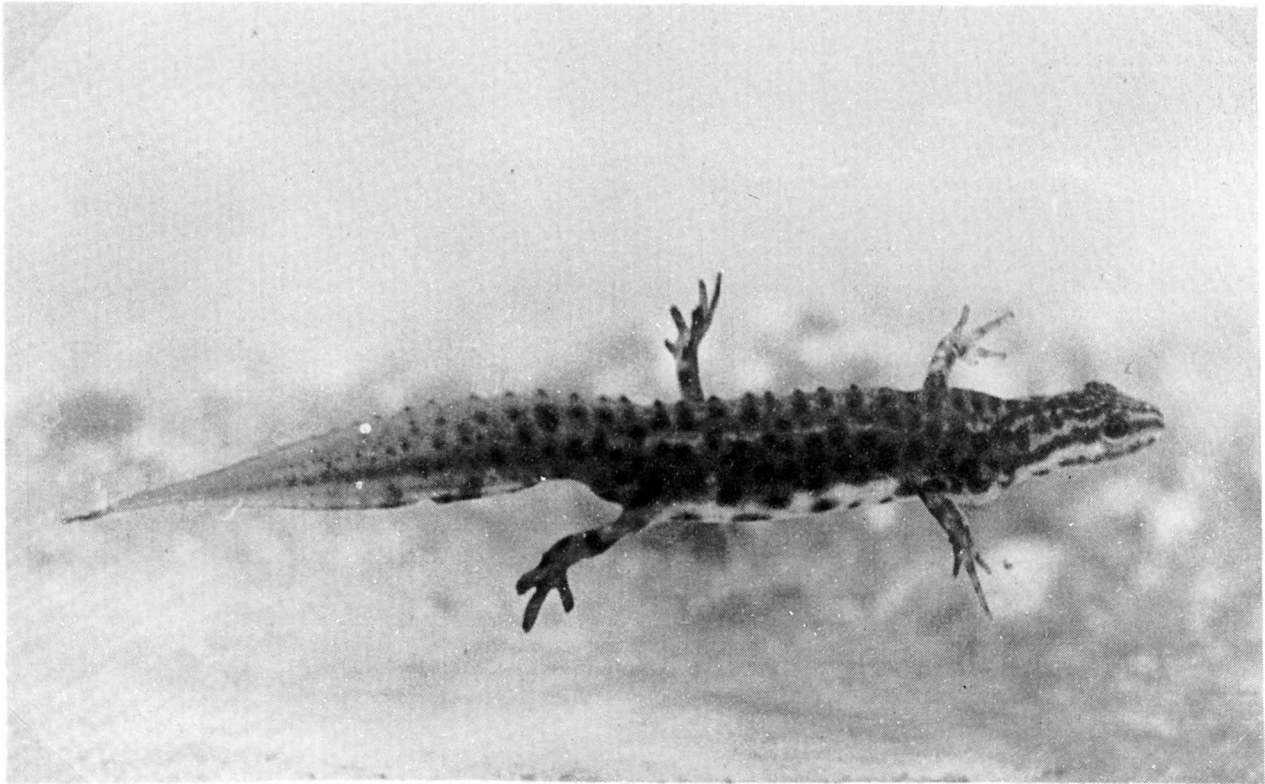


Fig. 5 *T. v. lantzi*, Tbilisi, U.S.S.R. (B. Ardabyevski).

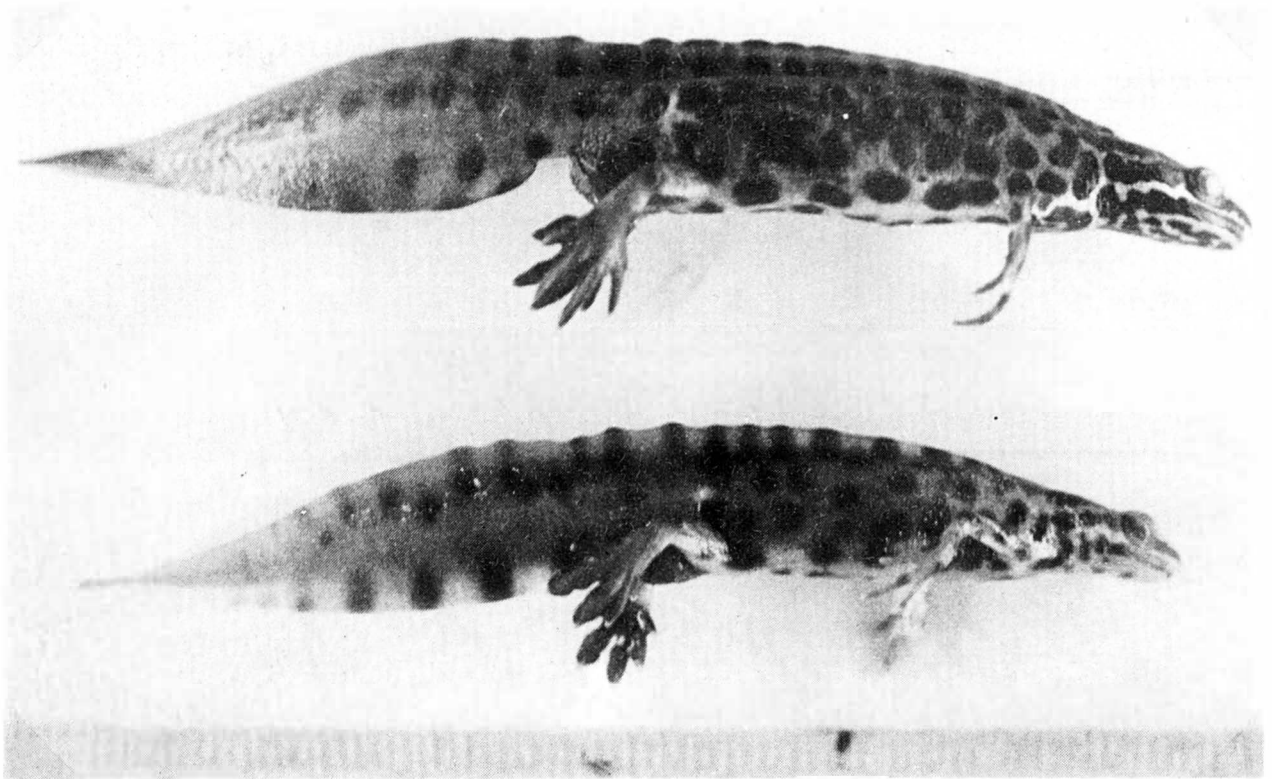


Fig. 6 *T. v. ampelensis*, Valea Dosului, Rumania. (D. Cogalniceanu).

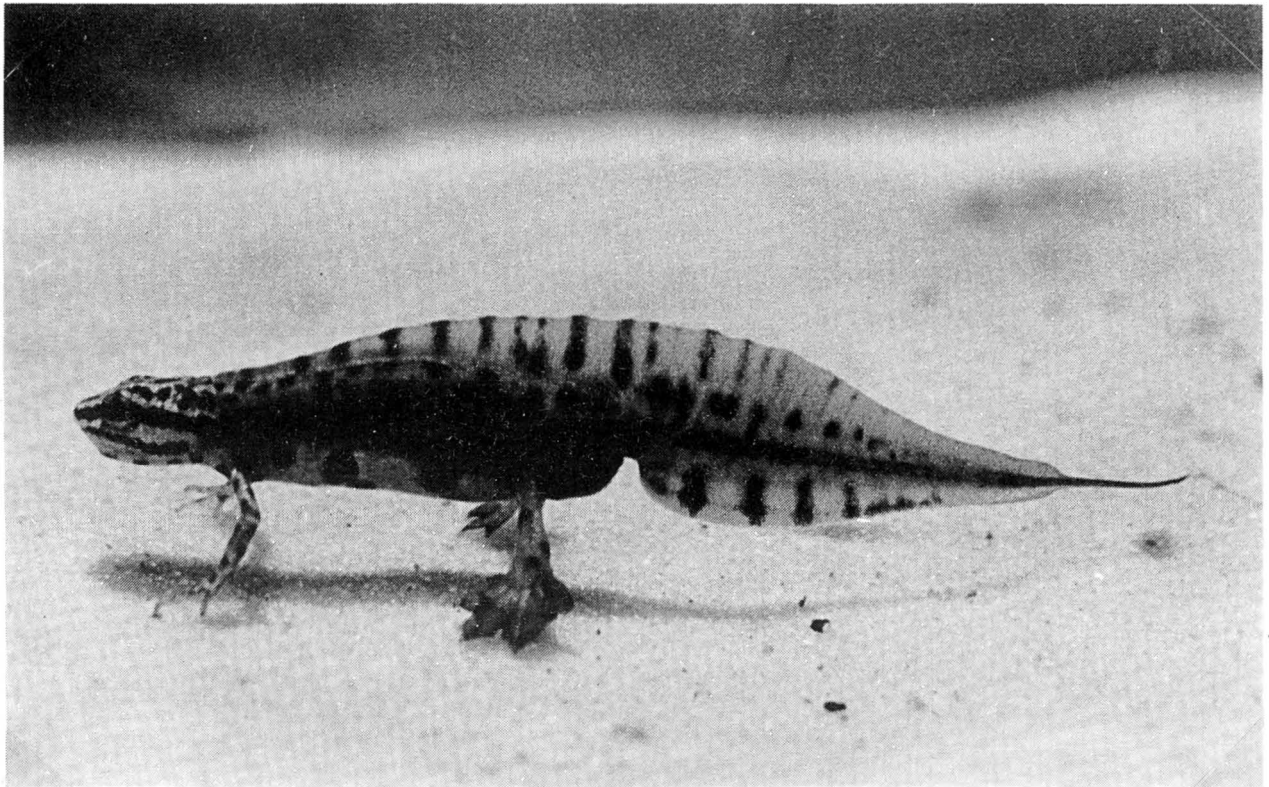


Fig. 7 *T. v. kosswigi*, Adapazari, Turkey. (C. J. Raxworthy).

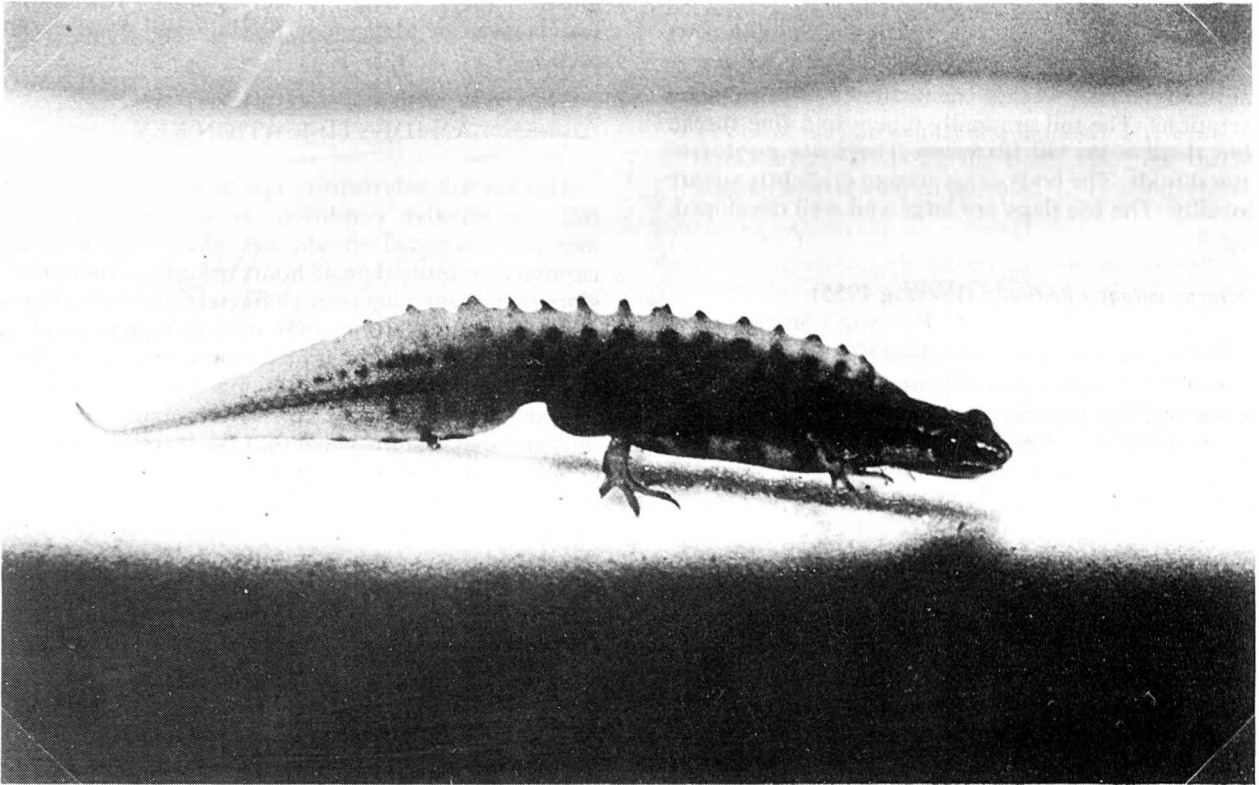


Fig. 8 *T. v. schmidtlerorum*, Karacabey, Turkey. (C. J. Raxworthy).

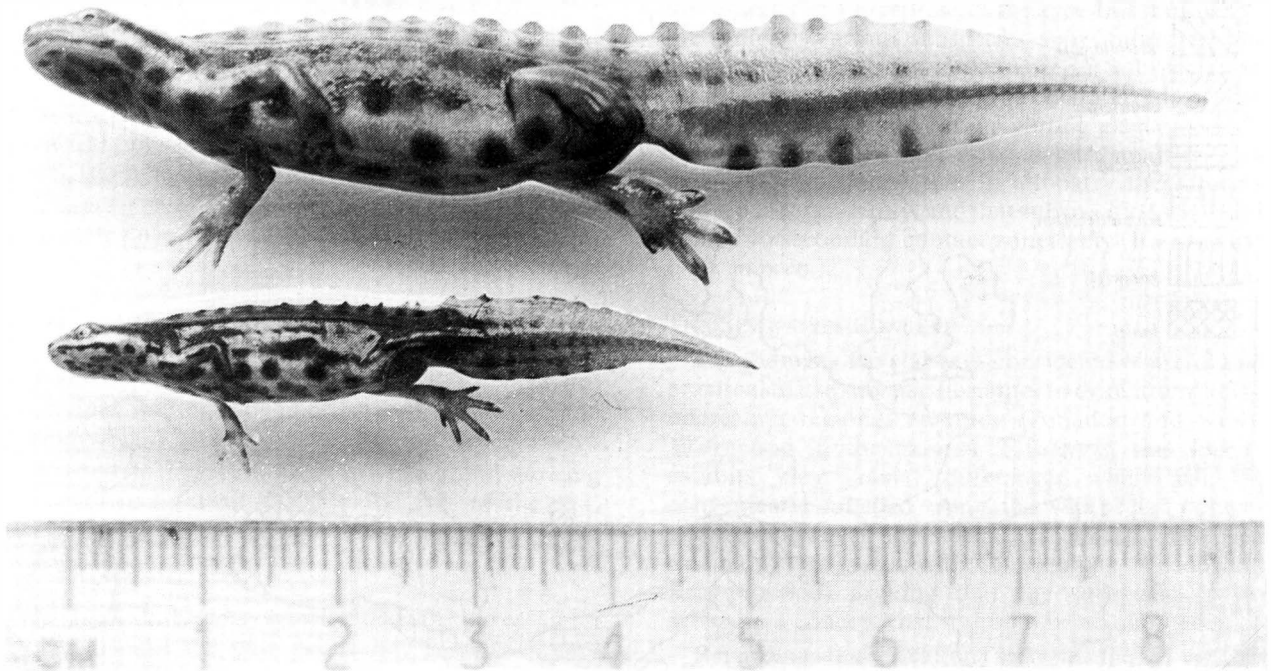


Fig. 9 Top: *T. v. vulgaris*, Milton Keynes, England. Bottom: *T. v. schmidtlerorum*, Karacabey, Turkey. (C. J. Raxworthy).

Triturus vulgaris ampelensis (Fuhn 1951)

Apuseni Smooth newt

The dorsal crest is of medium height (>1.0mm at mid-body) and weakly denticulated by rounded serrations. The tail gradually tapers to a fine thread (but there is no tail filament). There are no dorso-lateral folds. The body cross section is slightly square dorsally. The toe flaps are large and well developed. Fig. 6.

Triturus vulgaris kosswigi (Freytag 1955)

Kosswig's Smooth newt

The dorsal crest is smooth edged and very low on the body (<1.0mm at mid-body) but high at the basal area of the tail. The tail ends in a long tail filament. There are strongly developed dorso-lateral folds and the body cross section is square-shaped dorsally. The toe flaps are broad and very well developed. Fig. 7.

Triturus vulgaris schmidtlerorum (Raxworthy 1988)

Schmidtler's Smooth newt

The dorsal crest is of medium height (>2.0mm at mid-body) and denticulated by almost spine shaped serrations. The tail gradually tapers to an elongated point (but no tail filament). There are no dorsal-lateral folds but the body is slightly square-shaped dorsally. The tow flaps are only very weakly developed. Fig. 8 and Fig. 9.

Fig. 10 shows the geographical distribution of each subspecies based on the distribution information given by Schmidtler and Schmidtler (1967, 1983), Kalezić (1983), Sparreboom and Arntzen (1987) and Tark-

hnishvili (pers. comm.). A very similar distribution map is given by Macgregor, Sessions and Arntzen (in prep.).

AN IDENTIFICATION KEY

This key will only identify aquatic males which are in full reproductive condition. It is preferable that material examined should not have been kept in captivity for more than 48 hours prior to examination since important diagnostic characters such as toe flaps and crest denticulations may start to regress quickly under some conditions. The features used in this key can all be examined readily on live unrestrained aquatic animals, but the key works equally well with museum material provided that the secondary sexual characters are fully developed. This can be determined by examination of the crest and toe flaps. In all subspecies, one of these characters is always well developed for animals in full breeding condition. Occasionally animals may have suffered natural damage to the tail tip. Under these circumstances it is best to avoid using the tail tip features in the key.

- 1 The crest is obviously denticulated along the body. Fig. 11(a,b). 2
The crest is approximately smooth edged along its entire length. Fig. 11(c). 4
- 2 The tail tip gradually tapers to a fine point, frequently with a very fine thread like end. Fig. 11(d). The body cross section is slightly squares

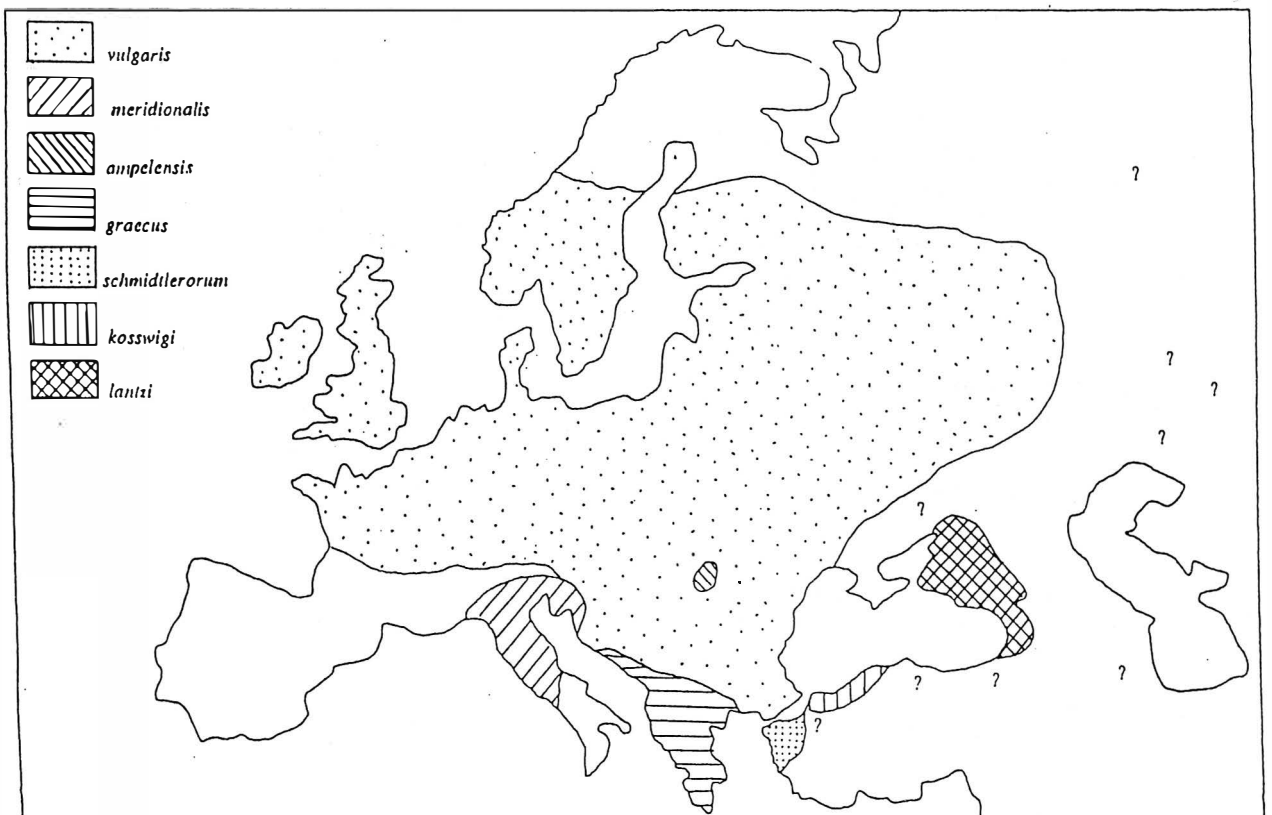


Fig. 10 The subspecies distribution of *T. vulgaris*.

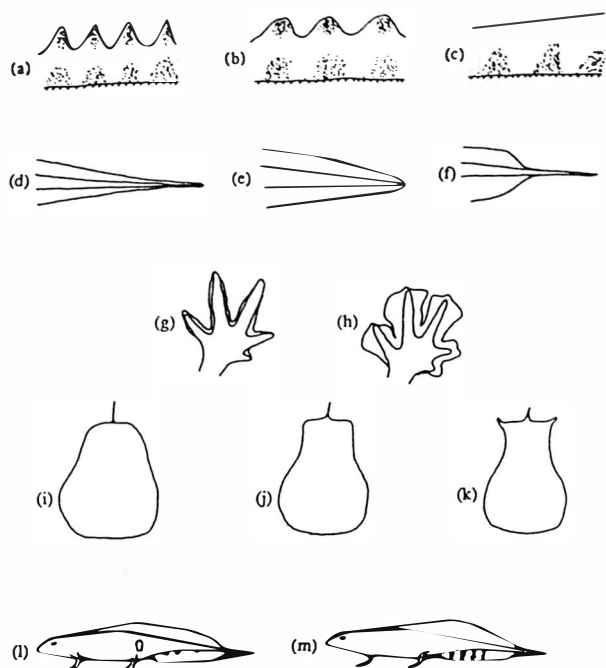


Fig. 11

shaped dorsally, Fig. 11(j). The crest denticulations may be pointed, Fig. 11(a), or rounded, Fig. 11(b).

The tail tip usually tapers gradually to a blunt point, Fig. 11(e). The body cross section is rounded in the dorso-lateral region, Fig. 11(i). The crest denticulations are rounded, Fig. 11(b). *T. v. vulgaris*

- 3 The toe flaps are not obvious, Fig. 11(g). The crest denticulations are almost pointed and extend onto the tail past the cloaca. Fig. 11(a).

T. v. schmidtlerorum

The toe flaps can be seen easily, Fig. 11(h). The denticulations may be rounded or pointed and extend onto the tail past the cloaca. *T. v. lantzi*

The toe flaps are large and very obvious, Fig. 11(h). The crest denticulations are rounded Fig. 11(b) and usually do not extend on to the tail past the cloaca.

T. v. ampelensis

- 4 The tail tip ends in a long tail filament which is devoid of tail fin and shows a distinct transition from the rest of the tail, Fig. 11(f). There are obvious well developed dorso-lateral folds on the body, Fig. 11(k).

The tail tip tapers gradually to a fine point, showing no distinct transition from the rest of the tail, Fig. 11(d). Dorso-lateral folds may be present, Fig. 11(k) or absent, Fig. 11(j).

- 5 No large dark spots typically touch the lower tail fin margin and the pale pelvic line is usually very obvious, Fig. 11(l). Only small spots on the belly (<1.5mm dia.)

T. v. graecus

Large dark spots typically touch the lower tail fin margin and the pale pelvic line is absent or very

poorly developed, Fig. 11(m). Usually a few large spots on the belly (>1.5mm dia.). *T. v. kosswigi*

- 6 The crest is always smooth edged. There are weak dorso-lateral folds on the body. *T. v. meridionalis*
The crest may be weakly denticulated. There are no dorso-lateral folds on the body although this is slightly square shaped dorsally. *T. v. ampelensis*

DISCUSSION

PHYLOGENETIC ASPECTS

The two most closely related species to *T. vulgaris* are *T. helveticus* and *T. montandoni*. The three species form their own monophyletic group (Rafinski and Arntzen, 1987, Arntzen and Sparreboom, 1987, Macgregor *et al.* in prep.). Hybridisation studies (Macgregor *et al.* in prep.), cytological evidence (Ragghianti, Bucci-Innocent and Mancino, 1978) and electrophoretic evidence (Rafinski and Arntzen, 1987) all indicate that *T. vulgaris* is most closely related to *T. montandoni*. Sympatric populations are known in Central Europe and natural hybrids have been reported which may be common in some populations (Hofmann, 1908, Geyer, 1953, Fuhn, Sova and Dumitrescu, 1975, Pecio and Rafinski, 1985).

Within *T. vulgaris* two main groups can be recognised (Raxworthy, 1989). The 'graecus' group is comprised of *T. v. graecus* and *T. v. kosswigi*. The 'vulgaris' group is comprised of *T. v. vulgaris*, *T. v. lantzi* and *T. v. schmidtlerorum*. *T. v. meridionalis* and *T. v. ampelensis* represent intermediate forms, with stronger affinities to the 'graecus' group for *T. v. meridionalis*, and stronger 'vulgaris' affinities for *T. v. ampelensis*. Outgroup comparison suggests that the 'graecus' group represents the ancestral state, while the 'vulgaris' group subspecies show more derived characters (Raxworthy, 1989, in prep.). Subspeciation of *T. vulgaris* appears to have occurred in the Pleistocene, when populations during glacial periods became fragmented and isolated into small refuges areas. It is suggested that in allopatry these forms evolved independently, and that subspecific fusion was limited to secondary contact zones only (Raxworthy, 1989, in prep.).

THE SUBSPECIES CONCEPT

Taxonomists have always considered it useful and practical to use subspecific names to draw attention to interesting regional variation (Amadon and Short, 1976), and in the case of *T. vulgaris*, this species exhibits clear racial differences which can be conveniently labelled using the subspecies nomenclature. However the subspecies concept has been frequently criticised, with for example Wilson and Brown (1953) arguing that the subspecies is so arbitrary a concept that it should be abandoned.

Regarding the situation seen in the *T. vulgaris* subspecies, all subspecies are defined, based on the development of morphological male secondary sexual characters, which are stable outside hybrid zones (Schmidtler and Schmidtler, 1983). These morpho-

logical characters do not show independent patterns of distribution and therefore this leads to the recognition of clearly defined (and non arbitrary) subspecific taxa. By use of such characters subspecies boundaries become real biological concepts represented by intergradation zones which can be readily identified (Fig. 12). The *T. alpestris* subspecies also appear to show non-independent geographical variation for both morphological and electrophoretic characters. Arano (1988) has found that most of the *T. alpestris* subspecies (described using morphological criteria) are supported by electrophoretic patterns of variability and the Yugoslavian *T. vulgaris* subspecies have also been supported by electrophoretic evidence (Kalezić, 1984).

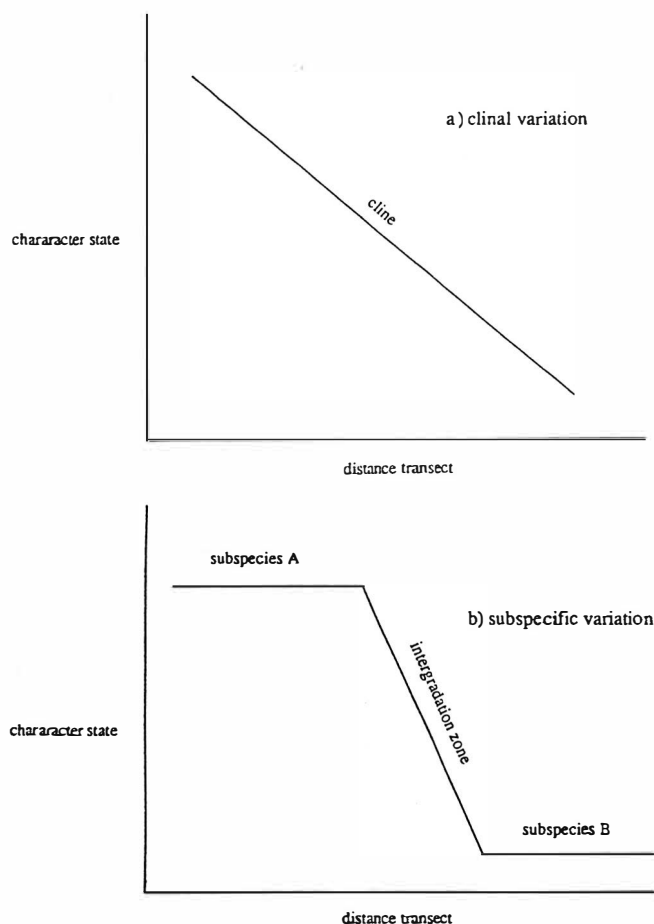


Fig. 12 The difference between clinal variation and subspecific variation.

The subspecific phylogenies of *T. vulgaris* and *T. alpestris* show a surprising level of biogeographical congruence, based on completely different types of data: morphological and courtship behaviour for *T. vulgaris* (Raxworthy, 1989) and electrophoretic evidence for *T. alpestris* (Arano and Arntzen, 1987, Arano, 1988). Both phylogenies have ancestral Balkan subspecies and a more derived lineage giving rise to the Italian and widespread Central European subspecies (Arntzen and Raxworthy, in prep.). The *T. vulgaris* subspecies appear to have arisen as a direct consequence of climatic changes in the Pleistocene. The glacial refugia identified by tree pollen analysis by

Huntley and Birks (1983) shows close correlations with the centres of current subspecies distributions of *T. vulgaris* subspecies (Raxworthy, 1989). It is therefore possible to propose the appropriate refugia where most subspecies were confined during at least the last glacial period.

The biogeographical congruence of subspecific phylogenies, the congruence of different taxonomic data sets and the correlation of subspecies distributions with glacial refugia provide strong evidence that these subspecies represent valid biological entities. Therefore I conclude that these subspecies are not arbitrary concepts, but rather represent real non-independent patterns of geographical variation.

SUBSPECIES OR SPECIES?

Is it appropriate to consider raising the taxonomic status of the *T. vulgaris* subspecies to the species level? Biological species are defined by Mayr (1942) as 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'.

Natural hybridisation is usually rare between *Triturus* species (the exception being between *T. montandoni* and *T. vulgaris*, and *T. cristatus* and *T. marmoratus*). When hybridisation is induced artificially in the laboratory, post-zygotic isolation mechanisms always result in unfit hybrids, e.g. between *T. marmoratus* and *T. cristatus* (Lantz, 1947), *T. vulgaris* and *T. helveticus* (Scali and Mancino, 1968) and the *T. cristatus* superspecies (Callan and Spurway, 1951, Wallis and Arntzen, 1989). In all these cases post-zygotic isolating mechanisms prevent genetic fusion and are therefore contribute to the reproductive isolation of each species. Geyer (1953) however has reported viable hybrid *T. vulgaris-montandoni* in the first and second generation. Although wild *T. vulgaris* x *montandoni* hybrids are well known (see earlier), recent studies have found mutually exclusive parapatric distribution patterns between these two species (Rafinski pers. comm., in Arntzen and Sparreboom submitted). Evidence for ecological and ethological pre-mating isolation mechanisms have been found in some species (Halliday, 1977, Arntzen, 1986) which would prevent gene flow between species.

Only a very limited amount of work has been undertaken concerning hybridisation experiments between the *T. vulgaris* subspecies. Lantz (1947) noted that intra-specific crosses between various subspecies of *T. vulgaris* were obtained without difficulty, yielding offspring which are normal in every respect. Observations made during this study found both reciprocal mixed pairs of *T. v. vulgaris* and *T. v. meridionalis* showed successful courtship with sperm transfer.

T. vulgaris subspecific intergradation zones have now been recognised and described throughout much of Europe. Intergradation zones have been found in: Yugoslavia: *T. v. vulgaris* x *T. v. meridionalis* and *T. v. vulgaris* x *T. v. graecus* (Schmidtler and Schmidtler, 1983). Rumania: *T. v. vulgaris* x *T. v. ampelensis* (Cogalniceanu pers. comm.) and in Turkey *T. v. vulgaris* and *T. v. kosswigi* (Tabrizi, 1980).

The size of some of these intergradation zones (up to 160km in length along the Dalmatian coast) and the reported normal fitness of hybrids do not provide any evidence of reproductive isolation between these subspecies. There is obvious gene flow occurring at these secondary contact zones, although subspecific fusion may be very slow if migration is low and there is some degree of subspecific assortative mating (Raxworthy, 1989). Clearly, there can be no question of raising these taxonomic units to species rank based on the biological species concept.

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REFERENCES

- Amadon, D. and Short, L. L. (1976). Treatment of subspecies approaching the species status. *Syst. Zool.* **25**, (2), 161-167.
- Arano, B. (1988). *Aspectos filogeneticos del genero Triturus con especial consideracion a la evolucion del complejo Triturus alpestris*. PhD Thesis. Madrid. Departamento de Zoologia. Museo Nacional de Ciencias Biológicas.
- Arano, B. and Arntzen, J. W. (1987). Genetic differentiation in the Alpine newt *Triturus alpestris*. In *Proceedings of the fourth Ordinary General Meeting of the Societas Euopaea Herpetologica*, 21-24. van Gelder, J. J., Strijbosch, H. and Bergers, P. J. M. (Eds.). Nijmegen. Faculty of Sciences. Nijmegen.
- Arntzen, J. W. (1986). Notes sur la coexistence d'espèce sympatrique de tritons du genre *Triturus*. *Bull. Soc. Herp. France*, **37**, 1-8.
- Arntzen, J. W. and Sparreboom, M. (1987). The use of biochemical and behavioural data for the phylogeny of Old World newts, genus *Triturus*. In *Proceedings of the fourth Ordinary General Meeting of the Societas Euopaea Herpetologica*, 25-28. van Gelder, J. J., Strijbosch, H. and Bergers, P. J. M. (Eds.). Nijmegen. Faculty of Sciences. Nijmegen.
- Bell, G. A. C. (1966). The size of a series of Leicestershire newts. *Brit. J. Herp.* **3**, 279-284.
- Boulenger, G. A. (1882). *Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the collection of the British Museum*. Second Edition. London. British Museum.
- Breuil, M. and Guillaume, C. P. (1984). Etude électrophorétique de quelques populations de Tritons alpestres néoténiques (*Triturus alpestris*, Amphibia, Caudata, Salamandriidae) du sud de la Yougoslavie. *Bull. Soc. Zool. Fr.* **109** (4), 377-389.
- Breuil, M. and Thuot, M. (1983). Etho-ecology of neotenic alpine newt (*Triturus alpestris montenegrimus* Radovanovic, 1951) in lake Bukumir (Montenegro, Yugoslavia): Examination of lake communities features and proposal of an ecological determination for neoteny. *Glas. Republ. Zavoda Zagst. Priode Prirodnjackog Muzeja, Titogradu*, **16**, 85-96.
- Callan, H. G. and Spurway, H. (1951). A study of meiosis in intermediate hybrids of the newt *Triturus cristatus*. *Journal of Genetics*, **50**, 235-249.
- Clifford, T. (1986). Notes on the morphometrics and spot patterns of female Smooth newts (*Triturus vulgaris*) at a coastal site in Lincolnshire. *Herpetological J.* **1**, 93-96.
- Dely, O. G. (1967). Neuere Angaben zur Kenntnis des Neotenischen Teichmolches (*Triturus vulgaris* L.). *Acta zool. hung.* **13** (3-4), 253-270.
- Dunn, E. R. (1918). The collection of Amphibia Caudata of the Museum of Comparative Zoology. *Bull. Mus. comp. Zool. Harv.* **62** (9), 445-471.
- Eiselt, J. (1966). Ergebnisse zoologischer sammelreisen in der Türkei: Amphibia Caudata. *Annl. naturh. Mus. Wien*, **69**, 427-445.
- Freytag, G. E. (1955). Ein neuer Teichmolch aus der Türkei. *Zool. Anz.* **154**, 195-200.
- Fuhn, I. E. (1951). Contributuni la sistematica salamandrelor din republica populara Romanana I. Studiul catorva populatii de *Triturus vulgaris*. L. *Buletin sti. Acad. Repub. pop. rom. Ser. geol. geog. biol. st. teh. ag. Sect. St. biol. agron. geol. geog.* **3** (3), 501-512.
- Fuhn, I. E., Sova, C. and Dumitrescu, M. (1975). Une population hybridogène *Triturus v. vulgaris* x *T. montandoni* Boul. du lac Craule (Mts. Nemira, Depart. Bacau). *Stud. Com. Mus. Stint. Natur. Bar.* **8**, 225-236.
- Gabriel, J., Sentein, P. and Gabriel, C. (1977). Les populations neoténiques de *Triturus helveticus* des causses et du bas-languedoc I. Répartition et caractéristiques. *Terre Vie* **31**, 489-505.
- Geyer, H. (1953). Über Bastarde zwischen Karpätenmolch (*Triturus montandoni*) und Teichmolch (*Triturus vulgaris*) und ihre F₂-Nachkommen. *Mitt. Naturk. Vorges. Mus. Kult.-Gesch. Magdeb.* **3**, 185-195.
- Gislén, T. and Kauri, H. (1959). Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta Vert.* **1** (3), 196-397.
- Griffiths, R. A. and Mylotte, V. J. (1989). Observations on the development of secondary sexual characters of male newts *Triturus vulgaris* and *Triturus helveticus*. *J. Herp.* **22**, 476-480.
- Halliday, T. R. (1977). The courtship of European newts. An evolutionary perspective. In *The Reproductive biology of amphibians*, 185-232. Taylor, D. H. and Guttman (Eds.). New York. Plenum Press.
- Hofmann, O. (1908). Über Triton *Montandoni* Blg. in Galizien. *W'chr. Aquar. - u. Terrarienk.* **1908**, 65-66.
- Huntley, B. and Birks, H. J. B. (1983). *An Atlas of past and present pollen maps for Europe: 0-13000 years ago*. Cambridge. Cambridge University Press.
- Kalezić, M. L. (1983). Geographical aspects of genetic variability in the Smooth newt (*Triturus vulgaris*). *Genetika* **15** (1), 93-103.
- Kalezić, M. L. (1984). Evolutionary divergences in the Smooth newt *Triturus vulgaris* (Urodela, Salamandriidae): electrophoretic evidence. *Amphibia-Reptilia* **5**, 221-230.

- Kolombatovic, G. (1907). Contribuzioni alla fauna dei vertebrati della Dalmazia. *Glasn. hrv. narodosl. Drust.* **19**, 1-24.
- Lantz, L. A. (1947). Hybrids between *Triturus cristatus* Laur. and *Triturus marmoratus* Latr. *Proc. Zool. Soc. Lond.* **117**, 247-258.
- Linnaeus, C. (1758). *Systema naturae per regna tria naturae* 10. Stockholm.
- Mancino, G. (1961). Anomalie meiotiche nella spermatogenesi dell' ibrido *Triturus italicus* female x *Triturus vulgaris* male. *Boll. Zool.* **28**, 691-701.
- Mayr, E. (1942). *Systematics and the origin of species*. New York, Columbia University Press.
- Mayr, E. (1963). *Animal species and evolution*. Cambridge, Mass.: Belknap Press.
- Méhely, L. (1905). Die herpetologischen Verhältnisse des Meesek-Gebirges und der Kapela. *Ann. Mus. Nat. Hung.* **3**, 256-273.
- Mertens, R. and Wermuth, H. (1960). Die Amphibien und Reptilien Europas 3. *Senckenberg. biol.* **38**, 1-264.
- Özeti, N. (1964). [Studies on the morphology, taxonomic position, seasonal activity and thermotaxis behaviour of *Triturus vulgaris* (Linnaeus) in the Aegean region.] *Sci. Rep. Fac. Sci., Ege Univ.* No. 15, 1-49. [in Turkish with English summary]
- Pecio, A. and Rafinski, J. (1985). Sexual behaviour of the Montandon's newt *Triturus montandoni* (Boulenger) (Caudata, Salamandridae). *Amphibia-Reptilia* **6**, 11-22.
- Peracca, M. G. (1898a). Descrizione di una nuova specie di Tritone Italiano. *Boll. Musei. Zool. Anat. comp. R. Univ. Torino.* **13** (317), 1-6.
- Peracca, M. G. (1898b). Note on an Italian newt, *Molge italica*. *Proc. Zool. Soc. Lond.* (1898), 482-487.
- Radovanovic, M. (1951a). *Vodozemci i gmizavci nase zemlje. Srpsko biologsko drustvo*. Beograd, Nancina Kmijica.
- Radovanovic, M. (1951b). A new race of Alpine newt from Yugoslavia. *Brit. J. Herp.* **1** (5), 93-97.
- Rafinski, J. and Arntzen, J. W. (1987). Biochemical aspects of the Old World newts, genus *Triturus*. Isozyme data. *Herpetologica* **43** (4), 446-457.
- Ragghianti, M., Bucci-Innocent, S. and Mancino, G. (1978). Karyology of the Carpathian newt *Triturus montandoni* and cytotoxic considerations on the species group *T. vulgaris* (Urodela: Salamandridae). *Caryologia* **31** (2), 243-256.
- Raxworthy, C. J. (1988). A description and study of a new dwarf sub-species of Smooth newt *Triturus vulgaris* from Western Anatolia, Turkey. *J. Zool. Lond.* **215**, 753-763.
- Raxworthy, C. J. (1989). The subspecific evolution of courtship behaviour and sexual dimorphism in the Smooth newt *Triturus vulgaris*. *PhD Thesis*. Milton Keynes, The Open University.
- Rocek, Z. (1974). Biometrical investigations of central European populations of the alpine newt *Triturus alpestris alpestris* (Laurenti, 1768). (Amphibia: Urodela). *Acta Univ. Carol. Biol.* **1972**, 295-373.
- Scali, V. and Mancino, G. (1968). Osservazioni sulla spermatogenesi di ibridi poliploidi *Triturus helveticus vulgaris* female x *T. vulgaris* male. *Memorie Atti. Soc. tosc. Sci. nat.* **75**, 8-18.
- Schmidtler, J. J. and Schmidtler, J. F. (1967). Über die Verbreitung der Molchgattung *Triturus* in Kleinasien. *Salamandra* **3**, 15-36.
- Schmidtler, J. J. and Schmidtler, J. F. (1983). Verbreitung, Ökologie und innerartliche Gliederung von *Triturus vulgaris* in den adriatischen Küstengebieten. *Spixiana* **6** (3), 229-249.
- Sparreboom, M. and Arntzen, P. (1987). Über die Amphibien in der Umgebung von Adapazari, Türkei. *Herpetofauna* **9** (50), 27-34.
- Steinitz, H. (1965). *Triturus vittatus* (Jenyns), geographic distribution and taxonomic subdivision. *Israel J. Zool.* **14**, 234-240.
- Steward, J. W. (1969). *The tailed amphibians of Europe*. Newton Abbot, David and Charles.
- Tabrizi, F. H. (1980). [On some new material of *Triturus vulgaris* (L.) from the area between Abant (Bolu) and Bosphorus in NW Anatolia] *Ege Univ. Fen. Fak. Der. (B)*, **4**, 115-140. [in Turkish with English summary].
- Thorn, R. (1968). *Les salamandres d'Europe, d'Asie et d'Afrique du Nord*. Paris, Lechavalier.
- Tucic, N. and Kalezić, M. L. (1984). Morphological variation within and among populations of the Smooth newt, *Triturus vulgaris*. *Biosistemika* **10** (1), 45-58.
- Verrell, P. A., Halliday, T. R. and Griffiths, M. (1986). The annual reproductive cycle of the South newt (*Triturus vulgaris*) in England. *J. Zool. Lond.* **210**, 101-119.
- Wallis, G. P. and Arntzen, J. W. (1989). Mitochondrial DNA variation in the Crested newt superspecies: limited cytoplasmic geneflow among species. *Evolution* **43** (1), 88-104.
- Wilson, O. E. and Brown, W. L. (1953). The subspecies concept and its taxonomic implications. *Syst. Zool.* **2**, 97-111.
- Wolterstorff, W. (1905). Über *Triton vulgaris*, L. subsp. *gracca* Wolt. n. subsp. *Zool. Anz.* **29** (5), 137-139.
- Wolterstorff, W. (1907). Über neue Tritonenformen Österreichs, insbesondere *Triton* (= *Molge*) *vulgaris* subsp. *typica* forma *Kammereri* n.f. *Zool. Anz.* **31**, 310-316.
- Wolterstorff, W. (1908). Ein neue Tritonenformen Dalmatiens. *W'schr. Aquar.- u. Terrarienk.* **5**, 23.
- Wolterstorff, W. (1914). Zwei neue Tritonenformen der paläarktischen region. *Abh. Ber. Mus. Naturk. Vorges. Magdeb.* **2** (4), 371-381.

SIZE DIFFERENCES OF NATTERJACK TOADS BREEDING IN THE NORTH MERSEYSIDE SAND-DUNES

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ABSTRACT

Snout-vent lengths of large samples of natterjacks were measured at four relatively isolated sand-dune breeding sites in two successive years. It was hoped that the size distributions would indicate whether satisfactory recruitment into the breeding cohort was taking place. Significant differences were found between males and females, between the four sites and between years. It is inferred that one group consists mainly of young individuals, reflecting high toadlet production, while the other three groups have a large proportion of older adults as a consequence of poorer breeding success. The possible reasons for these differences are discussed.

INTRODUCTION

The natterjack toad *Bufo calamita* Laur. is restricted to about forty, mainly coastal, localities in Britain (Cooke, Banks and Langton, 1984) and is specially protected under the Wildlife and Countryside Act 1981.

The north Merseyside sand-dune system supports one of the large populations of this species in the country (Smith and Payne, 1980). Since the 1970's, efforts have been made to conserve this population by statutory protection and positive management of its habitats. At the same time, almost annual monitoring of distribution and breeding success has been attempted in many parts of the dune system.

In 1978, Smith and Payne (1980) reported that the toads had enjoyed a sequence of successful breeding seasons, assisted by a rise in the water-table since 1974, the excavation of about fifty new breeding sites and licensed rescue operations to save tadpoles from desiccation. The adult female population was estimated to contain over 2000 individuals, while many immature toads were observed in the dunes and adjacent urban areas.

Continued monitoring during the 1980s suggests that breeding has been successful in some parts of the dune system but relatively poor in other areas. However, it has proved difficult to count the numbers of toadlets leaving the water and, despite recent research into natterjack population dynamics (e.g. Davis, 1985), it is not known what level of recruitment is necessary to sustain a breeding population (Banks and Beebee, 1988).

An indirect way of determining whether satisfactory recruitment is occurring is to examine the size range of individuals in the breeding groups (Cooke, 1981, 1982). Although growth rates are likely to be variable and related to environmental conditions (Hemmer and Kadel, 1972), a general relationship between size and age may be anticipated. Thus, Davis (1985) found significant positive correlations between snout-vent

length and age for both males and females in a Merseyside breeding colony.

On the Merseyside coast, *B. calamita* breeds in discrete groups of dune slacks and excavated scapes which are up to 3km from the next nearest breeding site. Although natterjacks are noted for their ability to 'migrate', especially if their breeding pools dry up (Beebee, 1983), most of the adults are probably relatively site faithful. Thus, Smith and Bownes (1978) found that 70 per cent of Merseyside toads marked in one breeding season and recovered in the next had moved a maximum of only 200m. The largest distance covered was 2.2km by one individual. Movements within a breeding season are likely to be less than this and it was therefore justified, for the purposes of this study, to treat the main breeding groups as isolated populations.

The aims of the study were to investigate natterjack body lengths at four major breeding sites in two successive years and to establish whether this technique can be used to monitor the success, or otherwise, of recruitment into the breeding populations.

MATERIALS AND METHODS

The four study areas were chosen on the basis of two criteria: they were at least 1km from the nearest known breeding site of *B. calamita* and they supported sufficient numbers of adults to provide a large sample size.

Fig. 1 shows the positions of the study areas which are described briefly as follows:

1. *Ainsdale Hills Local Nature Reserve*. This narrow strip of mobile and embryo dunes, 1.6km long and 0.3km wide, contains 13 semi-natural slacks with a total area of about 2.0ha, in which natterjacks have bred during the present decade. Parts of some slack basins were deepened from 1980 onwards.
2. *The National Trust Estate, Formby Point*. About 3km south of Ainsdale Hills, this site consists of four small pools (total area about 0.04ha) on the

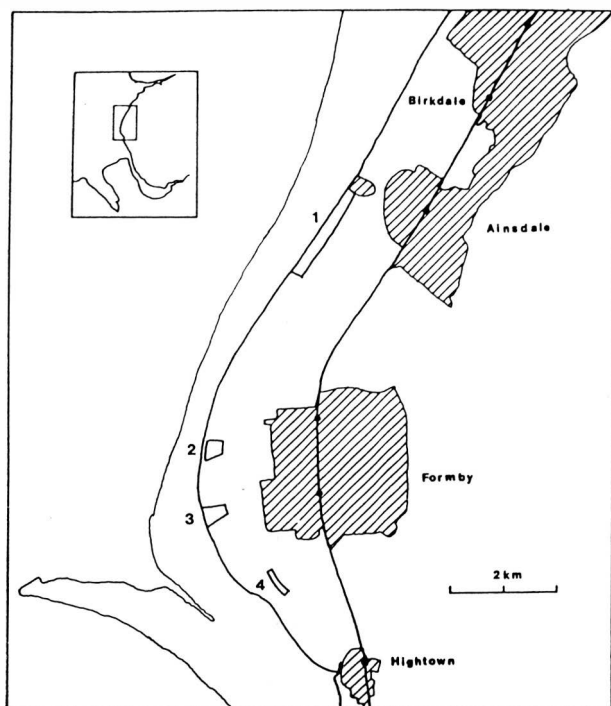


Fig. 1 Locations of study areas in the north Merseyside sand-dune system. 1 = Ainsdale Hills; 2 = National Trust tobacco dump; 3 = Lifeboat Road; 4 = Cabin Hill. Built-up areas are hatched.

so-called 'tobacco dump', a waste tip of denatured tobacco leaves which closed down in the mid-1970s. The high water-holding capacity of the waste maintains a perched water-table in an area of dunes lacking natural slacks. The pools, which date back to the early 1970s, have been deepened on several occasions.

3. *Lifeboat Road, Formby Point.* In a zone of heavy recreational pressure, this site is an area of degraded mobile dunes restored since 1978 under the auspices of the Sefton Coast Management Scheme. Four small scrapes (total area about 0.04ha) were excavated from 1981 onwards; they lie about 1 km south of the tobacco dump.
4. *Cabin Hill National Nature Reserve.* The breeding pools are situated in an area of fixed dunes 2 km south of Lifeboat Road. Most were formed as borrow pits during the construction of a flood defence bank in 1970. The largest of these shallow pits, covering about 1.6ha, was the sample site.

Visits were made to the study areas after dark during April and May when peak natterjack activity was expected. Pools were systematically searched with a torch; each unpaired animal found was caught with a pond net and sexed by reference to the nuptial pigmentation on the fore digits of the male (Beebee, 1983). Snout-vent length on the dorsal surface was measured to the nearest 1 mm by cupping the animal in the palm of the hand and gently compressing it under a transparent plastic ruler. Mating pairs were not disturbed. Measured individuals were immediately returned to the site of capture.

It has been suggested that larger individuals predominate early in the season, while smaller

natterjacks breed later (Flindt and Hemmer, 1968). As this could bias the samples, it was decided to take an early and late breeding season sample from each study area in 1988. In the event, only one sample was obtained at the National Trust site, but two were taken from the other three areas at intervals of 18-48 days. The results (see below) did not justify a second sample in 1989, so each area was sampled once in that season.

The data were analysed on a Dec-20 computer using the statistical package 'Minitab'.

RESULTS

DIFFERENCES BETWEEN MALES AND FEMALES

Snout-vent lengths of males ranged from 42 mm to 79 mm and of females, 51 mm to 82 mm. The largest female was 2 mm longer than the largest British Isles specimen known to Smith (1951) or Beebee (1983) and equalled the longest individual reported by Banks and Beebee (1986).

Frequency distributions of body lengths for each sample (Fig. 2, Fig. 3) are approximately normal and justify the use of parametric statistics.

A total of 622 males and 90 females was sampled in 1988, while 268 males and 57 females were measured

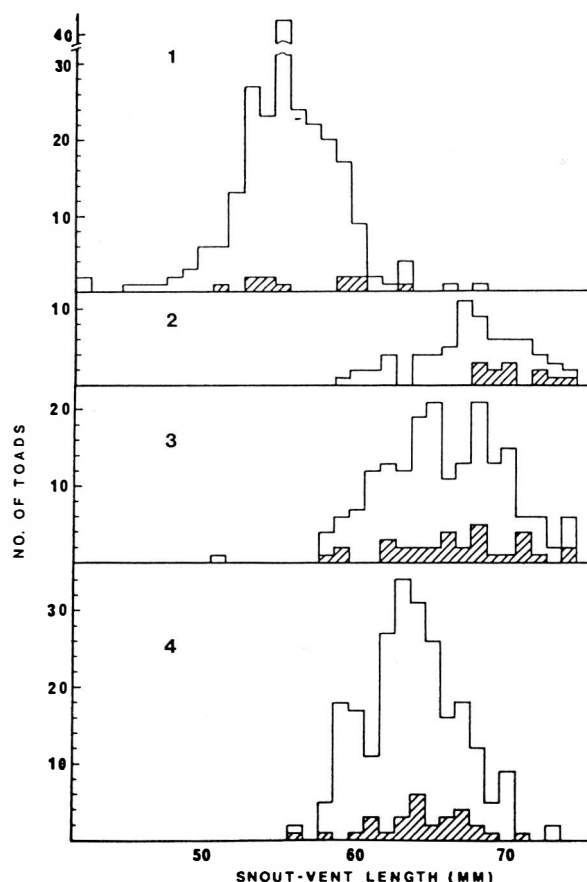


Fig. 2 Distributions of snout-vent lengths in samples of breeding natterjack toads measured in 1988 at:

1. Ainsdale Hills; 2. National Trust; 3. Lifeboat Road; 4. Cabin Hill. Open Columns = males; hatched = females.

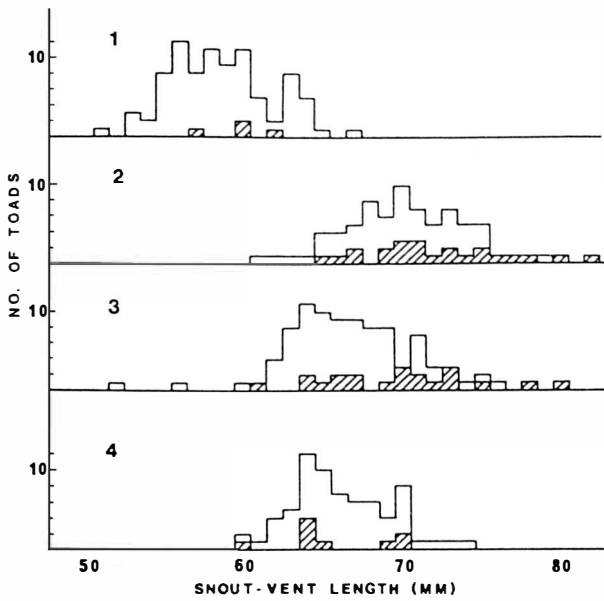


Fig. 3 Distributions of snout-vent lengths in samples of breeding natterjack toads measured in 1989 at: 1. Ainsdale Hills; 2. National Trust; 3. Lifeboat Road; 4. Cabin Hill. Open columns = males; hatched = females.

the following year. Apparent sex ratios of 6.9:1 and 4.7:1 in the two seasons reflect the fact that male natterjacks spend much more time at the breeding site than females (Arak, 1983) and therefore have a higher probability of capture. Davis (1985) reported sex ratios ranging from 12.1:1 to 5.5:1 in samples of natterjacks breeding at Cabin Hill between 1981 and 1983.

Table 1 compares the body lengths of males and females in the two seasons. Females were significantly larger than males ($p < 0.001$), being on average 3.7mm longer in 1988 and 4.9mm longer in 1989. Also, there was a significant ($p < 0.001$) increase in the lengths of both sexes between years, males averaging 3.0mm longer and females 4.2mm longer in 1989.

DIFFERENCES BETWEEN EARLY AND LATE SAMPLES IN 1988

Table 2 compares early and late breeding season samples of males at three sites. Female sample sizes were too small for a satisfactory test. At Ainsdale, the second sample has a significantly higher mean ($p = 0.03$), while, at Cabin Hill, the mean of the second sample is significantly lower than the first ($p = 0.01$). The mean of the second Lifeboat Road sample is higher than the first but not significantly so ($p = 0.1$). It seems reasonable to conclude that there is no systematic trend towards larger animals in the later samples. Therefore, a second sample was not taken in 1989. For subsequent comparisons, the two 1988 samples were pooled for each site.

DIFFERENCES BETWEEN SITES AND BETWEEN YEARS

There are considerable differences in mean body lengths between the four sites. Ainsdale toads being the smallest, National Trust the largest and Cabin Hill and Lifeboat Road animals intermediate in size. These trends are shown in both males and females and are consistent between seasons (Table 3). One-way analysis of variance (Table 3) shows that the differences between sites are significant in both years for both sexes ($p < 0.01$).

	1988		1989	
	males	females	males	females
No. sampled	622	90	268	57
Mean body length (mm)	61.5	65.2	64.5	69.4
S.D.	5.9	5.1	5.4	5.5
Two sample t	6.3		6.1	
p	<0.001		<0.001	

TABLE 1: Differences between male and female body lengths in 1988 and 1989.

	Ainsdale		Lifeboat Road		Cabin Hill	
	early	late	early	late	early	late
No. sampled	113	104	89	54	121	84
Mean body length (mm)	54.7	55.8	65.2	66.3	64.1	63
S.D.	3.2	3.6	4.3	4.0	3.1	3.2
Two sample t	2.24		1.51		2.53	
p	0.03		0.13		0.01	

TABLE 2: Differences between body lengths of males in early and late season samples, 1988.

	1988						1989					
	Males			Females			Males			Females		
	<i>n</i>	<i>x</i>	<i>SD</i>	<i>n</i>	<i>x</i>	<i>SD</i>	<i>n</i>	<i>x</i>	<i>SD</i>	<i>n</i>	<i>x</i>	<i>SD</i>
Ainsdale	217	55.2	3.44	11	56.5	3.86	83	58.6	3.26	4	59.8	2.06
Cabin Hill	205	63.7	3.17	29	64.3	3.29	60	66.2	3.02	9	65.6	3.40
Lifeboat Road	143	65.6	4.16	38	66.8	3.94	72	66.2	3.86	21	69.8	4.74
National Trust	57	66.9	3.55	12	70.3	2.05	53	69.6	3.65	23	72.2	4.43
ANOVA <i>f</i> ratio		362.3			33.8			130.6			12.4	
<i>p</i>		<0.01			<0.01			<0.01			<0.01	

TABLE 3: Analysis of body length differences between sites in the two seasons.

Site	Year								Mean Score
	1980	1981	1982	1983	1984	1985	1986	1987	
Ainsdale Hills	1	3	1	2	3	3	3	3	2.4
National Trust	2	2	1	3	0	1	1	—	1.4
Lifeboat Road	—	2	1	2	2	2	3	3	2.1
Cabin Hill	2	2-3	2	2	—	1	1	2	1.8

TABLE 4: Natterjack breeding success from 1980 to 1987 at the four study area based on estimates of toadlet production during routine monitoring. (0 = no toadlets, 1 = small numbers, 2 = moderate numbers, 3 = large numbers, — = no count).

DISCUSSION

It would be surprising if natterjack toads living only a few kilometres apart in the same dune system showed marked variations in growth rates. Therefore, it is likely that the differences observed reflect different age structures in the four breeding groups.

Davis (1985) measured natterjacks at Cabin Hill, ageing individuals of known sex by reference to growth rings in the phalanges. Comparisons with his data suggest that, in 1988, most males at Ainsdale were 3-4 years old, while most females were aged 4-5 years. The oldest group was at the National Trust Site where, in 1988, most males were at least 6 years old and most females about 7. At the other two sites, it seems that the majority of males were aged 5-6 years and most females 7. The difference in ages between the sexes is explained by Davis's (1985) finding that females mature one year later than males.

The 3-4mm increase in mean body length between years corresponds closely to the expected increment from one year's growth in older animals derived from Davis's (1985) regression equations. This suggests that there was little or no recruitment to the breeding cohorts in 1989.

Merseyside natterjacks can begin breeding at 2 years (males) or 3 years (females), although they may not be fully active until 1-2 years later (Davis, 1985). Therefore, in the 1988 breeding season, the first appearance of toads which metamorphosed in 1986 (males) or 1985 (females) could be anticipated. However, the Ainsdale adults seem to have been a year older than this while those at the National Trust site probably derive from the 1981 and 1982 spawnings,

implying a sequence of four years' poor recruitment at the latter site.

Low apparent recruitment could be due to a number of factors, including:

1. Emigration of juveniles or young adults to other parts of the dune system;
2. Young adults not appearing at the breeding sites;
3. Poor breeding success in earlier years;
4. High mortality of immature toads.

Although natterjacks are known to abandon breeding sites and move elsewhere (Beebee, 1983), there is no evidence that this has happened recently in the Merseyside dunes. Indeed, the colonisation of new scrapes dug in the last few years has been relatively slow.

Arak (1983) showed that large males can displace smaller males by antagonistic behavioural interactions at calling sites. This could lead to fewer small males being sampled, especially at the smaller pools, such as those at Lifeboat Road and the tobacco dump where high densities of males can occur. However, this should not affect the size distribution of females arriving to spawn. As has been shown in this study, the trend of female body size follows that of the males (Fig. 2, Fig. 3).

Breeding success has been routinely monitored by estimating the number of toadlets emerging from the pools. The results for the 1980s are summarised in Table 4. This shows that large numbers metamorphosed at Ainsdale, especially from 1984 onwards, but fewer toadlets appeared at other sites, the National Trust area having the worst record overall. However, it is important to note that some metamorphosis occurred

at the less successful sites in most years, giving the impression that satisfactory breeding was taking place, although with declining performance at Cabin Hill and the National Trust site.

The Lifeboat Road results appear anomalous in that, despite at least 'moderate' metamorphic success since 1983, few young adults have appeared in the breeding population. The most likely explanation is that what are perceived as 'moderate' toadlet numbers at these tiny, easily searched ponds are still too few to outweigh the high mortality suffered by immature animals in the years before they enter the breeding cohort.

Factors contributing to low toadlet numbers at some sites were spring/summer droughts in 1982, 1984 and 1985, predation of tadpoles by aquatic invertebrates and growth inhibition of natterjack tadpoles by those of other anurans, especially *B. bufo*.

Catastrophic mortality of developmental stages due to drying out of water bodies is an expected problem for an amphibian which habitually spawns in ephemeral pools (Beebee, 1979; Davis, 1985). However, emergency deepening, by hand, of some sites, particularly at Ainsdale, has undoubtedly aided metamorphosis in some years.

Tadpole predation has been shown to be major mortality factor by Banks and Beebee (1988) and Davis (1985). There is also some evidence that invertebrate predators of natterjack tadpoles are more abundant in deeper pools that are less likely to dry up (Banks and Beebee, 1988). In Merseyside, older scrapes appear to support higher densities of predators than younger ones. Those at Cabin Hill and Lifeboat Road have particularly large numbers of dragonflies (Odonata), especially *Sympetrum striolatum*. Banks and Beebee (1988) list nymphs of this genus as being effective predators of natterjack tadpoles. The two mild winters of 1987-88 and 1988-89 may well have enhanced predator numbers at the Merseyside sites.

It is known that high densities of other anuran tadpoles can inhibit the growth of natterjack tadpoles, making them more susceptible to desiccation and predation (Banks and Beebee, 1987). In Merseyside, *B. bufo* and to a lesser extent, *Rana temporaria*, are associated with older, more permanent water bodies in the fixed dunes, while *B. calamita* favours ephemeral or recently created pools nearer the sea. As yet, few common toads have bred in the Ainsdale frontal dune slacks, although they began to invade this area in the mid-1980s. At other sites, particularly Cabin Hill and the tobacco dump, common toad numbers increased during the 1970s and, by the 1980s, tadpole densities were probably high enough to produce inhibition effects.

Little is known about mortality factors affecting toadlets and immature natterjacks (Davis, 1985). It is possible that toadlets arising from growth-inhibited tadpoles show reduced survival because, for example, they have less time to gain weight before hibernation.

Adult natterjacks are long-lived (Beebee, 1983) and have previously survived several successive years with adverse breeding conditions in Merseyside (Smith and Payne, 1981). Cooke (1981), however, points out that

old females (over 70mm long) may lay spawn with reduced viability. He describes 'senile' populations, resulting from minimal recruitment over at least three years, in which males exceed an average of 60mm long, with no individuals less than 55mm. By 1989, this description applied to three of the four breeding groups studied here with the possible exception of Lifeboat Road where one male measured 52mm (Fig. 3). Banks and Beebee (1986) also found that old female natterjacks could produce spawn with reduced viability. Two out of about 20 aged females laid some non-viable eggs, those individuals being 11 and 12 years old.

Routine monitoring during 1988 and 1989 showed that all sites supported large numbers of breeding adults which laid many spawn strings. There was no evidence of reduced spawn viability. However, it seems clear that recruitment to three of the breeding groups in recent years has been insufficient to prevent the size distribution shifting towards a preponderance of larger and older individuals. This trend is most apparent at the tobacco dump and Lifeboat Road (Fig. 2, Fig. 3) where the small size of the pools may make natterjack tadpoles particularly susceptible to predation and inhibition problems.

Conservation measures to increase recruitment at three of the study areas seem justified. These could include removal of competing anurans, predator and scrub control and the excavation of more shallow scrapes, which should be situated in the frontal dunes and have as large an area as possible. Continued monitoring of adult size distribution is also desirable.

The results of this study confirm that recruitment can be monitored by measuring snout-vent lengths of adult natterjacks assembling to breeding sites. The technique is simple and seems to be more sensitive than the inevitably crude and possibly misleading estimation of toadlet production. One disadvantage is that a licence is required to handle the animals, this being unnecessary for counting toadlets. Also, comparisons should be confined to the same general area. Natterjacks from other regions of the country may well have different growth rates. The approach has potential both for alerting site managers to the need for action to promote recruitment and for monitoring the effects of conservation management over a period of years.

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REFERENCES

- Arak, A. (1983). Sexual selection by male-male competition in natterjack toad choruses. *Nature, London*. **306**, 261-262.

- Banks, B. and Beebee, T. J. C. (1986). A comparison of the fecundities of two species of toad (*Bufo Bufo* and *B. calamita*) from different habitat types in Britain. *Journal of Zoology, London (A)* **208**, 325-337.
- Banks, B. and Beebee, T. J. C. (1987). Spawn predation and larval growth inhibition mechanisms for niche separation in anurans. *Oecologia (Berlin)* **72**, 569-573.
- Banks, B. and Beebee, T. J. C. (1988). Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *Journal of Animal Ecology* **57**, 475-492.
- Beebee, T. J. C. (1979). A review of the scientific literature pertaining to the Natterjack Toad (*Bufo calamita*) throughout its geographical range. *Biological Conservation* **16**, 107-134.
- Beebee, T. J. C. (1983). *The natterjack toad*. Oxford University Press.
- Cooke, A. S. (1981). *Natterjacks in Britain, 1980*. Unpublished report. Nature Conservancy Council.
- Cooke, A. S. (1982). *Natterjacks in Britain, 1981*. Unpublished report. Nature Conservancy Council.
- Cooke, A. S., Banks, B. and Langton, T. (1984). *Natterjacks in Britain, 1983*. Unpublished report. Nature Conservancy Council.
- Davis, C. A. (1985). The population dynamics of the natterjack toad (*Bufo calamita* Laur.) in the north Merseyside sand-dune system. Unpublished PhD thesis. Liverpool Polytechnic.
- Flindt, R. and Hemmer, H. (1968). Beobachtungen zur Dynamik einer Population von *Bufo Bufo* und *Bufo calamita*. *Zoologische Jahrbücher (Systematik, Ökologie und Geographie der Tiere)* **95**, 469-476.
- Hemmer, H. and Kadel, K. (1972). Gewichtszustand und Wachstumsverlauf bei der Kreuzkröte (*Bufo calamita* Laur.). *Forma et Functio* **5**, 113-120.
- Smith, M. A. (1951). *The British Amphibians and Reptiles*. London: Collins.
- Smith, P. H. and Bownes, C. F. (1978). *The use of artificial breeding pools by adult Natterjack Toads in Ainsdale Sand Dunes National Nature Reserve in 1978*. Unpublished report. Liverpool Polytechnic.
- Smith, P. H. and Payne, K. R. (1980). A survey of Natterjack Toad *Bufo calamita* distribution and breeding success in the north Merseyside sand dune system, England. *Biological Conservation* **19**, 27-39.

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TEMPORAL CHANGES IN THE BEHAVIOUR OF FOAM-MAKING *LEPTODACTYLUS FUSCUS* TADPOLES

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ABSTRACT

Recently-hatched *L. fuscus* tadpoles kept out of water make a heap of foam which helps them to survive. At first, isolated tadpoles can make foam (by spitting mucus bubbles), but later, tadpoles can only make foam when in a group of five or more. If tadpoles are separated from one another, out of water, they can aggregate by active, apparently random wriggling movements, but this ability too declines with time since hatching.

INTRODUCTION

I have previously shown (Downie, 1984, 1989) that stage 27-28 tadpoles (Gosner, 1960) of the foam-nesting frog *Leptodactylus fuscus* are able to make a foam which replaces the original nest foam made by the parents. The tadpoles are able to live in this foam for up to several weeks, normally in the original nesting burrow, and to enter any nearby pool that forms, as feeding-stage tadpoles, once heavy rain falls. Foam making is a communal activity: the tadpoles stimulate each other by contact, to wriggle and spit out mucus-rich bubbles, and the wriggling movements themselves produce some bubbles. The 1984 study presented evidence that the ability to make foam diminished the longer the tadpoles remained in the nest. In this note, I report on aspects of this decline

—the aggregative ability of tadpoles out of water and the ability of individuals to make foam.

MATERIAL AND METHODS

COLLECTION AND MAINTENANCE OF TADPOLES

Two foam nests of *L. fuscus* were collected from burrows around the margin of a temporary pool site on the University of West Indies campus at St. Augustine, Trinidad, and from the bank of a ditch at Carmody Road, also in St. Augustine, in June and July 1989. The first nest was collected on 23 June, and the tadpoles were already stage 27-28 and making foam. However, heavy rain had occurred on 17 June, so this must have been a recently-laid nest (it takes 4-5 days to reach stage 27-28; Downie, 1984). The second nest was found on 15 July and the tadpoles were recently hatched, not

yet making foam (stage 24-25). After collection, foam-making tadpoles were maintained on the surface of moist tissue paper in 2 litre rectangular polythene tubs with the lids on. I have found moist tissue preferable to mud as a substrate for laboratory maintenance of foam-making tadpoles: it is easier to keep to the right degree of moisture and does not suffer from the occasional bacterial problems found with mud as a substrate.

BEHAVIOURAL OBSERVATIONS

To monitor progressive changes in tadpole behaviour, tadpoles were removed from foam at weekly intervals, and placed singly on the surface of damp tissue in 2 litre rectangular polythene tubs, six tadpoles to a tub, either 2cm or 6cm apart at the start. Tadpole movements were monitored at 24h intervals for up to two days. In addition, tadpoles were removed from foam, placed 2cm apart on moist tissue in petri dishes with the lid on and watched continuously for an hour or so.

RESULTS

AGGREGATION

Aggregation results are shown in Table 1. It is clear that tadpoles initially set 2cm apart aggregated more successfully than those set 6cm apart, and that the ability to aggregate declined with time since hatching. It is also clear that aggregation mostly occurred within the first day. This does not mean, however, that the tadpoles then became immobile: some aggregation did occur during the second day and, once an aggregate formed, the tadpoles remained in contact with one another, so the scope for further aggregation was lessened. Fig. 1 shows the actual movements of tadpoles in four representative cases.

GENERAL OBSERVATIONS ON TADPOLE BEHAVIOUR

Once an aggregate formed it could stay in the same place for the duration of the experiment: but this was

not always the case — a complete aggregate could move as a unit (shown in Fig. 1). This was also noticed in the stock tadpoles, where the foam heap, containing up to 100 tadpoles, could move from the centre of a tub to the margin.

An unexpected observation was that tadpoles isolated within the first week after hatching were able to make foam either as individuals or in small groups (2, 3 or 4 tadpoles). Of 24 week one tadpoles, after 48h, one single tadpole had made no foam, but three singles had made foam, as had two pairs, three groups of four and one group of five. This observation is shown in Fig. 1 and discussed later in the light of previous results. Although *L. fuscus* tadpole survival out of water is generally very good, for up to several days (Downie, 1984 and unpublished observations), I did experience a few casualties amongst older tadpoles. Amongst tadpoles three weeks post hatching, nine out of 48 died after 48h. Amongst tadpoles four weeks post hatching, one out of 18 died after 24h. Casualties always involved tadpoles that had remained as individuals.

Tadpoles watched continuously after isolation on moist tissue showed the following features. Movements were generally violent wriggles, often with no progress in any direction, but occasionally with a few millimetres movement from the original spot. Episodes of movement by isolated tadpoles were not rigorously quantified, but it was clear that recently hatched tadpoles were more active than older tadpoles, that tadpoles were more active soon after isolation than later, and that tadpoles were more active on very damp tissue than on rather dry tissue. Wriggles often led to the re-orientation of the head of a tadpole, but there was no sign that tadpoles were able to orientate and move towards one another: when aggregation occurred, it appeared to be the result of essentially random movements; and two tadpoles close together often then moved away from one another. However, once two tadpoles had touched, no case was observed where they then moved apart again.

Tadpole age	n	Time after setting up											
		24h						48h					
		Group size						Group size					
		1	2	3	4	5	6	1	2	3	4	5	6
a) 2cm apart													
1 week	2	0.5	0.5	—	0.5	0.5	—	0.5	0.5	—	0.5	0.5	—
2 weeks	5	1.2	1.2	0.2	0.2	0.2	—	0.8	1.0	0.2	0.4	0.2	—
3 weeks	5	5.6	0.2	—	—	—	—	4.8	0.6	—	—	—	—
4 weeks	2	4.0	1.0	—	—	—	—	4.0	1.0	—	—	—	—
b) 6cm apart													
1 week	2	1.5	0.5	0.5	0.5	—	—	1.5	0.5	0.5	0.5	—	—
2 weeks	5	6.0	—	—	—	—	—	5.2	0.4	—	—	—	—
3 weeks	5	5.6	0.2	—	—	—	—	5.6	0.2	—	—	—	—
4 weeks	1	6.0	—	—	—	—	—	6.0	—	—	—	—	—

TABLE 1: Aggregation of isolated *L. fuscus* foam-making stage tadpoles. a) tadpoles set 2cm apart at the start. b) tadpoles set 6cm apart at the start. n = number of trials at each tadpole age. Aggregation results are given as the mean number of groups of each size (2-6) or mean number remaining as individuals (1) per trial after 24h and 48h. Tadpoles were tested 1, 2, 3 and 4 weeks after hatching.

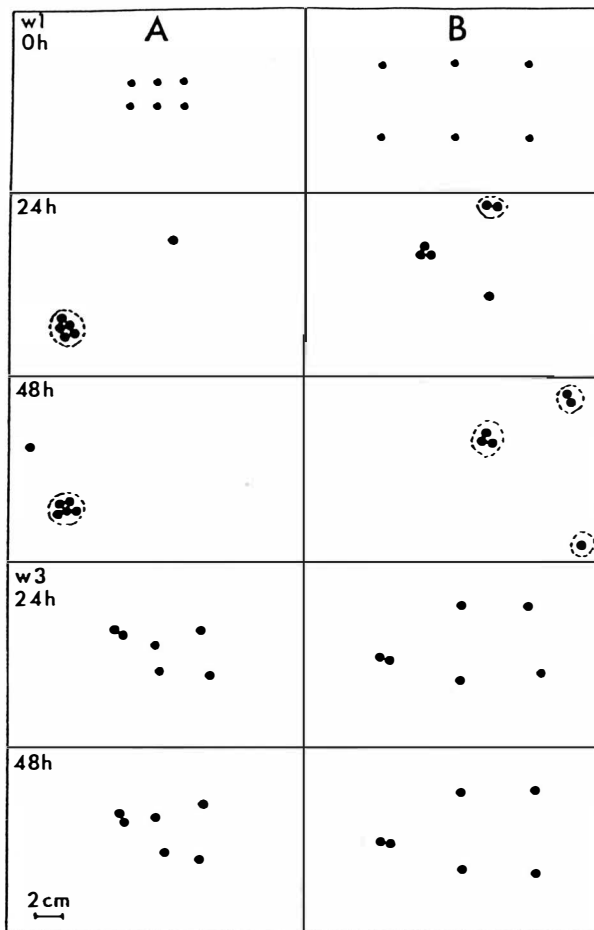


Fig. 1 Examples of movements of isolated *L. fuscus* foam-making tadpoles. Column A — tadpoles 2cm apart at the start. Column B — tadpoles 6cm apart at the start. Approximate initial positions are shown at 0h. All tadpoles are from the clutch taken on 15 July, and records are shown for tadpoles observed during the first and third weeks after hatching. Each tadpole is denoted by a black dot, indicating the position of the tadpole body. Tadpoles denoted as very close together are in contact. A dotted line surrounding an individual or group denotes foam made by the tadpoles.

DISCUSSION

The experiments reported here show that isolated stage 27-28 *L. fuscus* tadpoles are able to aggregate into groups, but that this ability declines with time since hatching. Presumably these tadpoles, which are not feeding, are continuously using up their yolk reserves, and this is reflected eventually in a decline in energy available for mobility. Tadpoles placed initially 2cm apart aggregated more effectively than those initially 6cm apart. This is not surprising given that each tadpole, fully extended, is around 1cm long, and that once in contact with one another, they tend to remain so. Random movements can easily explain aggregation: there is no evidence, from the observed behaviour of the tadpoles, for directed aggregative movement.

Tadpole survival out of water for the two days involved in these experiments was good, but some casualties occurred amongst older tadpoles that did

not aggregate. Since older tadpoles that survived well did not aggregate as well as younger tadpoles, the differences in aggregation ability were not simply due to tadpole death.

In addition, the most recently-hatched tadpoles were not only very active, showing highly aggregative behaviour: they were also able to make foam as individuals. Downie (1989) found that individuals could not make foam and that foam-making ability increased as group size increased from 3 to 5, to 10. Caldwell and Lopez (1989) have reported a similar finding for *L. mystaceus*. However, in both of these previous reports, the tadpoles tested were at least six days post-hatching. Here then is another sign of developmental decline: the longer the time since hatching, the lesser the ability to make foam. Foam-making requires a certain frequency of bubble formation: recently hatched tadpoles can make enough bubbles on their own; later ones require the stimulus of contact with their neighbours.

Caldwell and Lopez (1989) support the idea that foam made by tadpoles helps survival in the nest, but question my suggestion (Downie, 1984) that regeneration of such foam could help tadpoles that had left the nest if their pool happened to dry. Their argument is that such tadpoles would be scattered individuals unable to make foam. However, I have shown here that tadpoles are able to aggregate, and my field observations show that if a pool dries up, *L. fuscus* tadpoles are found in congregations, in low points of the pool, under leaves or rocks.

Foam-making by tadpoles has now been reported from two members of the *Leptodactylus fuscus* species group (Heyer, 1978). It would be interesting to test other members.

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REFERENCES

- Caldwell, J. P. and P. T. Lopez (1989). Foam-generating behaviour in tadpoles of *Leptodactylus mystaceus*. *Copeia* **1989**, 498-502.
- Downie, J. R. (1984). How *Leptodactylus fuscus* tadpoles make foam and why. *Copeia* **1984**, 778-780.
- Downie, J. R. (1989). Observations on foam-making by *Leptodactylus fuscus* tadpoles. *Herpetological Journal* **1**, 351-355.
- Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologia* **16**, 183-190.
- Heyer, W. R. (1978). Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County, Scientific Bulletin* **29**.

FUNCTIONS OF THE FOAM IN FOAM-NESTING LEPTODACTYLIDS: ANTI-PREDATOR EFFECTS OF *PHYSALAEMUS PUSTULOSUS* FOAM

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ABSTRACT

In a laboratory experiment, *L. fuscus* tadpoles, a known predator of *P. pustulosus* foam nests, took a much higher proportion of floating eggs presented as individuals than as groups embedded in foam: the bigger the group, the greater the protection. *L. fuscus* tadpoles did not take post-hatching stages of *P. pustulosus* but these were predated by dragonfly nymphs.

INTRODUCTION

In a previous paper (Downie, 1988), I discussed the possible functions of the floating foam nests produced by some anurans. Evidence based on experiments with foam nests of the widely-distributed neotropical Leptodactylid *Physalaemus pustulosus* suggested that, contrary to previous publications (Dobkin and Gettinger, 1985; Gorzula, 1977) the foam has no significant thermal properties; the foam also has very limited ability to protect eggs and hatchlings from desiccation. A third possible function is protection of eggs from predation: evidence presented showed that foam nests are attacked by predators, particularly the tadpoles of another Leptodactylid, *Leptodactylus fuscus*, and that *P. pustulosus* eggs are consumed by these tadpoles, and by odonate larvae. However, it seemed likely that embedding eggs in a mass of foam should help a proportion of them to survive. The experiments described in this note were designed to test this suggestion.

MATERIALS AND METHODS

COLLECTION OF NESTS AND PREDATORS

The *P. pustulosus* foam nests used in this study were found in drainage ditches near the University of West Indies campus at St. Augustine, Trinidad, during June and July 1989. Freshly-made nests were collected early in the morning after wet days or nights. Although June and July are normally very wet months in Trinidad, 1989 had unusually low rainfall, and the number of foam nests collected was therefore less than anticipated.

The potential predators used in this study were dragonfly nymphs, tadpoles of *L. fuscus* and tadpoles of *P. pustulosus*. Dragonfly nymphs were collected by handnet from the mud surface of the same ditches used for the collection of foam nests and kept in 2 litre polythene tubs, in water with a muddy bottom. *L. fuscus* tadpoles were reared in the laboratory in glass tanks from foam nests found in burrows adjacent to drainage ditches and temporary pool sites in the St. Augustine area. *L. fuscus* tadpoles were fed *ad lib* with a proprietary fish food. *P. pustulosus* tadpoles were

reared from foam nests in the same way as *L. fuscus* tadpoles.

PREDATION EXPERIMENTS

P. pustulosus eggs, hatchlings or stage 27 tadpoles (Gosner, 1960) were exposed to potential predators under standard laboratory conditions, in 2 litre rectangular polythene tubs, containing 1.5 litres water (6cm deep) for a period of 18h when the number of survivors was recorded. In most cases, the tubs had a clear bottom, but in a few, a thin covering of mud was present to simulate ditch conditions. Eggs floated on the surface of the water, buoyed by surrounding foam, as individuals, or groups of 5, 10 or 20 eggs, each tub containing 20 eggs in all. In isolating individual eggs and groups from foam, it was difficult to standardise the number of foam bubbles stuck to each egg or group, so this was quite variable. In experiments using *P. pustulosus* hatchlings or stage 27 tadpoles, 20 individuals were again used, but they were free to swim in the tub. Predators had no access to alternative food during the 18h of the experiment.

The predator classes used were: *L. fuscus* — four large mature tadpoles (around stage 35) or eight smaller tadpoles (around stage 30); dragonfly nymphs (species not known) — two medium-sized nymphs, around 1.5cm long; *P. pustulosus* — eight tadpoles around stage 30.

RESULTS

PREDATION OF FLOATING EGGS

The results of the predation experiments involving floating *P. pustulosus* eggs (individuals and groups) are shown in Table 1. The number of trials possible was not large, because of shortage of time and scarcity of material, but the overall trend in the results is clear. Exposed to large *L. fuscus* tadpoles, individual eggs were nearly all consumed, whereas eggs in groups survived better. Smaller *L. fuscus* tadpoles also predated individual eggs, though less heavily. Groups again survived better. In general, with both size classes of predator, the larger the group, the better the survival chance, with one result — groups of five exposed to

large *L. fuscus* being anomalous: unfortunately, only two trials were made in this class. With large *L. fuscus* as predators, foam bubbles were usually consumed as well as eggs; with smaller *L. fuscus* more foam was usually left. Occasionally, fragments of partly consumed eggs were left at the bottom of the tub. As previously described (Downie, 1988) *L. fuscus* tadpoles swam to the surface and bit at foam and eggs.

Dragonfly nymphs took a few individual floating eggs, but none from groups, and *P. pustulosus* tadpoles took no eggs at all. Dragonfly nymphs spent most of their time at the bottom, as did *P. pustulosus* tadpoles.

PREDATION OF HATCHLING AND OLDER TADPOLES

The results of a small number of predation experiments involving *P. pustulosus* hatchlings and stage 27 tadpoles are shown in Table 2. In no case did *L. fuscus* tadpoles consume any post-hatching *P. pustulosus*, whereas dragonfly nymphs took significant numbers of them. There was no evidence from the experiments that the nature of the bottom — clear or muddy — mattered to the effectiveness of dragonfly nymph predation, but the number of trials was very small.

BEHAVIOUR OF *P. pustulosus* HATCHLINGS AND OLDER TADPOLES

On hatching, *P. pustulosus* tadpoles were observed to hang motionless from the base of the foam nest, or the side of tub the nest was floating in; a few lay on the bottom; swimming occurred very occasionally. As development proceeded over the next two days to about stage 27, tadpoles became more active, but spent much of their time at rest on the bottom. On a mud bottom, these tadpoles were very cryptic, mostly motionless, but capable of rapid movement when disturbed.

ABUNDANCE OF PREDATORS IN NATURAL CONDITIONS

It would require a large scale survey to establish the overall relative abundance of the predators used in this study. In the drainage ditches and temporary pools I have sampled, *L. fuscus* and *P. pustulosus* nearly always occur together, and dragonfly nymphs are very abundant. The ditch used to collect the foam nests for this study was choked, with little through flow of water. It generally contained water about 2-3cm deep on a mud bottom, with sparse overhanging vegetation, and was 50cm wide. Two hand-net samples of 50cm

Potential Predator Class	Arrangement of Eggs											
	20 Individuals			4 Groups of 5			2 Groups of 10			1 Group of 20		
	n	no	%	n	no	%	n	no	%	n	no	%
4 stage 35 <i>L. fuscus</i>	4	0.25 (0-1)	1.25	2	11.5 (5-18)	57.5	5	1.6 (0-3)	8.0	6	7.2 (0-17)	35.8
8 stage 30 <i>L. fuscus</i>	4	2 (0-6)	10.0	2	9 (3-15)	45.0	4	12.8 (0-20)	63.75	3	14 (13-16)	70.0
2 dragonfly nymphs	2	18 (17-19)	90.0	—	—	—	—	—	—	2	20 (20)	100.0
8 stage 30 <i>P. pustulosus</i>	2	20 (20)	100.0	—	—	—	—	—	—	—	—	—

TABLE 1: Survival of *P. pustulosus* eggs as individuals or groups after 18h exposure to various classes of potential predator. (n = number of trials; No = mean number of survivors per trial (range in brackets); % = percentage of survivors).

Potential Predator Class	Potential Prey Class											
	20 hatchlings clear bottom			20 hatchlings mud bottom			10 stage 27 clear bottom			10 stage 27 mud bottom		
	n	no	%	n	no	%	n	no	%	n	no	%
4 stage 35 <i>L. fuscus</i>	2	20 (20)	100	—	—	—	—	2 (10)	10	100	—	—
8 stage 30 <i>L. fuscus</i>	2	20 (20)	100	—	—	—	—	—	—	—	—	—
2 dragonfly nymphs	2	17 (14-20)	85	2	17 (17)	85	2	5 (4-6)	50	4	5 (3-8)	50

TABLE 2: Survival of *P. pustulosus* hatchlings and stage 27 tadpoles after 18h exposure to various classes of potential predator. (n = number of trials; No = mean number of survivors per trial (range in brackets); % = percentage of survivors)

lengths from the muddy bottom of the ditch yielded 22 and 27 dragonfly nymphs, of a range of stages, respectively. These nymphs lay motionless on the bottom, often partly covered in mud particles: like the *P. pustulosus* tadpoles, they were very cryptic. The predators used in this study clearly occur and have access to *P. pustulosus* nests and tadpoles.

DISCUSSION

The main result of this study is the demonstration that *P. pustulosus* eggs do get some protection from predation by being surrounded in foam. Individual floating eggs were very likely to be eaten by *L. fuscus* tadpoles. The same number of eggs, exposed for the same time to the same number of predators had a much better chance of survival when presented in groups held together by foam bubbles.

In addition, the study showed that floating eggs, singly or in groups, are not much at risk from dragonfly nymphs, whereas on hatching, the risks are reversed, with *L. fuscus* tadpoles not attacking *P. pustulosus* larvae at all, but dragonfly larvae taking them, particularly when they become more active. Not surprisingly, perhaps, *P. pustulosus* tadpoles did not predate eggs of their own species. Predation tests in the laboratory need to be interpreted with caution, but, as pointed out earlier (Downie, 1988) *L. fuscus* tadpoles are serious potential predators of *P. pustulosus*. They inhabit the same temporary pools and drainage ditches, but *L. fuscus* eggs are laid in advance of rain, so that their tadpoles enter the water at the same time as eggs of other temporary pool nesting species like *P. pustulosus*. *L. fuscus* tadpoles have been seen to attack *P. pustulosus* nests in the wild, and the results reported here show how effectively they can consume eggs in the laboratory. It is a little puzzling that *L. fuscus* tadpoles stop predating *P. pustulosus* after they have hatched. The results for dragonfly nymphs are less surprising: they spend most of their time at the bottom as 'sit-and-wait' predators and would therefore be expected to attack mainly mobile swimming prey. Their very high numbers must make them the most serious threat to the survival of *P. pustulosus* tadpoles since fish are usually absent from these pools and drainage ditches. The absence of a difference between the predation success of dragonfly nymphs on muddy and clear bottoms is perhaps surprising. However, on muddy bottoms, both predator and prey are highly cryptic, and changing the background may therefore not alter significantly the outcome of the interaction. A larger scale experiment on tadpole-dragonfly nymph interactions would be of interest.

The protection offered to eggs by being in a floating foam nest may be of two kinds, not distinguished in

this study. As suggested by Martin (1967), Heyer (1989) and Ryan (1985), most of the eggs in a floating foam nest are above the water surface and therefore removed from the habitat of the most likely predators, tadpoles, fish and predatory aquatic insects. This effect must be much greater in intact nests, which contain several hundred eggs, than in even the biggest groups I tested of 20 eggs.

In addition, the stickiness and adhesiveness of foam may make removal of the eggs difficult for potential predators. Disentangling eggs from foam is not an easy business for humans, and *L. fuscus* tadpoles do seem to have to expend some effort in feeding on foam bubbles and eggs. Whether foam gives better mechanical protection than other devices used by frogs, such as egg strings or jelly masses, could perhaps be tested by experimentation. The discovery by Roberts (1989) of a population of the Australian myobatrachid *Limnodynastes tasmaniensis* which makes floating foam nests in one part of its range, but non-foamy egg masses in another part offers the opportunity of a natural test of the differences between foam and jelly nests.

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REFERENCES

- Dobkin, D. S. and Gettinger, R. D. (1985). Thermal aspects of anuran foam nests. *Journal of Herpetology* **19**, 271-275.
- Downie, J. R. (1988). Functions of the foam in the foam-nesting leptodactylid *Physalaemus pustulosus*. *Herpetological Journal* **1**, 302-307.
- Gorzula, S. (1977). Foam nesting in leptodactylids: a possible function. *British Journal of Herpetology* **5**, 657-659.
- Heyer, W. R. (1969). The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* **23**, 421-428.
- Martin, A. A. (1967). Australian anuran life histories: some evolutionary and ecological aspects. In Weatherley, A. H. ed. *'Australian inland waters and their fauna'* Ps 175-191. Australian National University Press, Canberra.
- Roberts, J. D. (1989). Non-foamy egg masses in *Limnodynastes tasmaniensis* (Anura: Myobatrachidae) from South Australia. *Copeia* **1989**, 488-492.
- Ryan, M. J. (1985). *'The tungara frog — a study in sexual selection and communication'* University of Chicago Press, Chicago.

AN ARCHAEOLOGICAL STUDY OF FROGS AND TOADS FROM THE EIGHTH TO SIXTEENTH CENTURY AT REPTON, DERBYSHIRE

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ABSTRACT

During excavation work around the Church of St. Wystans at Repton, Derbyshire, a large quantity of Common frog (*Rana temporaria*) and Common toad (*Bufo bufo*) bones were discovered at several sites. The robbing holes, suspected saw-pit, crypt, drain and burial mound all appeared to have acted as historical pitfall traps (between the eighth and sixteenth century), which in some cases caught frogs and toads in large numbers. In the eighth and ninth century the Common frog was abundant compared to the Common toad which was rare or even absent from Repton. However, by the fourteenth century, toads had become well established, and in modern times, extremely abundant in the area. This change may be associated with the formation of an ox-bow lake between the ninth and sixteenth century.

A very high proportion of frog bones were recorded among the disarticulate human bones of the ninth century Viking burial mound. This mound is known to have been disturbed in the seventeenth century. However the almost complete absence of toad bones suggests that there has been little contamination to these deposits during and after the fourteenth century, since the Common toad appears to have been common in Repton from this time onwards.

INTRODUCTION

Repton has been the subject of detailed archaeological investigations from 1974 to 1988, with excavation centred around the church of St. Wystans which was used in 873-4 as the Winter camp of the Great Viking army. At several excavation trenches unusually high densities of amphibian bone were discovered. Because of the care of excavation it has been possible to give precise datings for all these samples. The bone preservation has been so good that diagnostic identification down to species level can be made on even juvenile bones.

A BRIEF HISTORICAL OUTLINE

Before the end of the seventh century a monastery was founded at Repton, which became closely associated with the royal house of Mercia. The Anglo-Saxon crypt of St. Wystans church probably served as a mausoleum, containing the body of Wystan who was buried at Repton around 839 (Biddle and Kjølbye-Biddle, 1985). In 873 the Great Viking army came up the River Trent and made their winter camp at Repton. They departed the following autumn of 874, but during this short period of occupation at least 249 Vikings died and were buried in a burial mound formed from the ruined foundations of an earlier building (Biddle and Kjølbye-Biddle, 1986). In the twelfth century an Augustinian priory was established by the Cannon of Cake (Biddle and Kjølbye-Biddle, 1985). After the dissolution of the priory in 1538, the building eventually formed part of the School at Repton.

METHODS

Bone material was separated out by searching and sieving (with a 1mm mesh) soil layers found to contain small animal bone. For extensive layers only samples were taken. Bone material from the crypt deposits were also sorted out by water floatation. Amphibian bones were recognised using features shown by Engelmann, Fritzche, Gunther and Obst (1985). Species identification was confined to the ilium, and based on features given by Holman (1985) and Engelmann *et al.* (1985). The ilium of the Common frog *Rana temporaria* has an obvious although anteriorly depressed ilial blade. The Common toad *Bufo bufo* lacks any trace of an ilial blade but has a low rounded ilial prominence.

RESULTS

Amphibian bones were found at five sites. These are referred to here as the following:

1. The Robbing holes
2. The Drain
3. The Mound
4. The Crypt
5. The Saw-pit

Table 1 shows the number of identified ilia recovered from each site. The archaeological context and specific details of each site are briefly outlined below. The trench, layer and feature reference numbers used in this excavation are given in the Appendix, Table 2. The bone material has now been deposited at the Derby Museum.

SITE	CENTURY	NUMBERS OF ILIA	
		Common Frog	Common Toad
Robbing holes	eighth	2	0
Drain	eighth - ninth	63	0
Mound	ninth*	64	2
Crypt	fourteenth - fifteenth	16	8
Saw-pit	sixteenth	2	1

TABLE 1: The numbers of identified ilia found at each site. * = disturbed in the seventeenth century and later (see text).

1. The Robbing Holes

Before the crypt of St. Wystans was constructed an earlier building stood just to the north of the crypt. This building (referred to as Building 'B' in unpublished reports) was demolished before the construction of the crypt in the mid-eighth century. During its demolition holes were left in the ground where timbers and possibly stone had been removed. Two of these holes contained frog bones. These deposits are probably dated to the first half of the eighth century.

2. The Drain

The crypt was probably built as a free standing mausoleum in the middle of the eighth century, possibly to take the body of King of Æthelbald who died in 757. Associated with the crypt there was a substantial drain lined with green Keuper sandstone and covered with large sandstone cover slabs (Fig. 1). The floor of the drain was soil. This drain was fed water from the crypt floor which had to flow under the lowest stone of the crypt wall with a mere 5cm clearance. Exactly where the water flowed to is not known since excavation had to be restricted to the first three metres of the drains course. The precise function of the drain is also not yet understood; it may have taken water from a baptismal basin that would have been large enough for total submersion, or have simply drained the crypt floor. Certainly by 849 when Wystan was buried in the crypt, the crypt would no longer have functioned as a baptistry.

A very large collection of frog bones were collected from a soil sample taken from within the drain. The sample of bones contained all skeletal components and included 96 femora and 63 ilia. This gives a minimum estimate of 48 frogs; however, since it was not possible to sample the entire drain, the actual number of individuals would certainly have been considerably greater. The femur length varied from a minimum of 9mm to a maximum of 26mm, mean 14.4mm, S.D. 3.63.

3. The Mound

A two-room stone building, sunk to about 80cm, was found during excavation, less than 100 metres west of the crypt. This sunken building pre-dates the crypt and already had been long abandoned when the Great Viking Army came in 874. Following the death of at least 249 individuals, the building was cut down to

ground level and the disarticulated bones stacked neatly around the walls of the eastern compartment. Timbers were laid side by side over the burial chamber which was then covered by a low cairn of irregular stones and possibly a thin (less than 30cm) layer of top soil.

The burial mound was discovered and opened up around 1686 by Thomas Walker, opened up again in 1787, and briefly excavated in 1914 (Biddle and Kjølbye-Biddle, 1986).

Amphibian bones were found (during sieving of all soil excavated from the mound) in the disturbed human bone deposits, in the undisturbed and disturbed squatter deposits left while the building had been neglected, and lastly in the robber trenches made by Thomas Walker. Almost all of this amphibian bone was frog. A total of 64 Common frog ilia were found compared to just two Common toad ilia. The vast majority (79 per cent) of amphibian bone were found amongst the disturbed human bone. Because of the later disturbances to the mound the dating of most of these bones is uncertain (however see discussion).

4. The Crypt

In the late middle ages a stair had been inserted in the eastern recess of the crypt to give direct access from the outer court of the adjacent priory. The removal of the bottom step (the only surviving part of the stair) during archaeological excavations revealed a wedge of untouched deposits lying on and against the original eighth century structure of the crypt. Within these deposits were found a chip of red tile (dated not earlier than the thirteenth century) and a chip of glazed ceramic (not earlier than fourteenth century). These two items, taken in conjunction with the insertion of the stair which sealed these layers, suggest that the deposits should be dated at the earliest to the fourteenth century; they are unlikely to be much later.

Within these deposits many frog and toad bones were found. A total of 16 Common frog ilia and eight Common toad ilia were counted. The surviving wedge of soil would have only represented a tiny fraction of the total area of the crypt floor, which suggests that many more frog and toad bones would have been deposited in the crypt during this period.

5. The Saw-pit

North of the crypt, in the open besides the north-east corner of the north aisle, a large rectangular pit



Fig. 1 The excavated drain from Trench 3, Repton. View looking westwards towards the crypt of St. Wystans Church. The cover slabs are still in position for most of the drains length. The ranging rods are 50cm in total length.

(4m x 2m at the top, 1 m wide at the bottom) was discovered cutting through the remains of a priory-period trackway and cemetery. The pit was probably associated with some industrial process, and may be interpreted as a saw-pit. It probably belonged to the period after the dissolution of the priory in 1538, but the pottery and other finds suggest a date later not later than the mid-sixteenth century.

From the bottom of the saw-pit a small number of amphibian bones was found among a very large collection of larger (mainly domestic) animal bones. The identified amphibian bones consisted of two frog ilia and a single toad ilium.

DISCUSSION

The most obvious question is, how did these frog and toad bones get into these archaeological features? The simplest and most likely explanation is that these amphibians became trapped. The robbing-holes, the saw-pit and the crypt with its drain could all have acted as large pitfall traps from which escape was not possible for these amphibians. The mound is discussed later in this section.

The crypt floor had been sunken by about two metres from the original ground level (Biddle and Kjølbye-Biddle, 1985) and frogs and toads may

frequently have fallen down the entrance steps and become trapped in the building. The density of bones (representing at least 12 individuals) in the small wedge of soil under the step demonstrates that many frogs and toads may have been trapped in the crypt around the fourteenth century. In the drain, the very high density of frog bones (at least 48 frogs in the sample examined) suggests that these deposits probably built up over a number of years. About 50 per cent of these were juveniles. The body length can be approximately calculated from the femur length in *Rana temporaria* (see Esteban and Sanchiz, 1985). Smith (1973), Paris (1985) and Engelmann *et al.* (1986) agree that this species of frog matures at a minimum body length of 40–45mm, and we have concluded that femurs below 14mm in length are juveniles.

We do not know if the frogs in the drain were actually trapped or if they used the drain as a refuge from which they ventured out at night via the drain outflow (if there ever had been one). It is most likely frogs which become trapped in the crypt entered the drain from the crypt floor. Inside the drain, escape would have been impossible if the outflow became blocked once the drain fell into disuse.

The complete lack of toad bones from the drain and robbing holes of the eighth and ninth century contrasts the situation seen in the fourteenth and sixteenth century when Common toads were obviously present, representing 33 per cent of the total sample. The modern day situation is even more interesting, with the toad now extremely common in Repton, especially around the excavation trenches. Indeed the Common toad *Bufo bufo* is so abundant that Thorn (1989) records that each summer baby frogs (in fact toadlets) are allowed to migrate through the Hall at Repton school. These toadlets are all migrating from the breeding pond, the Old Trent Water. During the peak period of toadlet migration an archaeological trench 10 x 10 metres, about 85 metres south of the Old Trent, caught approximately 0.5 litres of toadlets each day, which had to be carefully gathered up and released before excavation work could proceed. The Smooth newt *Triturus vulgaris* is also common in the area with several animals having been found in the terrestrial phase during excavation work in the Cloister Garth and around St. Wystans Church. We have never seen Common frogs *Rana temporaria* at Repton during the Summer though it is reported by the local people to be present.

It can be argued that toads were not represented in the robbing holes, drain and mound because of an associated trap bias for frogs at these sites. The importance of archaeological trap bias for frogs or toads is not known but we note that the bone material at these sites contained a broad spectrum of small mammal species which suggests that these pitfall traps were surprisingly unselective. We suspect that the frogs and toads simply fell into these archaeological features by accident and therefore the bone material does provide an unbiased picture of local anuran abundance.

Why has the anuran population in Repton changed so drastically from frogs to toads since the eighth and

ninth century when only frogs appear to have been present? The Common toad had already become well established by the fourteenth century. A possible explanation may be the formation of an ox-bow lake produced when the Trent River changed its course.

The Viking army sailed up the Trent River which in 874 flowed past the seven metre high bluff on which Repton stands. However by 1576 the River had changes course to its modern channel some 850m to the north (Saxton, 1576 in Cameron, 1973), leaving an ox-bow lake (the Old Trent Water) which has gradually silted up since this time. This change in the river may have been produced as a result of serious flooding known to have occurred at the end of the thirteenth or early fourteenth century (Cameron, 1973). By 1699 Gilbert Thacker of Repton House was already concerned that the old channel would turn into a standing pond, although it would appear that water still flowed freely in the Old Trent at this time (Kitching, 1988).

The Common toad in modern times breeds successfully in the Old Trent despite it being well stocked with fish. The large pond appears to provide ideal breeding conditions for toads which are known to prefer deep water and permanent ponds, contrasting the Common frog which breeds in temporary or shallow ponds (Smith, 1973). Common toads will even breed at the edge of large reservoirs (Raxworthy, pers. obs.). Beebee (1979) reports that the Common toad is able to dominate the Common frog in larger older ponds which have fish populations. This probably reflects the unpalatable nature of toad tadpoles to fish. Perhaps the increased abundance of the Common toad in the fourteenth century can be attributable to the formation of the ox-bow lake during the floods of the late thirteenth or early fourteenth century. Provided the water was slow flowing, the old meander of the river could have provided a suitable breeding habitat which previously would not have been available.

We cannot offer a firm explanation for the apparent decline in the Common frog at Repton in modern times. There is no evidence of direct competition between the Common frog and Common toad therefore the most likely explanation is a change in the local habitat. Possible frog breeding sites such as smaller ponds in marshy areas close to the Trent river may have been drained in recent times. Certainly we were unable to find shallow ponds around the excavation sites at Repton, and breeding sites for the Common frog may now be scarce in the area.

The Mound

There are several questions associated with the amphibian bones found in the mound. Firstly how significant was the disturbance made by the previous excavations and secondly how were these bones deposited?

Considering the first question it is clear that some frog bones had never been disturbed after the mound was first formed in the ninth century. Eight frog ilia were found in the undisturbed squatter occupation layers and in the clean Keuper marl of the burial chamber. The remaining 58 ilia were found in Thomas

Walker's disturbed deposits of the seventeenth century. 56 ilia were Common frog and just two ilia were Common toad.

The evidence from the deposits of the fourteenth century crypt and the sixteenth century saw-pit both demonstrate that the Common toad was well established in Repton at this time. This contrasts the eighth and ninth century when only frogs were found in the robbing holes and drain. The rarity of the Common toad bones from the mound suggest that these bones from the mound do belong to the ninth century and have received little contamination during later excavation work. If the mound bones had been subject to contamination in the sixteenth century or more recently we feel certain that many more toad bones would have been discovered. However we can not say that no contamination has occurred, only that it appears that most of the amphibian bones are contemporary with other eighth and ninth century deposits.

Alternative evidence also suggests that the small bone material of the mound is ninth century. Many small mammal bones have been recovered from the charnel, including voles, shrews, woodmice, housemice and moles. However no brown rats or rabbits have been found (Pfeiffer, 1987). Both these species only invaded England in post-Anglo Saxon times.

Assuming that the frogs are from the ninth century, how did they get into the mound and among the charnel? The mound was covered by a low cairn of irregular stones. This has never been covered by more than a thin layer of top soil and initially the cairn may have been completely exposed. Under these conditions it is not too difficult to imagine frogs finding their way between the large stones into the sunken building containing the human bones, and some individuals may easily have become trapped. As top soil accumulated on the mound, either naturally or perhaps scraped up at a later date, then the voids between the stones would have become sealed, preventing subsequent immigration.

CONCLUSIONS

The unusual quantity of frog and toad bones collected at Repton appears to have been the accidental result of the robbing holes, saw-pit, crypt, drain and burial mound all acting as historical pitfall

traps. These amphibian bones suggest that in the eighth and ninth century the Common frog *Rana temporaria* was abundant at Repton, while the Common toad *Bufo bufo* was rare or even absent. However by the fourteenth century toads were well established and in modern times have become extremely abundant. This change may be associated with the formation of the Old Trent Water ox-bow lake which was formed between the ninth and sixteenth century.

The very high proportion of frog bones recovered from the charnel in the Viking burial mound suggest that these small animals bones date from around the ninth century and contain little subsequent contamination.

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REFERENCES

- Beebee, T. J. C. (1979). Habitats of the British amphibians (2): suburban parks and gardens. *Biol. Conser.* **15**, 241-257.
- Biddle, M. and Kjølbye-Biddle, B. (1985). The Repton stone. *Anglo-Saxon England*. **14**, 233-292.
- Biddle, M. and Kjølbye-Biddle, B. (1986). The Repton mound and the discovery of the coins. In *Anglo-Saxon Monetary History*, 111-115. Blackburn, M. A. S. (Ed.). Leicester.
- Cameron, A. (1973). Meering and the Merying Family. *Transactions of the Thornton Society of Nottinghamshire*. **77**, 43.
- Engelmann, W., Fritzsche, J., Gunther, R. and Obst, F. J. (1985). *Lurche und kriechtiere Europas*. Stuttgart, Enke.
- Esteban, M. and Sanchiz, B. (1985). Paleoclimatic inferences based on fossil Ranids. In *Studies in herpetology*, 379-382. Rocek, Z. (Ed.). Prague: Charles University.
- Holman, J. A. (1985). Herpetofauna of the late Pleistocene fissures near Ightham, Kent. *Herp. J.* **1** (1): 26-32.
- Kitching, C. (1988). The Old Trent. *Repton Parish Magazine*. March 1988, 9-11.

APPENDIX

SITE	TRENCH	FEATURE NUMBER	LAYER NUMBERS
Robbing holes	4	2731, 3029	2455, 2912
Drain	3	1116	1320-1322
Mound	8	922	293-4, 303, 718, 721, 735-6, 741, 804
Crypt	3	—	2004, 2007-10
Saw-pit	5	816	322, 329

TABLE 2: The trench, feature and layer numbers which contained amphibian bones.

- Pfeiffer, J. S. (1987). *The animal bones from Trench 8, Repton, Derbyshire. M.Sc. Thesis*. Philadelphia, University of Pennsylvania.
- Paris, M. C. (1986). *Los anfibios de España*. Madrid, Publicaciones Agrarias.
- Smith, M. (1973). *The British reptiles and amphibians. New Naturalist Series 20*, 5th edition. London, Collins.
- Thorn, J. (1989). *The road to Winchester*. London, Weidenfield and Nicolson.

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ECOLOGICAL RESPONSES IN A POPULATION OF SMOOTH NEWTS (*TRITURUS VULGARIS MERIDIONALIS*) IN AN UNPREDICTABLE ENVIRONMENT

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ABSTRACT

The annual cycle of a population of Smooth newts (*Triturus vulgaris meridionalis*) was studied at a temporary pond in Central Italy. Timing of migration differs from that described in northern countries. Immigration and reproduction take place as soon as weather conditions are favourable (December), males arriving earlier than females. Emigration lasts a short period (April-May) and ends before pond desiccation (June). Summer drought is therefore not a limiting factor for adult activity as it is for larval survival. The aquatic period is short compared to that of northern populations and during the summer terrestrial phase probably little activity occurs. Males exceed females in the breeding population. In particularly dry conditions not all the female population reaches the pond. The average growth rate during the aquatic phase is approximately 1mm. An hypothesis on the influence of environmental conditions on adult body size is suggested.

INTRODUCTION

Many studies have been carried out in the past few years on the ecology of *Triturus vulgaris* L., mainly in North and Central Europe. This research was on population dynamics (Bell, 1977, Blab and Blab, 1981, Griffiths, 1984, Verrell and Halliday, 1985), on several aspects of reproduction (Bell and Lawton, 1975, Halliday, 1977, Verrell *et al.*, 1986), on the niche (Dolmen, 1983, Dolmen and Koksvik, 1983, Griffiths, 1987), on the age determination and growth rates (Hagström, 1977, 1980, Verrell and Francillon, 1986, Verrell, 1987). The ecology of the Italian subspecies *Triturus vulgaris meridionalis* (Boulenger) has not yet been studied. The present distribution of newts in Italy might have been influenced by historical factors however climatic conditions, such as temperature and rainfall, probably also have a strong effect (Giacoma, 1988).

The pond which we investigated lies on the President's Estate of Castelporziano, a few kilometers south of Rome. The Estate is one of the last areas on the Tyrrhenian Coast still covered by floodplain forest. It is also close to the southern limit of the distribution area of *Triturus vulgaris meridionalis*. At Castelporziano the climate is particularly dry, the long summer drought causes ponds to dry up completely, this is the most dramatic event in the newts' annual cycle but it is also affected by other variable factors such as temperature, rainfall and the succession of the aquatic invertebrate community. Average pond water level varies from year to year since water comes exclusively from rainfall.

At Castelporziano *Triturus vulgaris meridionalis* spends less time in water than northern populations and it has little terrestrial activity in the summer, thus research on growth was undertaken during its aquatic phase in a temporary pond.

METHODS

The President's Estate of Castelporziano, strictly closed to the public, extends from the sea coast towards Rome for about 18km. The climate in this area is very dry especially during the long summer period when also the temperature is high (Fig. 1 and Fig. 2).

The pond which we chose for our study site, has a surface area of about 400m² and a maximum depth of 80cm. It is a temporary pond which lies at sea level in typical Mediterranean maquis. The aquatic vegetation consists of filamentous algae (*Spyrogira* and *Cladophora*) and herbaceous plants such as *Ranunculus* and *Mentha*. The pond is a breeding site for *Triturus meridionalis*, *Triturus carnifex*, *Rana dalmatina*, *Rana esculenta* 'complex' and *Hyla arborea*.

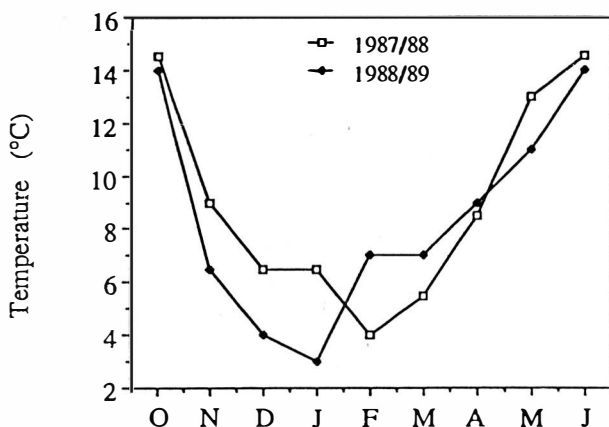


Fig. 1 Mean of the minimum air temperature recorded each month, during the two years of observations.

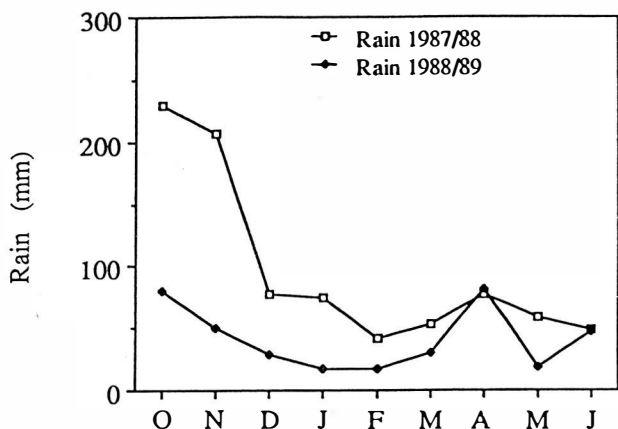


Fig. 2 Mean rainfall recorded each month, during the two years of observations.

Data reported in this paper refer to the period from November 1988 to June 1989 (data recorded the previous year have been used for comparison). We attempted to install a drift fence with pitfall traps but these were continuously damaged by the numerous wild boars which live on the Estate. Newts were caught weekly by dipnetting. Due to the turbid water the pond could only be investigated randomly. Dipnetting was performed for a total of one hour and a half by at least two people simultaneously all over the pond.

An 0.3:1000 solution of phenoxyethanol was used to anesthetize the newts. The sex of each animal caught and its secondary sexual characters were recorded, together with its snout-vent length (to the nearest 1mm). Individuals were then marked by clipping toes to show date of capture: each combination of toes clipped was unique for a weekly sampling. Furthermore the belly-pattern of every newt was recorded (photographically) for individual recognition. Any characteristics such as tail indentation and limb deformities were also recorded to aid in identification. Toe-clipped recaptured newts were measured again in order to verify whether the animals had grown. The experimenter who took the measurements was unaware of the previous size measured.

The weekly size of the population (N_i) was estimated using Chapman's modification of the Petersen Index. The absolute size of the population was obtained calculating $N = \sum N_i / s - 1$ (where s = samplings), and variance (V) was calculated as $V(N) = \sum V_i / (s-1)^2$, (where V_i = variance obtained each week), (Seber, 1973). The mean time spent in water by each individual was calculated considering the mean recapture intervals between first and last captures (Griffiths, 1984). Animals recaptured after one week only were excluded from the mean.

RESULTS

THE TIMING OF MIGRATION

Weekly sample data show the seasonal migration patterns (Fig. 3). The first capture in 1988 was on 13th December. The number of animals caught increased until March 1989. The estimated size of the population (\pm standard deviation) which had visited the pond at that point was 229 ± 33 . In 1987-88 newts had first been caught on 3rd November and the increase was observed until March.

Emigration started in the same period in both years (beginning of April) but it proceeded faster in the first year. In 1988 the last newts were caught in water on 2nd May whereas in 1989 animals were still present on 1st June.

SEX RATIO AND POND RESIDENCY

In 1988-89 the overall male:female ratio was 1.72:1 (93 males and 54 females). Males migrated to the pond a few days earlier than females, and their number always exceeded that of females (Fig. 4a). The sex ratio in February was 1.70:1 and in May it was 1.25:1. In March the size of the population was estimated as 141 ± 21 and 78 ± 17 for males and females respectively. In 1987-88 males initially exceeded females, during the breeding period (December-March) the ratio approached 1:1 or was slightly female-biased, and males emigrated faster (Fig. 4b).

The average time spent in the water in 1988-89 is shown in Table 1. In 1987-88 the recapture interval was never longer than 84 days in either males or females.

BODY SIZE AND GROWTH RATE

The mean snout-vent lengths (SVL \pm s.d.) were 34.7 ± 2.4 mm ($n = 93$) and 35.3 ± 2.7 mm ($n = 54$) in males and females respectively. Table 2 shows the

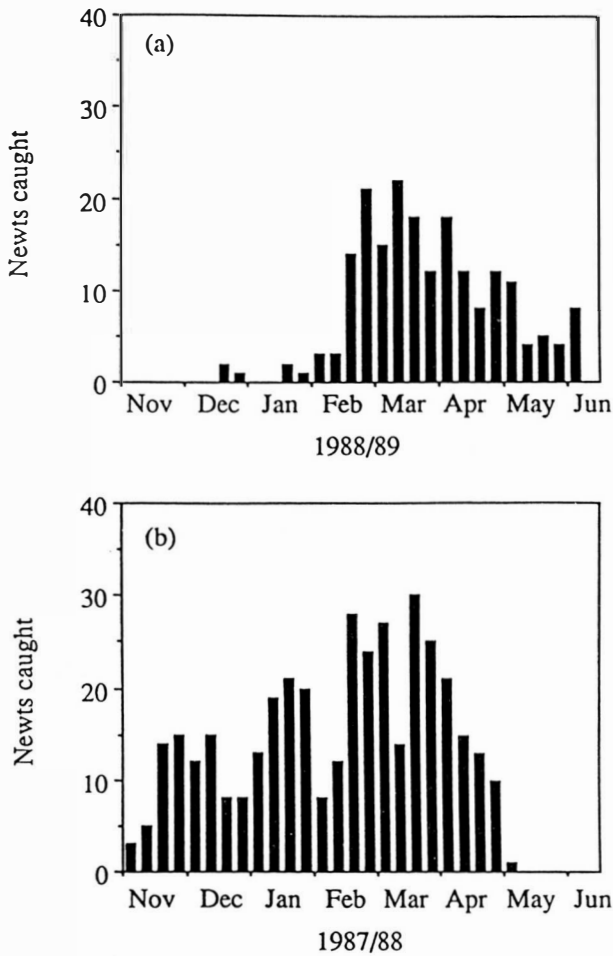


Fig. 3 Number of newts caught weekly in fixed time samplings, in 1988/89 (a) and 1987/88 (b).

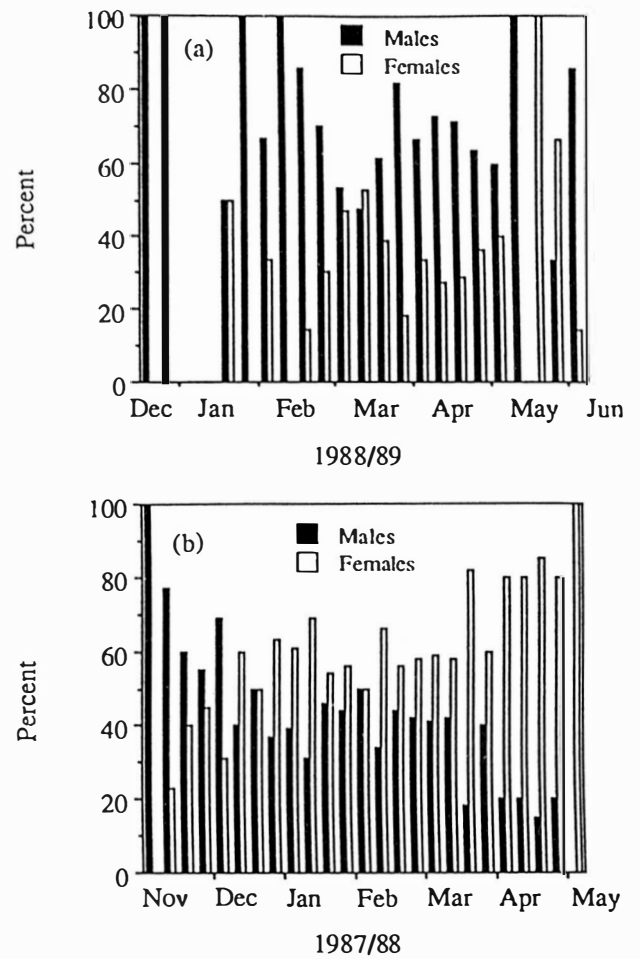


Fig. 4 Sex ratio expressed in percentage of males and females caught each week in 1988/89 (a) and 1987/88 (b).

mean snout-vent lengths measured each month. (Monthly samplings < 10 individuals have been omitted.)

	<i>min.</i>	<i>max.</i>	<i>mean</i> \pm <i>s.d.</i>
Males	12	106	37 \pm 26 (n = 14)
Females	14	42	25 \pm 9 (n = 6)

TABLE 1: Recapture intervals, in days, of newts caught in 1988/89. (n = sample size; s.d. = standard deviation)

	<i>February</i>	<i>March</i>	<i>April</i>	<i>May</i>
Males	33.8 \pm 2.9 28 \div 40 (n = 30)	34.4 \pm 2.0 31 \div 38 (n = 35)	35.4 \pm 1.9 31 \div 39 (n = 29)	35.4 \pm 2.0 32 \div 39 (n = 15)
Females	34.7 \pm 4.4 28 \div 42 (n = 10)	35.0 \pm 2.0 31 \div 40 (n = 24)	35.8 \pm 2.2 33 \div 41 (n = 14)	36.0 \pm 2.1 33 \div 39 (n = 10)

TABLE 2: Mean of the body sizes, in mm. (\pm s.d.), range and sample size of the newts caught monthly in 1988/89.

Of the 27 recaptured newts (20 males and 7 females) 8 males (40 per cent) and 3 females (43 per cent) had increased by 1mm in size, only one individual 31mm long was recaptured 3 weeks later measuring 34mm. Newts were never found decreased in size. No correlation was noted between recapture time interval or length at first capture and increase in size. Three males were recaptured twice after quite a long time. At their first recapture (after 21, 28 and 42 days respectively) their lengths had increased by 1mm, the second time they were recaptured (after 14, 28, 35 days) they had not grown any more.

DISCUSSION

THE TIMING OF MIGRATION

Our newt population was present in the water from November to May, much earlier in the year compared to populations of northern countries. For instance in England immigration starts in February-March and emigration lasts from July to December (Harrison *et al.*, 1983, Verrell and Halliday, 1985). Different water seasons have also been observed in Italy according to latitude and altitude of the breeding sites (Lanza, 1983). Temperature certainly has an influence on the annual reproductive cycle (Galgano, 1944, Mazzi, 1982). In our study area rainfall is also important: in autumn 1988 rain was very scant limiting pond refill (Fig. 2), thus immigration started later than the previous year. Early pond drought due to lack of spring rainfall is widely known to be a limiting factor for larval survival, and may prevent metamorphosis occurring at all. In very dry areas one must also consider that scarce autumn rainfall may dangerously delay reproduction.

Bell (1977) and Blab and Bláb (1981) refer to autumn migrations of newts which spend winter in the water and breed in advance. Lanza (1983) states that a breeding period has occasionally been observed in late autumn in Italy. In sea level ponds in central Italy Smooth newts start breeding usually in late January-beginning of February. In our study area reproduction may also occur earlier (In 1987 Smooth newt eggs were first observed on 16th December, in 1989 egg laying started at the end of February).

The increase in the number of newts caught continued until March. Immigration lasted at least one month longer than that observed by Verrell and Halliday (1985). When weather conditions were unfavourable, i.e. scarce rainfall affecting pond refill (water level < 15cm), few newts reached the pond and their number did not increase continuously. As soon as water level steadily exceeded 25cm mass migration occurred (our case in 1988-89).

Emigration lasted for a short period (April-May), probably because environmental conditions became unfavourable for newts. We believe water temperature to be a very important factor in the determination of emigration time: animals started to leave the pond when maximum water temperature approached 15°C. It is relevant to note that adults leave water long before desiccation, when the water level is higher (50cm) than that observed when immigration starts. Desiccation is therefore a limiting factor for larval survival but not for adult activity.

POND RESIDENCY AND SEX RATIO

At Castelporziano estivation lasts from June to September. On both years newts were caught in the water over a period of six months, but each individual was never recaptured for a period of over three months. In England each individual spends an average of five months in the water (Verrell and Halliday, 1985), and hibernation is only two months long. The average time spent in water, calculated using the mean recapture intervals (Griffiths, 1984), is not as reliable a method as the use of a fence. Our data (underestimated

due to the method used) show that newts spend a shorter period in the water at the southern border of their distribution area.

Males and females migrate at different times. Males were caught earlier and in greater numbers than females, this is in agreement with Harrison *et al.* (1983), Griffiths (1984), Giacomini (1985). The sex ratio varies during pond residency, in 1987/88 initially males exceeded females, later the trend was inverted, whereas in 1988/89, even though the number of both males and females grew, males always exceeded females.

In literature data on the sex ratio of *Triturus vulgaris* are contradictory. Glandt (1978) and Hagström (1979) find a 1:1 ratio in water. Harrison *et al.* (1983) and Verrell and Halliday (1985) find an excess of females that is less marked as the aquatic period progresses. Griffiths (1984) catches an excess of males in the water but the opposite happens on land. Two hypotheses are suggested (Griffiths, 1984, Gill, 1978, 1979 for *Nothophthalmus viridescens*) to explain the excess of males in the aquatic population: 1) mortality is higher among females than among males, 2) females do not breed every year. A shorter period of pond residency by females might also explain why the sex ratio appears to be male biased. Our observations suggest that the sex ratio of the population is not affected by mortality. The females' rate of increase was lower than that of males in 1988-89, whereas during the previous year the number of females exceeded that of males during most of the aquatic period. A similar pattern was observed over the two years in a sympatric population of *Triturus carnifex*. A possible explanation of this phenomenon (not breeding of females) might be the exceptionally dry weather of the year 1988/89. Biennial sexual cycles have been observed in female populations of Plethodontidae by Maiorana (1976). They were related to energetic reasons due to limited activity in unfavourable dry weather conditions.

GROWTH RATE AND BODY SIZE

Triturus vulgaris is known to have indeterminate growth (see Verrell, 1987). Adults spend part of the aquatic season to feed and grow. Throughout this season not every single individual grows, nevertheless at the level of the population average body size increases. An increase in mean snout-vent length of +1.6 in males and +1.3 in females was observed in the newts caught. At individual level the growth rate was approximately 1mm. These data are in agreement with those reported by Verrell (1987), although 40 per cent of the newts recaptured had increased in size, while this author found an increase in 77 per cent of them. Differences between these results may be due to the shorter recapture interval in our case, or to different approximation in the measurements (0.5mm vs 1mm). The short recapture interval probably also explains the lack of relationship between size at first capture and increase in size.

Adult growth rate varies among populations and years (Hagström, 1977). No data on this rate within a year are available except Verrell's (1987). A 1mm increase in *Triturus vulgaris meridionalis* 35mm long is greater in percentage than the same increase in *Triturus*

vulgaris vulgaris 45mm long. (2.85 per cent vs 2.22 per cent). However growth rate slows after attainment of sexual maturity (Hagström, 1977, 1980), scarcely affecting adult body size. Tilley (1973) reports altitudinal size clines in adult *Desmognathus ochrophaeus* as a consequence of: '1) constant age at maturity and variable juvenile growth rates, 2) constant juvenile growth rates and variable age at maturity, or 3) both.' In *Triturus vulgaris* sexual maturity is determined by age, not size (Verrell and Francillon, 1986), thus body size reflects mainly juvenile growth rate.

The mean body size registered in Castelporziano is the smallest among other populations of central and northern Italy. Unfavourable weather and habitat conditions, i.e. coastal and xeric habitats, make food consumption irregular during the terrestrial juvenile phase. In cooler and higher breeding sites, surrounded by moist litter, faster growth probably occurs. This assumption is based only on ecological surveys, we are not aware of the degree to which this phenomenon has a genetic basis.

Fecundity in *Triturus vulgaris* is size-specific: larger females lay more and larger eggs which hatch earlier (see Bell, 1977 and Verrell *et al.*, 1986). A smaller body size may also affect several features of the population: size, age distribution, egg and larval survival. Further research on this topic would be of interest.

REFERENCES

- Bell, G. (1977). The life of the Smooth newt (*Triturus vulgaris*) after metamorphosis. *Ecol. Monogr.* **47**, 279-299.
- Bell, G. and Lawton, J. H. (1975). The ecology of the eggs and larvae of the Smooth newt (*Triturus vulgaris* (Linn.)). *J. Animal Ecology*, **44**, 393-423.
- Blab, J. and Blab, L. (1981). Quantitative analysen zur phenologie, erfassbarkeit und populationsdynamik von Molchbeständen des kaltenforstes bei Bonn. *Salamandra*, **17**, 147-172.
- Dolmen, D. (1983). Diel rhythms and microhabitat preference of the newts *Triturus vulgaris* and *T. cristatus* at the northern border of their distribution area. *J. Herpetol.* **17** (1), 23-31.
- Dolmen, D. and Koksvik, J. I. (1983). Food and feeding habits of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia), in two bog tarns in central Norway. *Amphibia-Reptilia*, **4**, 17-24.
- Galgano, M. (1944). Il ciclo sessuale annuale di *Triturus cristatus carnifex* (Laur). Il ciclo naturale nei due sessi. *Arch. Ital. Anat. Embriol.* **50**, 1-148.
- Giacoma, C. (1988). The ecology and distribution of newts in Italy. *Annuaire. Ist. Mus. Zool. Univ. Napoli*, **26** (1983), 49-84.
- Gill, D. E. (1978). The metapopulation ecology of the Red-spotted newt, *Nothophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* **48**, 145-166.
- Gill, D. E. (1979). Density dependence and homing behaviour in adult Red-spotted newt, *Nothophthalmus viridescens* (Rafinesque). *Ecology*, **60**, 800-813.
- Glandt, D. (1978). Notizen zur populationsökologie einheimischer Moleche (Gattung, *Triturus*) (Amphibia: Caudata: Salamandridae). *Salamandra*, **14**, 9-28.
- Griffiths, R. A. (1984). Seasonal behaviour and intrahabitat movements in an urban population of Smooth newts, *Triturus vulgaris* (Amphibia: Salamandridae). *J. Zool. London*, **203**, 241-251.
- Griffiths, R. A. (1987). Microhabitat and seasonal niche dynamics of Smooth and Palmate newts, *Triturus vulgaris* and *Triturus helveticus*, at a pond in mid-Wales. *J. Animal Ecology*, **56**, 441-451.
- Hagström, T. (1977). Growth studies and ageing methods for adult *Triturus vulgaris* L. and *Triturus cristatus* Laurenti (Urodela: Salamandridae). *Zool. Scr.* **6**, 61-68.
- Hagström, T. (1979). Population ecology of *Triturus cristatus* and *Triturus vulgaris* in S. W. Sweden. *Holarctic Ecology*, **2**, 108-114.
- Hagström, T. (1980). Growth of newts (*Triturus cristatus* and *Triturus vulgaris*) at various ages. *Salamandra*, **16**, 248-251.
- Halliday, T. R. (1977). The courtship of European newts: an evolutionary perspective. In 'The Reproductive Biology of Amphibians' Taylor D.H. and Guttman S.I. (Eds). New York: Plenum Press.
- Harrison, J. D., Gittins, S. P. and Slater, F. M. (1983). The breeding migration of Smooth and Palmate newts (*Triturus vulgaris* and *Triturus helveticus*) at a pond in mid-Wales. *J. Zool. London*, **199**, 249-258.
- Lanza, B. (1983). Anfibi, rettili. *Guide per il riconoscimento delle specie animali delle acque interne italiane*. C.N.R. No. 27.
- Maiorana, V. C. (1976). Size and environmental predictability for Salamanders. *Evolution*, **30**, 599-613.
- Mazzi, V. (1982). Meccanismi di controllo del ciclo riproduttivo in anfibi urodela. *La ricerca scientifica No. 110. Atti del Convegno Scientifico Naz. Progetto Finalizzato. Biologia della riproduzione*. Roma CNR, 427-430.
- Seber, G. A. F. (1973). The estimation of animal abundance. *Griffin, London*.
- Tilley, S. G. (1973). Life histories and natural selection in populations of the Salamander *Desmognathus ochrophaeus*. *Ecology*, **54** (1), 2-17.
- Verrell, P. A. (1987). Growth in the Smooth newt (*Triturus vulgaris*) during the aquatic phase of the annual cycle. *Herpetological Journal*, **1**, 137-140.
- Verrell, P. A. and Francillon, H. (1986). Body size, age and reproduction in the Smooth newt, *Triturus vulgaris*. *J. Zool. London*, **210**, 89-100.
- Verrell, P. and Halliday, T. (1985). Reproductive dynamics of a population of Smooth newts, *Triturus vulgaris*, in southern England. *Herpetologica*, **41** (4), 386-395.
- Verrell, P. A. and Halliday, T. R. and Griffiths, M. L. (1986). The annual reproductive cycle of the Smooth newt (*Triturus vulgaris*) in England. *J. Zool. London*, **210**, 101-119.

DOMINANCE OR TERRITORIALITY? THE COLONISATION OF TEMPORARY LAGOONS BY *CAIMAN CROCODILUS* L. (CROCODYLIA)

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ABSTRACT

The behaviour of 51 individually known spectacled caimans (*Caiman crocodilus*) was studied in the Llanos savannahs during the first half of the rainy season. At the onset of the rains caimans left their dry season refuge, a permanent pond, to colonise the appearing temporary lagoons. Caimans less than one year old did not leave the pond. Despite reports of territoriality in this species, no indication of territorial behaviour was found during the colonisation of lagoons. Ninety per cent of the caimans were nomadic. Their movements between water bodies included the permanent pond. Residence in a study lagoon was up to one week long and was followed by prolonged periods of absence. During their residence time in the lagoon, some caimans showed site fidelity, others did not. There was considerable overlap of caiman ranges in the lagoon, but caimans showed spacing behaviour when simultaneously in the water. Priority of access to resources in caimans and other crocodilians is apparently determined by the body size of competitors and not by the site of agonistic encounters. It is argued that the social behaviour of crocodilians is characterised by an absolute dominance hierarchy based on body size, rather than territoriality.

RESUMEN

El comportamiento de 51 caimanes (*Caiman crocodilus*) marcados individualmente fue estudiado en las sabanas de los Llanos durante la primera mitad de la estación lluviosa. Al comenzar las lluvias, los caimanes abandonaron el charco de aguas permanentes (morichal) donde se refugiaron durante la estación seca y colonizaron las lagunas temporales (esteros) que se comenzaban a formar. Caimanes menores de un año de edad no abandonaron el morichal. No obstante previos informes de territorialismo en esta especie, no hubo ninguna indicación de comportamiento territorial durante la colonización de esteros. El noventa por ciento de los caimanes fueron nómadas e incluyeron el charco permanente en sus movimientos entre lagunas. El tiempo regular de residencia en el estero estudiado fue de hasta una semana, seguido por periodos de ausencia prolongada antes de un regreso eventual. Durante la residencia en el estero solo algunos caimanes se mostraron fieles a un determinado sector. Cuando estaban simultaneamente en el agua los caimanes mostraron especiamiento entre sí, pero el traslapo entre las áreas usadas por cada individuo fue considerable. En caimanes y otros crocodílicos el acceso prioritario a recursos es aparentemente determinado por el tamaño de los competidores y no por la localidad del encuentro agonístico. Se argumenta que en vez de territorialismo, el compartamiento social de los crocodílicos se caracteriza por una jerarquía absoluta de dominio basada en tamaño corporal.

INTRODUCTION

Reports of territoriality among spectacled caimans (*Caiman crocodilus*) may be misleading due to a lack of consistency in the definition of territorial behaviour. Territoriality has been inferred from observations of site fidelity (Medem, 1962; Gorzula, 1978), displacement behaviour (Medem, 1962; Staton and Dixon, 1975) and breeding site defence by captive females (Alvarez del Toro, 1974). Although these are typical elements of territorial behaviour, none are sufficient to demonstrate territoriality according to more recent definitions of the term. Kaufmann (1983) reviewed the concepts of territoriality and dominance, defining the first as a space-related dominance, whereby the territory is '... a fixed portion of an individual's or group's range in which it has priority of access to one

or more critical resources over others which have priority elsewhere or at another time. This priority of access must be achieved through social interaction...'. Territoriality is a form of relative dominance (relative to location of the contestants) whereas an absolute dominance hierarchy (e.g. based on body size) is independent of location and time.

In the savannahs of northern South America, large aggregations of spectacled caimans are found in the scarce permanent ponds during the dry season (Staton and Dixon, 1975; Marcellini, 1979). During the rainy season, extensive areas of grassland are flooded, forming temporary lagoons. Caimans move from their dry season refuge to the new lagoons and return to the permanent ponds when the lagoons dry out (Staton and Dixon, 1975; Gorzula, 1978). The present study describes the behaviour of 51 individually known

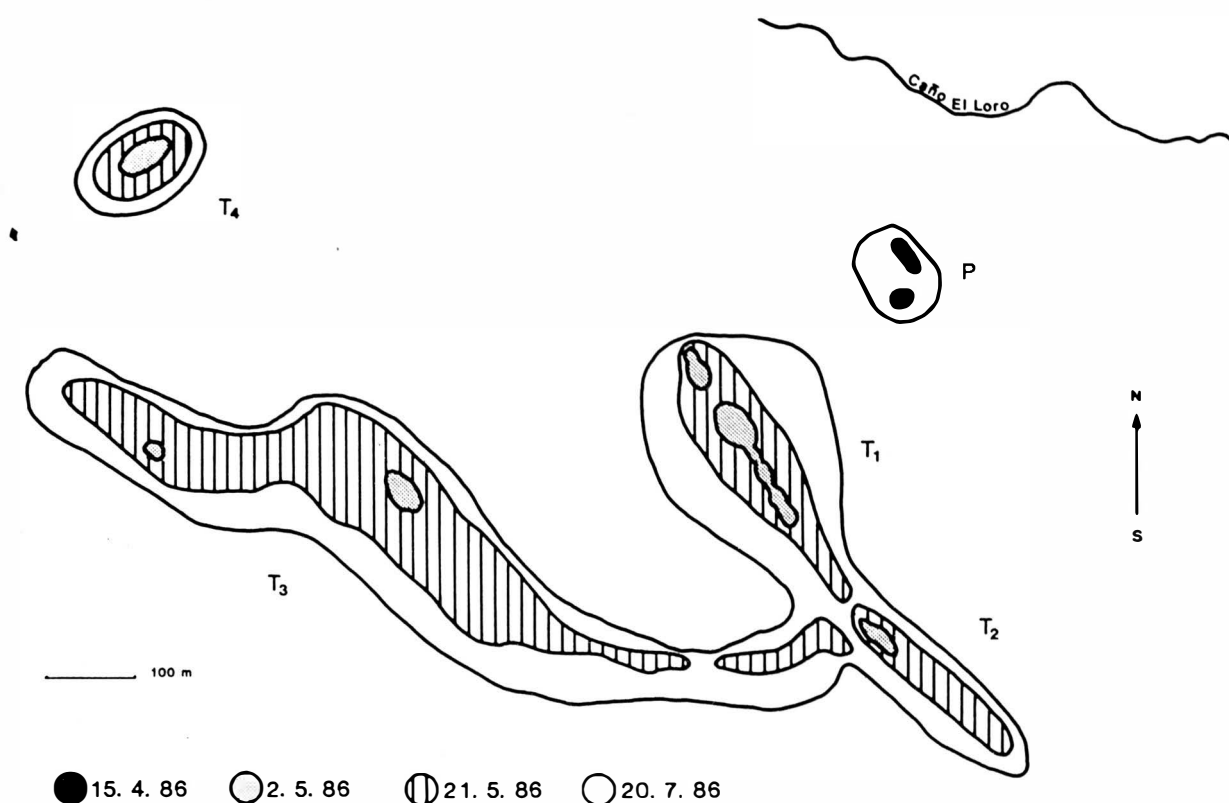


Fig. 1 The study site, showing the permanent pond P and the growth of the temporary lagoons T over the course of the rainy season. T1, T2 and T3 are considered together in the text as the temporary lagoon of the study. They became a continuous water body in June. T4 was visited sporadically and not included in the nightly census. The next temporary lagoon (T5, not on the map) was located 1 km to the northeast of P.

caimans during their colonisation of temporary lagoons. The study period corresponds to the mating season of caimans in this environment (Staton and Dixon, 1976). The inadequate use of the concept of territorial behaviour is discussed in respect to former reports of territoriality in this species and other crocodylians.

METHODS

The study took place at the Hacienda Los Naranjos (4° 13' N, 73° 16' W, 400 m above sea level) in the Colombian Llanos. The Llanos are the seasonal grassland savannah located northeast of the Andean range, both west and east of the Orinoco river. For descriptions of this region see publications by Hueck (1966), Staton and Dixon (1975) and Cabrera and Willinck (1980). There is a single rainy season usually from April to November, and a dry season from December until March. Average annual rainfall in the study area is 3438 mm and the average temperature is 25.7°C (written comm. HIMAT, Bogotá). The data were collected daily between 12 April 1986 and 20 July 1986. This period corresponds to the first half of the rainy season. Rainfall at the study site was recorded daily.

The spectacled caiman (*Caiman crocodilus* L.) is common in the study region, where it is sympatric with two other *Alligatoridae* species: *Paleosuchus palpebrosus* and *Paleosuchus trigonatus* (Medem, 1981). The study

population was never hunted for commercial purposes. During this study 19 female, 22 male and 10 unsexed (juvenile) caimans were captured, measured, marked and released. Their size range was 16.6 cm to 75.1 cm snout-vent-length (SVL, measured to the anterior end of the cloaca). Three age categories were defined using growth data for free-ranging spectacled caimans published by Gorzula (1978):

- Juveniles (13): SVL < 36.0 cm. Animals less than three years old.
- Immatures (26): SVL 36.0 cm–50.0 cm.
- Adults (12): SVL > 50.0 cm. Animals 7 years in age or more. Females sexually mature (Rivero-Blanco, 1974).

Individuals smaller than 100 cm total length were captured by hand, seizing the neck and the base of the tail simultaneously. Larger caimans were hooked around the neck against the ground, then secured with a noose to pull them out of the water. Captured caimans were weighed, restrained on a board and then sex was determined by cloacal probing (after Brazaitis, 1968) and/or visual examination of the cloaca with an otoscope. After taking morphometrical data, the caimans were individually marked using a code of holes punched into the proximal vertical scales of the tail and a number painted on their backs with fast drying metallic paint for model airplanes. This number remained recognisable for about six weeks. An attempt to mark the caimans using reflective tape was unsuccessful. The different coloured dots attached to

the cranial plate with cyanoacrylate bonder fell off within one week due to shedding of the *Stratum corneum*. A detailed description of scars, injuries and other conspicuous marks was recorded on each individual's file. Within one hour of capture the caiman was released at the capture location. Data on morphometry, injuries, population structure, and habitat choice will be published elsewhere.

The present study was carried out at night for two reasons: 1. The assumption that during the rainy season caimans are most active at night. 2. Close approach for identification and eventual capture of submerged caimans during the day is almost impossible due to the shyness of the animals. Data on the activity of caimans in the dry season indicate that over 80 per cent of the individuals are found in the water between 2000h and 200h at night (Marcellini, 1979). Nightly water temperature variation between 24.3°C and 29.6°C at the time of censusing did not correlate with caiman activity (Staton and Dixon, 1975). Comparable data for the rainy season is not yet available.

Caimans can be easily located at night using spotlights since their *Tapetum lucidum* reflects the light intensively reddish to orange and, at close range, white. Night censuses have been estimated to record over 90 per cent of the caimans in a pool (Staton and Dixon, 1975). The study lagoon (Fig. 1, T1 + T2 + T3) was censused within 15 minutes between 1900h and 300h each night. The time depended on weather conditions. The position of each caiman was recorded using compass triangulation and landmarks around the lagoon. Approach and identification of marked individuals and the capture of unmarked ones were performed after finishing the census. During rains the water surface became rough and submerged caimans could not be seen, making identification difficult. Successful identification was achieved in 52 per cent of all sightings ($N=189$). Data on the relative positions of caimans and censuses at the permanent pond are excluded from the analyses, because observations here became inaccurate as cyperaceous vegetation increased. Statistical analyses, unless otherwise indicated were performed using the software statistics package Minitab (C) at the Computer Main Frame of Cambridge University (UK).

RESULTS

1. Colonisation of temporary water bodies

At the onset of the rainy season in mid-April temporary lagoons started to appear in the vicinity of the single permanent pond of the study area (Fig. 1). At the beginning of observations (12 April 1986) 30 caimans were counted in the 0.14 ha permanent pond. Thereafter, a successive decline of caiman numbers was recorded. Five weeks after the initial census less than three caimans could be regularly found in the permanent pond. The first lagoon appeared on 22 April 1986 with an area of less than 0.2 ha. Five nights later three caimans were sighted in it.

Ten caimans, less than one year old, were marked in the permanent pond during the first three weeks of the

study. They were often resighted in the same pond, but never in the temporary lagoon. The two year old female F-7 (SVL = 26.9cm) was the youngest caiman recorded covering the 180m which separated the permanent pond from the adjacent lagoon (Fig. 1). A similar result is reported by Gorzula (1978), who found caiman hatchlings only in permanent ponds of a seasonal savannah in Venezuela (but see Ouboter and Nanhoe, 1988, for swamp forest habitat).

Out of 27 caimans (yearlings included) marked in the permanent pond between 15 April 1986 and 4 June 1986, 22 per cent were resighted during that period in the same pond, 44 per cent were resighted in the adjacent lagoon, and 34 per cent were not seen again. No caiman identified in the temporary lagoon between 26 April 1986 and 28 May 1986 was resighted in the permanent pond ($N=13$). Thus, during the first month of the rainy season caimans moved from the permanent pond to temporary lagoons, but apparently not in the opposite direction. Later in the season, however, movements from the lagoon to the permanent pond were observed (see below).

Although vegetation in the permanent pond made the nightly censuses from June onwards inaccurate, sightings in June included two adult females, two adult males, one immature male and several juveniles. This shows that during the rainy season the permanent pond was still used by caimans of all age categories and both sexes.

2. Movements between lagoons

Twelve instances of movements from the permanent pond to the lagoon by known individuals were recorded. Movements between lagoons or from these to the permanent pond were recorded five times. One example of such movements was the immature male M-9 (SVL = 47.5cm), marked in the permanent pond on 28 April 1986, resighted there on 29 April 1986 and 5 May 1986, then seen in the lagoon T3 on 12 May 1986 and, one month later, in lagoon T4 (Fig. 1). Short distance movements between the lagoons T1, T2 and T3 (Fig. 1) when these were still discrete water bodies are considered as movements *within* the study lagoon. Thirty caimans recorded for an average total time of 2.4 days in the study lagoon, out of 76 days of observations (see below), are assumed to have moved between distant water bodies including a brief stop at the study lagoon. Caimans were seen travelling through the savannah on two occasions during daylight (900 hours, 1000 hours) and once in the evening (1900 hours). No individual from the marked population sample was resighted in the temporary lagoon T5, located 1km away from the permanent pond, but spectacled caimans have been reported to travel overland distances of 2.4km and 5.0km (Gorzula, 1978; Marcellini, 1979).

The behaviour of the caimans during the first half of the rainy season can be characterised as nomadic. After the appearance of temporary lagoons and their colonisation by caimans, resightings of known individuals in neighbouring water bodies indicated that they did not become sedentary in the new lagoons, but rather moved between them. Such movements were made by caimans of all age and sex classes, except

	N	proportion resighted	median value of resightings/caiman	range of resightings/caiman
Males	22	15 (68%)	3.0	0 - 23
Females	19	12 (63%)	2.0	0 - 9

Table 1: Resighting rates of male and female spectacled caimans during the study.

for yearlings (see above). No significant difference in the resighting rates of males and females was observed (Table 1). Each caiman apparently moved between lagoons independently of other conspecifics, since no two or more individuals visited and left the study lagoon simultaneously.

The movement between water bodies ceased during the last week of the study, when high caiman numbers were consistently attained during the nightly censuses, and the same individuals recorded each night in the study lagoon. The average number of caimans counted in the lagoon increased from two individuals per night over the last six weeks, to 10 individuals per night during the week thereafter. This change was not related to changes in the rainfall pattern. It probably corresponds to the onset of the breeding season when adult females become sedentary and build nests (Staton and Dixon, 1976). This study did not verify if this sedentary behaviour persisted until the end of the rainy season.

3. Total time present in the lagoon

Fig. 2 shows the frequency distribution of the total number of days that each caiman ($N = 33$) was recorded in the lagoon during the study (76 observation days considered). The observed mean was

3.9 days. In order to correct for the unknown number of caimans which did not visit the lagoon at all, a mean of 3.0 days was chosen to calculate the random Poisson distribution. Each observed value in Fig. 2 represents a minimum value since individuals were only identified in 52 per cent of the sightings ($N = 189$). The observed distribution was not significantly different from the Poisson (Fig. 2, $P < 0.1$, chi-square = 9.12, $df = 4$). The large value of chi-square is due to three individuals who significantly exceeded 12 days in the lagoon (Fig. 2, $P < 0.0001$ in the Poisson distribution). If they are omitted from the sample the mean time in the lagoon is 2.4 days and the value of chi-square drops to 1.19 ($df = 3$, NS) in a comparison with a random Poisson distribution with a mean of 2.0.

Three male caimans, M-1 (SVL = 41.6cm), M-5 (SVL = 41.5cm) and M-11 (SVL = 50.2cm), were identified in the lagoon on 16, 17 and 24 days respectively. Since their time recorded at the lagoon was significantly higher than that of 30 other caimans, the former are referred to as *residents* (10 per cent of the sample) and the latter as *visitors* (90 per cent of the sample). The residents M-1 and M-5 visited the lagoon in bouts of several consecutive days, but M-11 was more or less constantly present (Fig. 3). The unusual behaviour of M-11 may have been related to a severe snout wound evidently inflicted with a machete by a

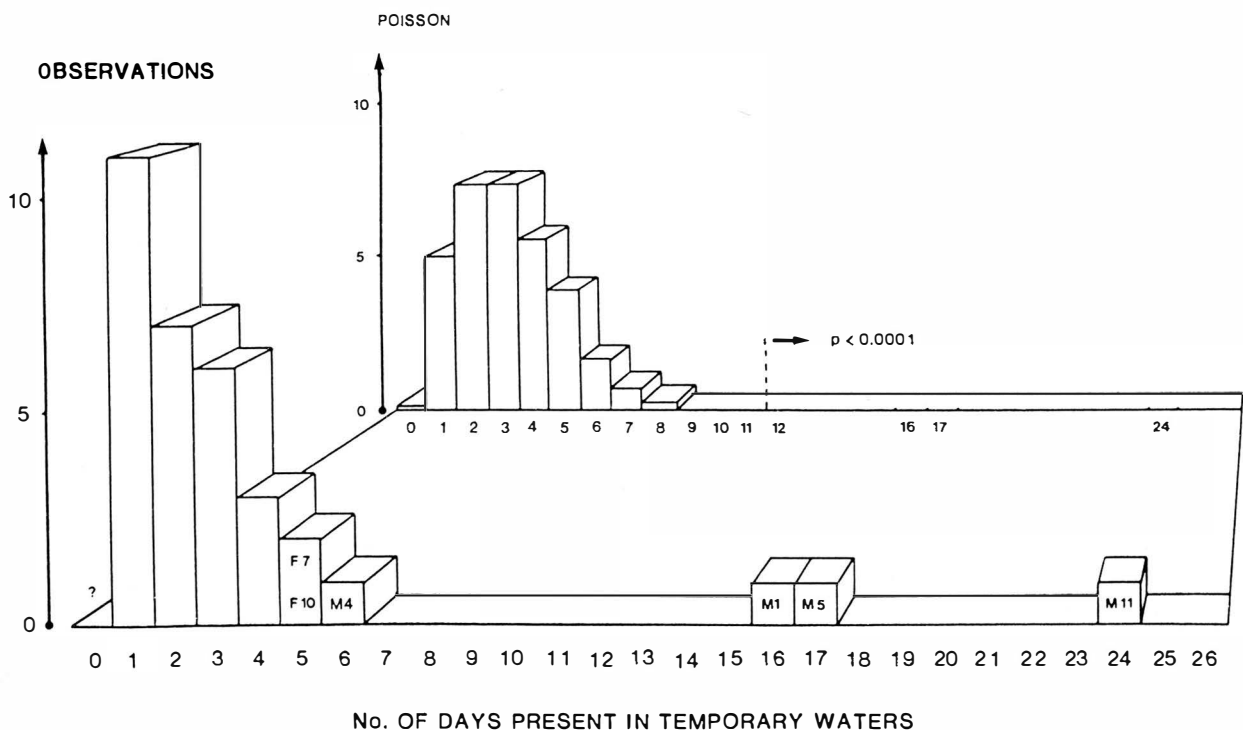


Fig. 2 Frequency distribution of the total number of days that each caiman was recorded in the temporary lagoon over the 76 days of observation. The identity of the six caimans recorded five or more days at the lagoon is indicated. The distribution of the data (foreground) is compared with a random Poisson distribution (background) (see text).

CAIMAN

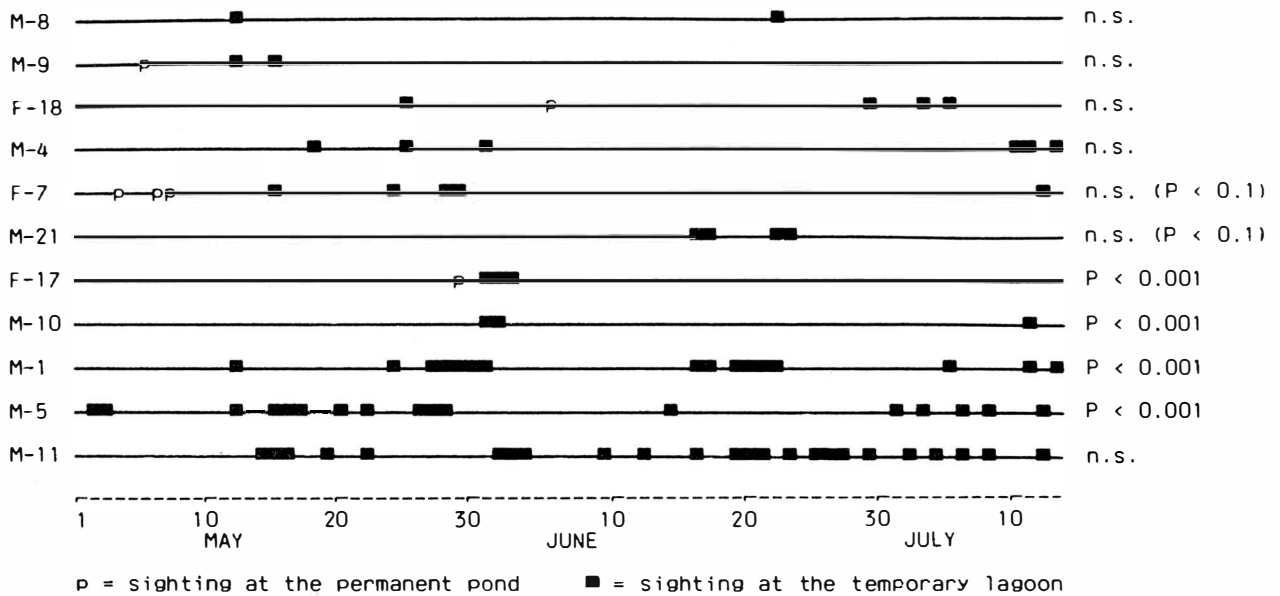


Fig. 3 Occurrence of some caimans at the temporary lagoon. Each square represents one day. This sample was used for a sequence analysis (Siegel, 1958) testing clumpiness of each caiman's sightings over time. The significance of this test is indicated by P values for each caiman.

hunter. This wound probably interfered with feeding for a long time, since M-11 had the lowest body condition of the population sample at the beginning of the study. Thirty days after its first capture, M-11 had reached a just below average body condition.

4. Temporal pattern of visits to the lagoon

Each caiman visited the temporary lagoon at intervals (see Fig. 3 for an exemplary subset of data). The days between visits to the lagoon are referred to as the absence interval. The sample is composed of the pooled absence intervals of 22 caimans recorded more than once in the lagoon. The frequency distribution of the absence intervals recorded was bimodal (Fig. 4) and differed significantly from the expected geometric

distribution ($P < 0.001$, chi-square = 70.3, $df = 14$). This difference was still significant at the 0.1 per cent level, when the three resident caimans were removed from the sample. The large value of chi-square is due to the high number of very short absence intervals (one to two days) and very long absence intervals (longer than 34 days). In general, caimans visited the lagoon in bouts up to one week with brief absence intervals within bouts, and there were prolonged absence intervals between bouts. Out of 30 caimans recorded at the temporary lagoon, 12 (40 per cent) returned to the lagoon after an absence period of at least two weeks.

This pattern is supported by sequence analysis (Siegel, 1956) of the presence and absence days of 10 single individuals seen in the lagoon at least three

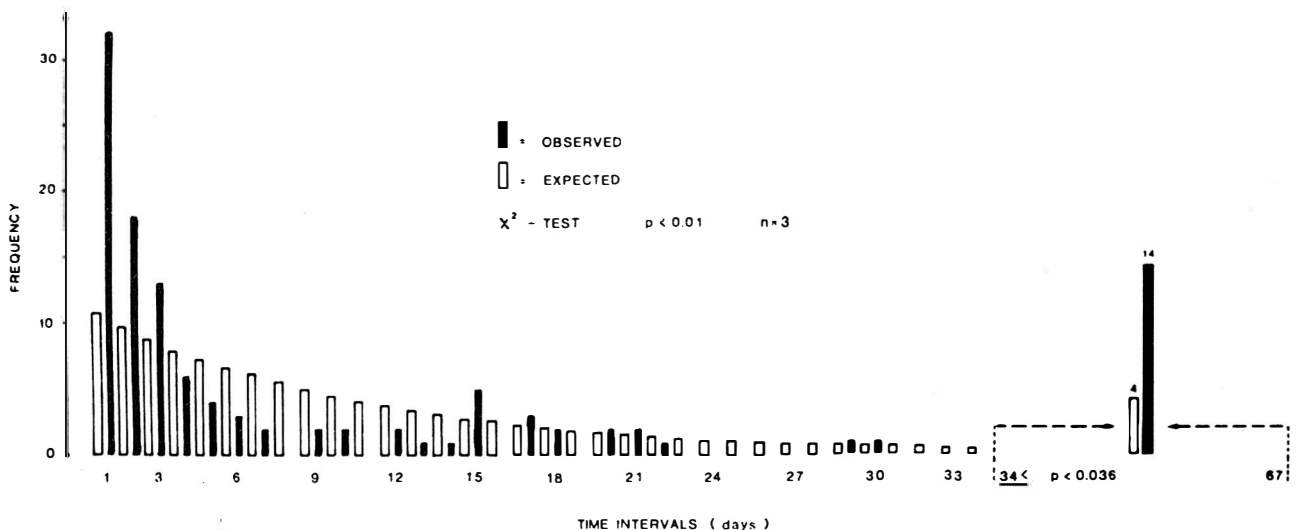


Fig. 4 Frequency distribution of absence intervals between two sightings of the same individual at the temporary lagoon (33 caimans pooled). Absence values between 34 and 67 days are pooled. The distribution of observed values is bimodal and differs significantly from a calculated geometric distribution.

times. The days present were significantly clumped in time for four caimans (Fig. 3): the resident males M-1 and M-5, and the visitors male M-10 (SVL = 67.0cm) and female F-17 (SVL = 53.5cm). They displayed the pattern of short visits followed by prolonged absence intervals. The visits of four other caimans were sporadic events. Because the resident immature M-11 rarely left the lagoon, its days of presence were not clumped in bouts.

5. Ranges within the temporary lagoon

Seven nightly focal observations of 85 to 555 minutes duration were made on the resident caiman M-11. These indicated that there was no consistent ranging pattern within the lagoon. Movement rates varied between 7m/h and 180m/h (median value = 42m/h, $N = 7$). The absolute distance covered during the 555 minutes observation was 875m, and the longest straight line between two locations for the same night was 338m. Values obtained from two other individuals lay in the same range. The caimans used to move parallel and close to the shore. In general, they swam submerged in short bursts followed by prolonged stops at the water surface, usually facing the shore or parallel to it. These stops could last for several hours. When caimans were stationary the body hung down vertically and the tail tip rested on the ground as a point of support. Caimans usually were not stationary in water deeper than a body length, since tail movements were required to keep the eyes and nostrils above the water surface. Caimans often crawled through the grass along the shore in a water depth of about 5cm, leaving a trail of flattened grass with a serpentine shape.

The average distance between the location of a caiman on one night and its location the night after was 180m (SD = 214, range 25-940m, $N = 30$, eight caimans pooled). Capture and handling did not induce caimans to leave that area of the lagoon. The mean distance from the capture site to the location the following night was 184m (SD = 183.2, $N = 7$), while the mean distance for caimans identified but not captured was 182m ($N = 21$).

The maximum distance covered between two locations over seven days, in which the caiman was sighted three or more times, was measured. This value corresponds to the range covered within the lagoon during an average visiting bout. The median for eight caimans was 240m (range 25-800m). The size of the seven-day-ranges compared with the average moving rate of 180m/night and the size of the lagoon (Fig. 1) suggests that caimans showed fidelity to the lagoon portion chosen at the start of a visiting period. This is referred to as short term site fidelity.

There was no consistency in the area of the lagoon chosen after a prolonged absence (i.e. absence of more than seven days). Some individuals showed long term site fidelity, for example the adult female F-9 (SVL = 54.4cm), which returned after 35 days absent to a site within 50m of its last location. Others were resighted hundreds of metres away from their last location. The male M-8 (SVL = 63.9cm) was found 650m away from the site of the last record after 34 days

of absence. Values obtained from 11 more caimans lay between these two extremes.

Sufficient location data was obtained from the resident caimans to estimate ranges within the lagoon for the three month observation period. M-1 ($N = 16$) preferred the eastern part of the lagoon (Fig. 1, T2), but occasionally visited the western areas also. M-5 ($N = 17$) and M-11 ($N = 24$) were mostly found along the western side of the lagoon (Fig. 1, T3), but were also sighted in eastern areas. Considerable overlap between ranges was observed. Most visitor caimans were recorded within the ranges of residents. However, few caimans were seen in the temporary lagoon during most censuses (median = 3 caimans, range 0-22, $N = 66$). Hence, range overlap did not necessarily mean simultaneous use of an area. If caimans occurred simultaneously in an area, they showed spacing behaviour (see below).

6. Spatial distribution of caimans in the lagoon

The spatial distribution of immature and adult caimans in the temporary lagoon, was analysed using a computer program for spatial analysis written by D. Brown (Statistics Group, Cambridge University, UK). The lagoon was subdivided into two equal size sectors (Fig. 1, T1 + T2 and T3). The sample was 11 cases in which four to nine caimans occurred simultaneously in the lagoon sector analysed. For eight cases the probability calculated by the simulation indicated regularity, showing a significant tendency for regularity in the spatial distribution of caimans ($P < 0.01$, combined probabilities test, Fisher, 1958).

The shortest nearest-neighbour distance between two stationary caimans was 15m, but more commonly a minimum nearest-neighbour distance of 30m was observed. This distance may depend on the body sizes of the individuals concerned, but such a relationship was not analysed due to the small sample size. Quantitative analysis of social displacement was not possible because only three social interactions between caimans were observed during the study.

DISCUSSION

There was no indication of territoriality among caimans in the Llanos during the first half of the rainy season. Observations on the reproductive biology of caimans in the Venezuelan Llanos (Staton and Dixon, 1976) suggest that the study period corresponded to the mating season. According to Kaufmann (1983), a territorial individual is expected to be almost continuously in its territory, in order to displace intruders and guarantee its priority access to resources. Caimans in the studied lagoon system did not fulfil this elementary condition for territoriality: 1. Most caimans were nomadic between lagoons. 2. Visits to a lagoon were brief, lasting a maximum of one week. These visits were often interrupted by some nights of absence. 3. Some caimans did not show any preference for any location, while others did remain within a certain sector of the lagoon during their visit. Ranges within the lagoon overlapped considerably. During the short absence periods within a visiting bout caimans may have been in the vegetation next to the lagoon.

Caimans in captivity are known to rest in the vegetation for several days after a substantial meal (Pachon, pers. comm.). During the long absence periods between visits to the study lagoon caimans presumably seeked distant lagoons as supported by three observations of movements across the savannah and five resightings of marked individuals in water bodies other than the study lagoon. Movements between lagoons were not unidirectional, as indicated by 40 per cent of the caimans returning to the study lagoon after a minimum of two weeks absent.

The nomadic behaviour of caimans may be partly related to differences in frog availability between lagoons. Frogs are probably the most common food item in the study lagoon (pers. obs.). Alternative food items found in similar environments, such as fish, snails or crabs (Staton and Dixon, 1975; Gorzula, 1978; Seijas and Ramos, 1980), were not found in the study lagoon. Prior to the start of the rainy season, caimans were found in high densities in the permanent ponds. With the onset of the rains, the calling activity of a common frog, *Physalaemus neglectus dunni*, at the permanent pond increased noticeably. However, as lagoons appeared in the vicinity, the calling activity of frogs decreased to zero in the permanent pond and became deafening in the newly formed lagoons (pers. obs.). Most caimans were found in these lagoons from then onwards. Caiman numbers and calling activity of frogs were particularly high in new lagoons on nights following heavy rainfall (pers. obs.). As the lagoon level rose, caiman numbers and the calling activity of frogs decreased. Two weeks after the onset of the rains, the number of caimans seen in the lagoon was no longer related to rainfall. Although caiman movements between temporary water bodies have been reported before (Gorzula, 1978; Marcellini, 1979), the nature of this behaviour is still not understood.

The nomadic behaviour of caimans during the study suggests that access to resources in the lagoon was not determined by a site-dependent dominance hierarchy (territoriality, *sensu* Kaufmann, 1983). Instead, the distribution of the caimans in the lagoon was probably determined by a body-size dependent hierarchy (Staton and Dixon, 1975), which resulted in spacing behaviour. Spacing behaviour may be a response to potential cannibalism and the aggressive nature of agonistic encounters, which can lead to severe injuries (Staton and Dixon, 1975; Gorzula, 1978).

A site-dependent hierarchy is likely if opponents have a similar body size, as is the case among adult mammals, birds and many arthropods. But similar sized opponents seldom meet among crocodilians due to the large variance in body size. In spectacled caimans, a young sexually mature female can increase its body weight threefold before reaching full size. A fully grown adult caiman achieves 100 to 200 times the weight of a juvenile (Rivero-Blanco, 1974; Medem, 1981). Since most agonistic interactions involve different sized caimans, the outcome of such interactions is generally determined by a body size determined absolute dominance, rather than the location of an encounter. The present study shows lack of territoriality during a limited period. The theoretical considerations above predict also lack of

territoriality during the rest of the year, when caimans are sedentary around breeding sites or in permanent ponds during the dry season.

Territorial behaviour has been reported for other crocodilians, such as *Crocodilus niloticus* (Modha, 1967; Pooley and Gans, 1976; Hutton, 1982), *Crocodilus acutus* (Lang, 1975) and *Alligator mississippiensis* (Garrick, 1975; Garrick and Lang, 1977). Most of these reports use the term 'territory' for an area defended by adults and mention body-size dependent displacements. The defence of an area cannot be termed territoriality, unless the outcome of fights depends on the site of the encounter and is largely independent of body size. So far there is no evidence for site-dependent hierarchies among crocodilians. Even if such a hierarchy existed among fully grown males defending mating areas or females defending breeding sites, the proportion of displacements determined by the site of the encounter rather than the body-size of opponents would still be low. Considering the large variance in the body size of contestants and the accumulated evidence for body-size dependent displacements, the social system of crocodilians is more adequately regarded as an absolute dominance hierarchy in which body size determines access to resources.

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REFERENCES

- Alvarez del Toro, M. (1974). Los Crocodylia de Mexico (estudio comparativo). *Inst. Mex. Rec. Nat. Renov.* 1-70
- Brazaitis, P. J. (1968). The determination of sex in living crocodilians. *Brit. J. Herpetol.* 4, 54-58.
- Cabrera, A. L. and Willinck, A. (1980). *Biogeografía de América Latina* (Ed. E. V. Chesneau). 2nd ed. Washington, DC: Secretaría General de la Organización de los Estados Americanos, Programa Regional de Desarrollo Científico y Tecnológico.
- Fisher, R. A. (1958). *Statistical Methods for Research Workers*. 13th ed. London: Oliver and Boyd.
- Garrick, L. D. (1975). Love among the alligators. *Anim. Kingd.* 78(2), 2-8.
- Garrick, L. D. and Lang, J. W. (1977). Social signals and behaviours of adult alligators and crocodiles. *Amer. Zool.* 17, 225-239.

- Gorzula, S. J. (1978). An ecological study of *Caiman crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. *Oecologia*, **35**, 21-34.
- Hueck, K. (1966). *Die Wälder Südamerikas*, (pp.389-392). Stuttgart: Gustav-Fischer Verlag.
- Hutton, J. M. (1982). Home range and territoriality in the Nile crocodile. *Zimbabwe Science News*, **16**, 199-201.
- Kaufmann, J. H. (1983). On the definitions and functions of dominance and territoriality. *Biol. Rev.* **58**, 1-20.
- Lang, J. W. (1975). The Florida crocodile: Will it survive? *Chicago (Field) Mus. Nat. Hist. Bull.* **46**, 4-9.
- Marcellini, D. L. (1979). Activity patterns and densities of Venezuelan caiman (*Caiman crocodilus*) and pond turtles (*Podocnemis vogli*). In: *Vertebrate Ecology in the northern Neotropics* (Ed. J. F. Eisenberg), pp.263-270. Washington, DC: Smithsonian Institution Press.
- Medem, F. (1962). La distribución geográfica y ecología de los *Crocodylia* y *Testudinata* en el departamento del Chocó. *Revista Acad. Col. Cienc. Exact. Fis. Nat.* **11** (44), 279-303.
- Medem, F. (1981). *Los Crocodylia de Sur America. Vol. 1. Los Crocodylia de Colombia*. Bogotá: Colciencias.
- Modha, M. L. (1967). The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *E. Afr. Wildl. J.* **5**, 74-95.
- Ouboter, P. E. and Nanhoé, L. M. R. (1988). Habitat selection and migration of *Caiman crocodilus crocodilus* in a swamp and swamp forest habitat in Northern Suriname. *J. Herpetol.* **22**, 283-294.
- Pooley, A. C. and Gans, C. (1976). The Nile crocodile. *Sci. Amer.* **234**, 114-24.
- Rivero-Blanco, C. (1974). Hábitos reproductivos de la baba en los Llanos de Venezuela. *Natura*, **52**, 24-29.
- Seijas, A. E. and Ramos, S. (1980). Características de la dieta de la baba (*Caiman crocodilus*) durante la estación seca en las sabanas moduladas del estado de Apure, Venezuela. *Acta Biol. Venez.* **10** (4), 373-389.
- Siegel, S. (1956). *Nonparametric statistics for the behavioral sciences*. New York: MacGraw-Hill.
- Staton, M. A. and Dixon, J. R. (1975). Studies on the dry season biology of *Caiman crocodilus* from the Venezuelan Llanos. *Memoria Soc. Cienc. Nat. La Salle*, **101**, 237-265.
- Staton, M. A. and Dixon, J. R. (1976). Breeding biology of the spectacled caiman, *Caiman crocodilus*, in the Venezuelan Llanos. *Wildl. Res. Report*, **5**, 1-21.

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A LATE PLEISTOCENE HERPETOFAUNA FROM BELL CAVE, ALABAMA

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ABSTRACT

Three stratigraphic units in Bell Cave, northwestern Alabama, have yielded fossil herpetofaunas that are mainly analogues of the modern ones in the area. Two of the fossiliferous zones have been dated by the Carbon 14 method: Zone 1/2 at 11,820 ± 480 to -500 BP and Zone 4 at 26,500 ± 870 to -990 BP. An intermediate unit (Zone 3) did not yield a Carbon 14 date, but is faunistically nearly identical to Zone 1/2. Excessive damage was present in many of the fossils due to predators and gnawing scavengers, thus only 18 per cent of the 3,953 herpetological fossils could be identified to the generic or to the specific level. The wide variety of habitats represented by the fossils (small, clear streams; larger, slower streams; marshy wetlands; waterfalls and associated talus seeps; woodlands and woodland edges) is attributed to transportation by palaeopredators. None of the amphibian or reptile species is extinct, in contrast to the mammalian fauna which has several extinct taxa. Zone 1/2 has at least 24 species, including one northern and two slightly eastern extralimital ones. Zone 3 has at least 24 species, including the same three extralimital species that occur in Zone 1/2. Zone 4 has 13 species, including only two slightly eastern extralimital ones. It is difficult on the herpetological remains to suggest a palaeoclimate much different from the climate of the area today. Certainly, the presence of many egg-laying turtles, lizards and snakes in all units negates a tundra-like or boreal-like interpretation of the palaeoclimate.

INTRODUCTION

Late Wisconsinan faunas in midlatitude North America typically have extralimital, northern, mammalian species. This has led regularly to the conclusion that the climate was tundra-like or boreal-like. On the other hand, the herpetofaunas of these sites are usually similar or identical to those inhabiting such areas today, and this has led to an interpretive dilemma (Fay, 1984, 1986, 1988; Holman, 1986; Holman and Grady, 1987).

The lack of stratigraphic control in most of these faunas, many of them in caves, rock shelters, or fissure fillings, has led some workers to suspect that herpetological species were modern intrusives, and not contemporaneous with the mammalian species (references in Fay, 1988). Thus, the Bell Cave herpetofauna reported here is of considerable importance as it is from Carbon 14 dated, stratigraphically controlled, units. Moreover, it is the first large Pleistocene herpetofauna from Alabama.

The Bell Cave bone deposit lies in the NE corner of Section 9, Township 4 S, Range 12 W, 10.8k W of Tuscumbia, Colbert County, Alabama, 87° 47' 45" W, 34° 43' 48" N. The cave is located in a bluff, adjacent to the Tennessee River, within the Tuscumbia Limestone of Middle Mississippian age. It consists of a 26.2m horizontal crawlway which ends at a large, 4 by 11.9m oval, pit-like room.

This room acted as a settling basin for fissure-transported sediment, and has accumulated about 40cm of bone-packed mud. The deposit is distinctly separated into three bone-bearing units; Zone 1/2, Zone 3 and Zone 4, representing different depositional events. These units lie on top of a layer, at least 70cm

thick, of sterile clay (Fig. 1). The sterile unit and its overlying bone-bearing unit (Zone 4) are both believed to have been subaqueously deposited. A lowering of the local water table resulted in the subsequent desiccation and consolidation of these two units and the onset of travertine formation. Zone 3 appears to have been deposited as a viscous mud flow from the fissure, and Zone 1/2 was deposited later in the same manner. Radiocarbon dates are as follows:

Zone 1/2 — 11,820 +480 to -500 BP (*Ursus americanus* femur)

Zone 3 — Not sufficient bone for a sample

Zone 4 — 26,000 +870 to -990 (various longbone fragments)

Matrix from each stratigraphic fossiliferous unit was collected in sacks and removed from the cave for processing. The matrix was dried and screened, mainly using the standard techniques of Hibbard (1949). The concentrate was then sorted into taxonomic groups. Nine different workers are studying the mammalian fossils of this rich site, greatly delaying the time of publication of that component of the cave fauna.

SYSTEMATIC PALAEOONTOLOGY

The fossils of this study are deposited in the Red Mountain Museum, Birmingham, Alabama, 35205, USA (abbreviated to RMM), and their collection numbers identify the specimens reported herein.

Class Amphibia

Order Caudata

Family Cryptobranchidae

Cryptobranchus alleganiensis (Daudin)

Hellbender

Zone 1: Pit 1, vertebra RMM 3943; Pit 3, left premaxilla 5081. Zone 1/2: Pit 1, atlas 3878, eight vertebrae 3858; Pit 2, atlas 4905, five vertebrae 4279; Pit 3, seven vertebrae 5057, six vertebrae 5079, vertebra 6764; Pit 4, 12 vertebrae 5264. Zone 3: Pit 1, right premaxilla 4806 (Fig. 2a), left maxilla 3999, three vertebrae 4320; Pit 3, nine vertebrae 4703 (Fig. 2b), vertebra 6675; Pit 4, five vertebrae 5348. Zone 4: Pit 2, atlas and three presacral vertebrae 4353 (Fig. 2c). Disturbed Zone: two vertebrae 3832 and 4047.

Holman (1977, 1982b) has discussed the identification of *Cryptobranchus alleganiensis* and *C. guildayi* on the basis of isolated bones. *Cryptobranchus alleganiensis* occurs in the Tennessee River System in northwestern Alabama today (Mount, 1975, Fig. 116). These animals are completely aquatic and occur in rocky streams with relatively clear water. Fossil hellbenders have been found in Pleistocene cave deposits in Virginia (Holman, 1986), West Virginia (Holman, 1982b; Holman and Grady, 1987) and Maryland (Holman, 1977).

Family Ambystomatidae

Ambystoma sp. indet.

Mole Salamander

Zone 1/2: Pit 1, 11 vertebrae RMM 4773; Pit 3, three vertebrae 5060; Pit 4, two vertebrae 5255. Zone 3: Pit 1, three vertebrae 4811, vertebra 6766; Pit 3, two vertebrae 4697; Pit 4, vertebra 5604.

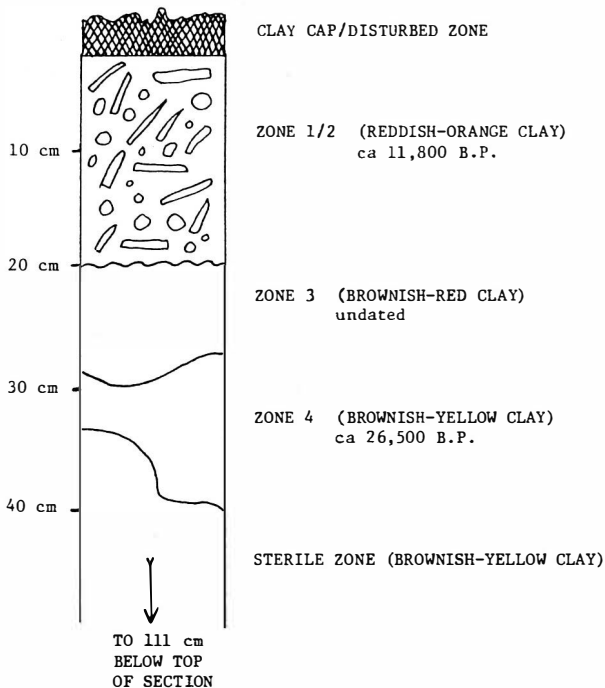


Fig. 1 Stratigraphic units of Bell Cave, Alabama, USA at Pit 1. The Clay Cap/Disturbed Zone is variable in thickness. Travertine slabs and large rounded pebbles are indicated in Zone 1/2.

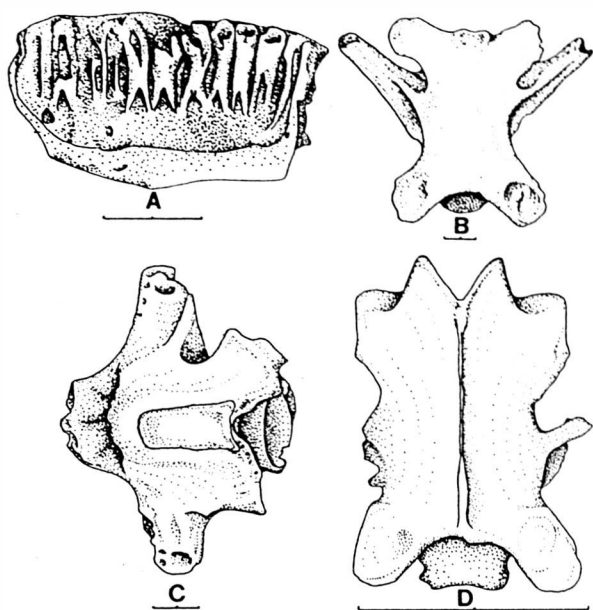


Fig. 2 Salamander fossils of Bell Cave. A, right premaxilla of *Cryptobranchus alleganiensis* RMM 4806; B, trunk vertebra of *C. alleganiensis* RMM 4703 in dorsal view; C, atlas of *C. alleganiensis* RMM 4553 in dorsal view; D, trunk vertebra of *Desmognathus ochrophaeus* RMM 6770 in dorsal view. Each scale line equals 2mm.

Tihen (1958) has given vertebral characters for the genus *Ambystoma*. The above vertebrae were too fragmentary for specific identification.

Ambystoma maculatum Shaw

Spotted Salamander

Zone 1/2: Pit 4, two vertebrae RMM 6767. Zone 3: Pit 1, vertebra 6768; Pit 3, vertebra 6769.

Tihen (1958) and Holman and Grady (1987) discuss the identification of *Ambystoma maculatum* on the basis of vertebrae. This animal occurs in the area today (Mount, 1975, Fig. 102) where it inhabits low areas where hardwood trees are present and pools are available for breeding.

Family Plethodontidae

Desmognathus sp. indet.

Dusky Salamander

Zone 4: Pit 4, vertebrae RMM 5606.

Holman and Grady (1987) have discussed the identification of this genus on the basis of vertebrae, but the above specimen is too fragmentary for specific identification.

Desmognathus ochrophaeus Cope

Mountain Dusky Salamander

Zone 4: Pit 1, vertebra RMM 6770 (Fig. 2d); Pit 4, two vertebrae 6771.

The identification of this species on the basis of vertebrae has been discussed by Holman and Grady (1987). A very deeply notched posterior end of the neural spine is characteristic of this species (Fig. 2d). Today, this species occurs in Alabama only in the extreme northeastern corner of the state (Mount, 1975, Fig. 127) where it occurs near moist cliff faces and talus areas beneath water falls.

Eurycea sp. indet.

Brook Salamander

Zone 1/2: Pit 4, vertebrae RMM 6772. Zone 4: (pit undesignated) five vertebrae.

Eurycea have amphicoelous or falsely opisthocelous vertebrae that are slender; have a high, rounded or sometimes pointed neural spine; two small foramina behind the rib-bearers; and with the rib-bearers distinctly divided. We are unable to identify the above vertebrae specifically. Species of this genus occur in moist woodlands today.

Plethodon glutinosus (Green)

Slimy Salamander

Zone 1/2: Pit 1, vertebra RMM 6774; Pit 2, vertebra 4910. Zone 3: Pit 1, vertebra 6775. Overlying Clay Cap: 6776.

The identification of *P. glutinosus* middle trunk vertebrae was discussed by Holman and Grady (1987). The anterior trunk vertebrae of *P. glutinosus* also appear to be diagnostic in having a relatively short and wide form; with a well-developed, rounded neural spine; slender anterior zygapophyses; widely-spaced, cylindrical rib-bearers, two foramina anterior to the rib-bearers, a wide ventral surface; and with this surface with a constricted medial portion. This salamander occurs in the area today (Mount, 1975, Fig. 152) in many woodland habitats. All of the authors of this paper have seen living specimens in Bell Cave.

Order Anura

Family Bufonidae

Bufo sp. indet.

Zone 1: Pit 1, six sacra RMM 6677. Zone 1/2: Pit 1, one left and four right ilia 3780; Pit 2, left ilium 6778, sacrum 6779; Pit 3, sacrum 6780; Pit 4, sacrum 6781. Zone 3: Pit 3, three sacra 6782.

These elements were too fragmentary for specific identification.

Bufo americanus Holbrook

Zone 1/2: Pit 1, two left and one right ilia RMM 6783; Pit 2, left ilium 6784; Pit 3, right ilium 6785; Pit 4, right ilium 6788 (Fig. 3a). Zone 3: Pit 1, one left and two right ilia 6787; Pit 3, three left and one right ilia 6788, two left and two right ilia 6789.

The identification of isolated ilia of *B. americanus*, *B. terrestris* and *B. woodhousii* was detailed by Wilson (1975). The base of the ilial protuberance of *B. americanus* is wider than that of *B. woodhousii fowleri*. We have also noticed in skeletons of 12 *B. americanus* and 12 *B. w. fowleri* that the ilial protuberance is less distinctly marked from the prominence in *B. americanus* than in *B. w. fowleri*. *Bufo americanus* has not been recorded from northwestern Alabama today (Mount, 1975, Fig. 42), but it occurs in the northeastern part of the state. This species has ubiquitous habitats in basically woodland areas.

Bufo woodhousii fowleri Hinckley

Fowler's Toad

Zone 1/2: Pit 3, left ilium RMM 6790. Zone 3, left ilium 6791 (Fig. 3b), right ilium 6792.

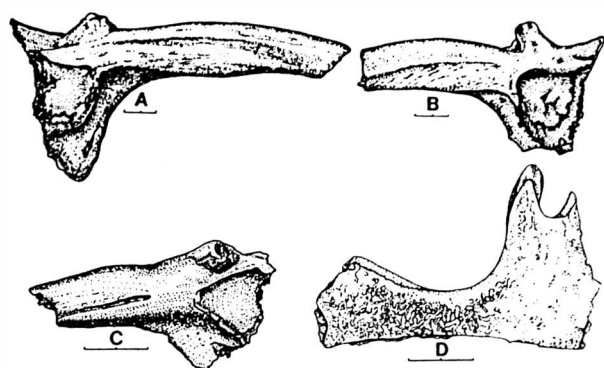


Fig. 3 Anuran and chelonian fossils of Bell Cave. A, right ilium of *Bufo americanus* RMM 6786 in lateral view; B, left ilium of *Bufo woodhousii fowleri* RMM 6791 in lateral view; C, left ilium of *Hyla gratiosa* RMM 6793 in lateral view; D, left hypoplastron of *Trionyx spiniferus* RMM 4580 in dorsal view. Scale lines A, B and C equal 2mm. Scale line D equals 20mm.

Bufo woodhousii fowleri is easily distinguished from its western counterpart *B. woodhousii woodhousii* on the basis of its much lower ilial protuberance. Fowler's toad occurs in the area today (Mount, 1975, Fig. 48). This species has ubiquitous habitats in basically woodland areas today.

Family Hylidae

Hyla gratiosa LeConte

Barking Treefrog

Zone 1: Pit 1, left and right ilia RMM 4767. Zone 1/2: Pit 4, left ilium 6793 (Fig. 3c).

Hyla gratiosa has an ilium that is distinguishable from other *Hyla* in being quite large; with an extensive ventral acetabular expansion; rounded dorsal protuberance that occurs posterior to the anterior edge of the acetabular cup; and with the protuberance close to the edge of the acetabular cup. There is a record of the barking treefrog quite near Bell Cave today (Mount, 1975, Fig. 62). This is a woodland treefrog.

Family Ranidae

Rana sp. indet.

Zone 1/2: Pit 1, sacrum RMM 6794. Zone 4: Pit 1, two sacra 6795; Pit 4, two sacra 6796.

These elements cannot be distinguished to species.

Rana pipiens complex

Leopard Frogs

Zone 1: Pit 1, left ilium RMM 4758, sacrum 6797. Zone 1/2: Pit 2, five left and four right ilia 6887; Pit 3, five left and two right ilia 6798; Pit 4, three right ilia 6799. Zone 3: Pit 1, left ilium and sacrum 4798, one left and two right ilia 6800; Pit 4, one left ilium 4595. Zone 4: Pit 1, four left and eight right ilia 6801; Pit 3, one left and one right ilia 5171, three left and 12 right ilia 6802, two left and two right ilia and one sacrum 6803; Pit 4, 22 left and 24 right ilia 6804. Overlying Clay Cap: right ilium 5544.

Characters for the identification of ilia of the *R. pipiens* complex are given in Holman (1984). Today, *R. palustris* and *R. sphenoccephala* of this complex occur in the Bell Cave area (Mount, 1975,

Figs. 93 and 95). Both species occur in marshy wetlands.

Rana catesbeiana Shaw

Bullfrog

Zone 1/2: Pit 3, right ilium RMM 5056.

Holman (1984) discussed the identification of ilia of *R. catesbeiana*. This species occurs in the area today (Mount, 1975, Fig. 84) in wetlands and streams.

Order Testudines

Trionyx sp. indet.

Zone 1: Pit 1, two carapace fragments RMM 4580. Zone 1/2: Pit 1, nine shell fragments 6805, 27 shell fragments 3709; Pit 2, 10 shell fragments 3633, 22 shell fragments 4858; Pit 3, 30 shell fragments 4952; Pit 4, 14 shell fragments 5185. Zone 3: Pit 1, 12 shell fragments 4186; Pit 3, two shell fragments 4723, 20 shell fragments 4644; Pit 4, 13 shell fragments 5341. Zone 4: Pit 1, one costal 4474, two shell fragments 4482; Pit 2, three shell fragments 4916; Pit 3, four shell fragments 5119. Disturbed Zone: one costal fragment 3779. Overlying Clay Cap: two shell fragments 5517, one shell fragment 5526.

These fossils were too fragmentary to identify to the specific level.

Family Trionychidae

Trionyx spiniferus Lesuer

Spiny Softshell Turtle

Zone 1: Pit 1, left hypoplastron RMM 4580 (Fig. 3d). Zone 1/2: Pit 2, one juvenile right hypoplastron 6808.

The hypoplastron of *T. spiniferus* is distinguished from that of *T. muticus* in having a much less acute greater xiphiplastral notch and a much shorter lesser xiphiplastral notch. This species occurs throughout Alabama today (Mount, 1975, Fig. 348), but there are no specific records near the cave site. This species occurs in rivers, lakes, and permanent ponds.

Family Emydidae

Chrysemys picta (Schneider)

Zone 4: Pit 1, nuchal and left epiplastron RMM 6807. Ledge in Fissure: right hypoplastron 4539 (Fig. 4a).

The serrated anterior end of the nuchal scute area of the nuchal bone appears to be diagnostic in many individuals of this species. The hypoplastron of *C. picta* differs from that of *Pseudemys concinna*, *P. floridana* and *Trachemys scripta* in having the inguinal scute shorter and broader. This bone further differs from *T. scripta* in its smoother texture, smaller size and more vertically directed inguinal buttress. This species occurs in the area today (Mount, 1975, Fig. 297) in ponds, lakes and slowly moving streams with soft bottoms and abundant aquatic vegetation.

Graptemys geographica (Le Sueur)

Common Map Turtle

Zone 1/2-3: Pit 5, lower mandible of a female and three peripherals RMM 6888.

The lower mandible of female *G. geographica* differs from the male of *G. geographica*, and from both sexes of the sympatric *G. pseudogeographica* in having the posterior part of the crushing surface of each dentary

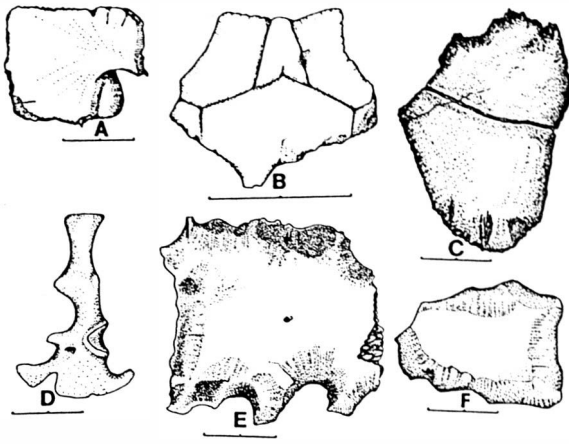


Fig. 4 Chelonian and lizard fossils of Bell Cave. A, right hypoplastron of *Chrysemys picta* RMM 4539 in dorsal view; B, nuchal bone of *Pseudemys concinna* RMM 6813 in dorsal view; C, left xiphiplastron of *P. concinna* RMM 6814 in ventral view; D, left scapulocoracoid of *Anolis carolinensis* RMM 4822 in lateral view; E, indeterminate emydid turtle plastron RMM 3724 (in dorsal view) that had been crushed by a large predator; F, indeterminate emydid turtle plastron RMM 5184 (in dorsal view) that had been gnawed by rodents. Scale lines A, B, C, E and F equal 20mm. Scale line D equals 2mm.

broadly expanded posteriorly as a mollusk-crushing specialisation. *G. geographica* occurs in the area today (Mount, 1975, Fig. 305) in rivers, creeks and brooks.

Pseudemys sp. indet.

Cooters and Red-bellied Turtles

Zone 1/2: Pit 1, left hypoplastron RMM 6810; Pit 2, right hypoplastron 6811. Disturbed Zone: right hypoplastron 3690.

These bones are too damaged by predators to identify to species.

Pseudemys concinna (Le Conte)

River Cooter

Zone 1/2: Pit 1, two right hypoplastra RMM 6812; Pit 3, two right hypoplastra 4445. Zone 3: Pit 3, nuchal 6813 (Fig. 4b), left xiphiplastron 6814 (Fig. 4c).

The nuchal of *P. concinna* appears to be separable from other emydid turtles of southeastern United States, having a triangular nuchal scute that is about twice as long as it is high, and that is slightly upraised; no sculpturing on the dorsal surface of the bone; and the anterior edge of the bone slightly indented. The hypoplastron of *P. concinna* has the inguinal longer and narrower than in *C. picta* and *T. scripta* and less etched into the bone than in *Pseudemys floridana*. The xiphiplastron *P. concinna* has its posterior end more narrowly rounded than in *C. picta*, *P. floridana* or *P. scripta*. *P. concinna* occurs in the area today (Mount, 1975, Fig. 323) where it is said to prefer streams and large lakes.

Order Squamata

Family Iguanidae

Anolis carolinensis Voigt

Green Anole

Zone 4: Pit 1, left scapulocoracoid RMM 4822 (Fig. 4d).

Although the scapulocoracoid of lizards has been infrequently reported in the fossil record, this element appears to be diagnostic. This is probably because of its complex structure (Romer, 1956) that probably reflects differences in posture and locomotion. This element in *A. carolinensis* is very distinct from those of other lizards of the eastern United States. The complex of processes on the anterior face of the bone as well as the position of the lateral nutrient foramen and relationship of the posteroventral process to the acetabulum (Fig. 4d) are all distinct and diagnostic characters.

The species occurs almost anywhere that vegetation and shade are abundant in Alabama today (Mount, 1975).

Family Colubridae

Carphophis amoenus (Say)

Worm Snake

Zone 1/2: Pit 4, three vertebrae RMM 6815. Zone 3: Pit 1, two vertebrae 6816. Zone 4: Pit 4, two vertebrae 6817. Disturbed Zone: one vertebra 6818. Clay Cap: Pit 3, one vertebra 6819.

Holman and Grady (1987) give characters that distinguish the vertebrae of *C. amoenus* from those of the very similar *Diadophis punctatus*. The worm snake occurs in the area today (Mount, 1975, Fig. 195), in open woodlands and woodland edges, and is frequently discovered near *Diadophis punctatus*.

Coluber constrictor Linnaeus

Black Racer

Zone 3: Pit 1, one vertebra RMM 6820; Pit 3, one vertebra 6821; Pit 4, one vertebra 6822.

Holman (1981) gave references to publications that discussed the identification of *C. constrictor* on the basis of individual fossil vertebrae. The black racer occurs in the area today (Mount, 1975, Fig. 200) in open woodland and forest edges, as well as along brushy stream edges.

Diadophis punctatus (Linnaeus)

Ringneck Snake

Zone 3: Pit 1, one vertebra RMM 6823.

Holman and Grady (1987) give characters that distinguish the vertebrae of *D. punctatus* from the similar *Carphophis amoenus*. *Diadophis punctatus* occurs in the area today (Mount, 1975, Fig. 202) where it is often found in the vicinity of *Carphophis amoenus*.

Elaphe sp. indet.

Ratsnake

Zone 1/2: Pit 1, nine vertebrae RMM 6824; Pit 2, one vertebra 6825; Pit 3, one vertebra 6826. Zone 3: Pit 1, one vertebra 4099, one vertebra 4300; Pit 3, one vertebra 6827; Pit 4, three vertebrae 6828.

These vertebrae are too fragmentary for specific identification.

Elaphe cf. *Elaphe guttata* (Linnaeus)

Cornsnake

Zone 1/2: Pit 2, one vertebra RMM 6829.

Auffenberg (1963) discusses the identification of isolated vertebrae of species of *Elaphe*. This vertebrae fits his criteria for *E. guttata* in most respects, including

the height of the neural spine. On the basis of having only a single vertebra, we are tentatively referring the fossil to *E. guttata*. This species occurs in the area today (Mount, 1975, Fig. 206) where it is frequently found near woodland edges.

Elaphe vulpina Baird and Girard

Foxsnake

Zone 1/2: Pit 1, one vertebra RMM 6830; Pit 2, one vertebra 6831. Zone 3: Pit 1, two vertebrae 6832; Pit 4, one vertebra 6833.

This snake gets no closer to the area today than northeastern Missouri and southwestern Illinois (Conant, 1975, map 148).

Vertebral characters of this snake are given in Holman (1982a). This species is one of the most easily identified large colubrid snakes in North America based on individual vertebrae. The foxsnake had a much wider distribution in the eastern and southeastern United States in the Pleistocene than it has today (Holman, 1981, 1984); it has recently been recorded from the late Pleistocene of Georgia (Holman, 1985a,b). This species is found in grasslands and woodland edges.

Heterodon cf. Heterodon platirhinos Latreille

Eastern Hognose Snake

Zone 1/2: Pit 1, two vertebrae RMM 6834; Pit 2, one vertebra 6835. Zone 3: Pit 1, three vertebrae 6836; Pit 3, three vertebrae 6837. Zone 4: Pit 1, two vertebrae 6838.

Holman (1981) quotes literature that deals with the identification of vertebrae of the species of *Heterodon*. Mount (1975) considers this species to be of statewide occurrence in Alabama, in areas of broken terrain.

Lampropeltis getulus (Linnaeus)

Eastern Kingsnake

Zone 1/2: Pit 3, one vertebra RMM 6839. Zone 3: Pit 4, one vertebra 6840. Zone 4: Pit 1, one vertebra 6841.

Holman (1981) quotes references to the identification of isolated vertebrae of this species. The eastern kingsnake occurs in the area today (Mount, 1975, Fig. 223) at the edges of aquatic habitats.

Lampropeltis triangulum triangulum (Lacepede)

Northern Milksnake

Zone 1/2: Pit 1, five vertebrae RMM 6842; Pit 4, one vertebra 6843. Zone 3: Pit 1, six vertebrae 6844; Pit 3, seven vertebrae 6845; Pit 4, four vertebrae 6846. Zone 4: Pit 3, three vertebrae 6847; Pit 4, 25 vertebrae 6848.

The identification of this large subspecies based on individual vertebrae is discussed in Holman (1985a). The northern milksnake occurs only in extreme northeastern Alabama today (Mount, 1975, Fig. 227) where it is a secretive woodland form.

Nerodia sp. indet.

Watersnake

Zone 1/2: Pit 1, 18 vertebrae RMM 6849; Pit 2, four vertebrae 6850; Pit 3, one vertebra 6851; Pit 4, two vertebrae 6852. Zone 3: Pit 4, six vertebrae 6853.

These vertebrae are too fragmentary to identify to the specific level.

Nerodia sipedon (Linnaeus)

Northern Watersnake

Zone 1/2: Pit 1, one vertebra RMM 6854; Pit 3, three vertebrae 6855; Pit 4, five vertebrae 6856. Zone 3: Pit 1, one vertebra 6857; Pit 3, two vertebrae 6858; Pit 4, two vertebrae 6859. Zone 4: Pit 4, six vertebrae 6860.

Brattstrom (1967) and Holman (1967) discuss the identification of *Nerodia* and species of *Nerodia* on the basis of isolated vertebrae. The species occurs in the area today (Mount, 1975, Fig. 246) in a variety of aquatic habitats.

Opheodrys aestivus (Linnaeus)

Rough Green Snake

Zone 1/2: Pit 1, two vertebrae RMM 6861; Pit 3, one vertebra 6862. Zone 3: Pit 4, six vertebrae 6863.

Holman and Richards (1981) distinguish between vertebrae of *O. aestivus* and *O. vernalis*. *Opheodrys aestivus* is found in the area today (Mount, 1975, Fig. 250) where it is common in vegetation around lakes and streams.

Storeria sp. indet.

Brown or Redbelly Snake

Zone 1/2: Pit 1, three vertebrae RMM 6864; Pit 3, one vertebra 6865; Pit 4, 11 vertebrae 6866. Zone 3: Pit 1, two vertebrae 6867; Pit 3, two vertebrae 6868; Pit 4, six vertebrae 6869.

Holman (1981) gives references for the identification of *Storeria* vertebrae. We cannot determine the species of the above vertebrae. Mount (1975) believes that the two species of *Storeria* that occur in Alabama today (*S. dekayi* and *S. occipitamaculata*) occur statewide.

Thamnophis sp. indet.

Garter or Ribbon Snake

Zone 1/2: Pit 1, 19 vertebrae RMM 6870; Pit 2, three vertebrae 6871; Pit 3, one vertebra 6872; Pit 4, two vertebrae 6873. Zone 3: Pit 1, nine vertebrae 4812; Pit 3, seven vertebrae 6874; Pit 4, four vertebrae 6875. Zone 4: Pit 1, one vertebra 6876.

Brattstrom (1967) discusses the identification of isolated *Thamnophis* vertebrae. These fossils are too fragmentary for specific identification.

Thamnophis sirtalis (Linnaeus)

Gatersnake

Zone 1/2: Pit 1, seven vertebrae RMM 6877; Pit 3, one vertebra 6878. Zone 3: Pit 3, one vertebra 6879. Zone 4: Pit 1, one vertebra 6880.

Holman (1984) has discussed how vertebrae of large *T. sirtalis* may be separated from those of the similar *T. proximus* and *T. sauritus*. Mount (1975) considers *T. sirtalis* to occur statewide in Alabama.

Family Viperidae

Agkistrodon sp. indet.

Copperhead or Cottonmouth

Zone 4: Pit 3, one vertebra RMM 6882.

Holman (1981) gives references for the identification of *Agkistrodon* and *Crotalus* vertebrae. We are unable to determine this broken vertebra to the specific level.

Crotalus horridus Linnaeus

Timber Rattlesnake

Zone 1/2: Pit 2, one vertebra RMM 6883; Pit 3, five vertebrae 5055. Zone 3: Pit 1, two vertebrae 6884, one vertebra 4195, one vertebra 6885; Pit 3, nine vertebrae 4638. Zone 4: Pit 1, one vertebra 4142, two vertebrae 6886; Pit 3, four vertebrae 5173.

Holman (1967) gives characters that distinguish *C. horridus* from other viperid species in eastern United States. This species is considered by Mount (1975) to have a statewide occurrence in Alabama today. The timber rattlesnake is a species that prefers forested areas, especially if rocky ledges are available for hibernation.

DISCUSSION

Herpetological evidence from late Wisconsin cave faunas in the United States has sometimes been neglected or misinterpreted (Holman, 1986; Fay, 1988). Several of these faunas have amphibian and reptile species that would not be ecologically compatible with some of the mammalian species today; but some workers have disregarded these herpetological species on the supposition that they were modern intrusions into the fauna. But the Bell Cave herpetofauna is temporally in context with the rest of the fauna. Moreover, Carbon 14 dates in identifiable stratigraphic units provide a stratigraphic control that is unusual in some previously reported North American Pleistocene cave faunas.

Excessive damage was present on many of the fossil bones due to the activities of predators and scavengers. Thus, only 718 of 3953 individual bones (18 per cent) were identified to the generic or to the specific level. Fig. 4e,f shows two turtle bones that could not be identified to genus or species. Fig. 4e is from the plastron of a large emydid turtle that had been bitten by a very large predator. Emmons (1989) has detailed how jaguars (*Planthera onca*) feed upon turtles by crushing the shells in their jaws. It is likely that many of the large turtle remains from the Ladds, Georgia, USA, Pleistocene site had been crushed by these large-headed felines (Emmons, 1989, Fig. 1; Holman, 1985a, Fig. 4). It therefore seems possible that the large tooth marks on the Bell Cave, Alabama, turtle shells could also have been made by *Panthera onca*. Fig. 4f is from the plastron of a smaller emydid turtle that had been gnawed by rodents.

A wide variety of aquatic and terrestrial habitats is indicated by the fossil herpetofauna, and this may be most logically attributed to transportation of prey to the cave by various predators. Bears and large felids (still being studied) were present in the cave as attested by fossil remains.

Small clear streams are indicated by *Cryptobranchius alleganiensis*. Larger, slower streams are indicated by *Chrysemys picta*, *Graptemys geographica*, *Pseudemys concinna*, *Trionyx spiniferus*, and *Nerodia sipedon*. Marshy wetlands are indicated by *Rana catesbeiana*, *Rana pipiens* complex, *Storeria* sp. and *Thamnophis sirtalis*. Talus areas below waterfalls or seeps are indicated by *Desmognathus ochrophaeus*. Woodlands

and woodland edges are indicated by *Ambystoma maculatum*, *Eurycea* sp., *Plethodon glutinosus*, *Bufo americanus*, *Bufo woodhousii fowleri*, *Hyla gratiosa*, *Anolis carolinensis*, *Carphophis amoenus*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe* cf. *E. guttata*, *Elaphe vulpina*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis getulus*, *Lampropeltis t. triangulum*, *Ophedrys aestivus* and *Crotalus horridus*.

All of the fossil amphibians and reptiles from the Pleistocene of Bell Cave are represented by species that are living today, a situation that is not unusual in North American late Wisconsin herpetological assemblages. This is in sharp contrast to North American late Wisconsin mammalian assemblages which suffered much extinction at the end of the Pleistocene. Extinct felids, cervids, armadillos and horses, as well as smaller mammals, were recovered from Bell Cave and are currently being studied by several experts on the various taxonomic groups.

The absence of the extinct giant land tortoise, *Geochelone crassiscutata*, which was present in the late Wisconsin fauna of northwestern Georgia, USA, (Holman, 1985a,b) is unexplained, but could be related to some unknown or uninterpreted taphonomic event. The lack of extinction in the North American herpetofauna during the past 1.8 million years compared to that of the mammals, and to a lesser extent, the birds, is becoming a subject of considerable discussion (Holman, 1989).

Bell Cave is typical of several late Wisconsin faunas (Fay, 1984, 1986, 1988; Holman, 1986; Holman and Grady, 1987) in having a herpetofauna that resembles the modern one in the area. The relative stability of these herpetofaunas in the face of the changes that occurred in the late Pleistocene has posed a problem that has been discussed, but not actually resolved (Holman, 1986; Holman and Grady, 1987; Fay, 1988).

We have no reason to believe that there has been a systematic misidentification of taxa from these sites. Moreover, several of these faunas are from caves with beds that are very well stratified and that have been dated by the Carbon 14 method (Holman, 1986; Holman and Grady, 1987; Fay, 1988). Therefore, there is every reason to believe that all of the fossil vertebrate taxa from these sites were living contemporaneously.

Thus, the most parsimonious explanation for these seemingly disharmonious assemblages appears to be the one proposed in reference to the late Pleistocene vertebrate fauna of New Trout Cave, West Virginia by Holman and Grady (1987). This hypothesis was *that somewhat cooler summers and a more mosaic vegetation would allow for the selective survival of some of the mammalian species that were forced southward by the advancing glacial front; and that the presence of northern amphibian and reptile populations forced southward would not be easily detected because of the lack of herpetological species with restrictive northern distributions*.

The Ladds herpetofauna of northwestern Georgia (Holman, 1985a,b) remains an exceptional one, having striking northern and southern extralimital species from coeval Carbon 14 dated late Wisconsin

TAXON	ZONE 1/2	ZONE 3	ZONE 4
<i>Cryptobranchus alleganiensis</i>	X	X	X
<i>Ambystoma</i> sp. indet.	X	X	
<i>Ambystoma maculatum</i>	X	X	
<i>Desmognathus</i> sp. indet.			X
<i>Desmognathus ochrophaeus</i>			X
<i>Eurycea</i> sp. indet.	X		X
<i>Plethodon glutinosus</i>	X	X	
<i>Bufo</i> sp. indet.	X	X	
<i>Bufo americanus</i>	X	X	
<i>Bufo woodhousii fowleri</i>	X	X	
<i>Hyla gratiosa</i>	X		
<i>Rana</i> sp. indet.			X
<i>Rana pipiens complex</i>	X	X	X
<i>Rana catesbeiana</i>		X	
<i>Trionyx</i> sp. indet.	X	X	
<i>Trionyx spiniferus</i>	X		
<i>Chrysemys picta</i>			X
<i>Graptemys geographica</i>	X	X	
<i>Pseudemys</i> sp. indet.	X		
<i>Pseudemys concinna</i>	X	X	
<i>Anolis carolinensis</i>			X
<i>Carphophis amoenus</i>	X	X	
<i>Coluber constrictor</i>		X	
<i>Diadophis punctatus</i>		X	
<i>Elaphe</i> sp. indet.	X	X	
<i>Elaphe</i> cf. <i>E. guttata</i>	X		
<i>Elaphe vulpina</i>	X	X	
<i>Heterodon</i> cf. <i>H. platirhinos</i>	X	X	X
<i>Lampropeltis getulus</i>	X	X	X
<i>Lampropeltis t. triangulum</i>	X	X	X
<i>Nerodia</i> sp. indet.	X	X	
<i>Nerodia sipedon</i>	X	X	X
<i>Opheodrys aestivus</i>	X	X	
<i>Storeria</i> sp. indet.	X	X	
<i>Thamnophis</i> sp. indet.	X	X	X
<i>Thamnophis sirtalis</i>	X	X	X
<i>Agkistrodon</i> sp. indet.			X
<i>Crotalus horridus</i>	X	X	X

TABLE 1: Pleistocene amphibians and reptiles of Bell Cave, Alabama

fissures. An explanation for the anomalous Ladds fauna is still being sought.

Table 1 indicates the distribution of fossil amphibian and reptile species by stratigraphic zone at Bell Cave. Zone 1/2 has a Carbon 14 date of about 12,000 B.P., thus the bones were deposited during the restoration of interglacial conditions that lasted from about 15,000 to about 10,000 B.P. in North America (Watts, 1983). Zone 3 does not have a Carbon 14 date, but it has a similar sedimentary profile and is faunistically very similar to Zone 1/2 (Table 1).

Twenty-four species occur both in Zone 1/2 and Zone 3; and the same extralimital species (*Bufo americanus*, *Elaphe vulpina* and *Lampropeltis t. triangulum*) are present in both zones. *Bufo americanus* and *Lampropeltis t. triangulum* occur only in the

northeastern tip of Alabama today, but *Elaphe vulpina* gets no closer to the vicinity of the cave today than northeastern Missouri and southwestern Illinois. But *E. vulpina* had a much wider distribution in the east and southeast in the Pleistocene (Holman, 1981) and has been recorded from the late Wisconsinan fauna of northwestern Georgia (Holman, 1985a,b). These slightly eastern species and the northern species might be interpreted as suggesting a somewhat moister and/or cooler palaeoclimate. But the fauna as a whole does not suggest a climate much different than occurs in the area today. Most certainly, the presence of egg-laying reptiles (*Pseudemys concinna*, *Trionyx spiniferus*, *Carphophis amoenus*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe* cf. *E. guttata*, *Elaphe vulpina*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis t. triangulum*, and *Opheodrys aestivus*) negates a Tundra-like or

Boreal-like climate during the deposition of the bones in Zones 1/2 and 3.

Zone 4 has a Carbon 14 date of about 26,000 B.P., thus the bones were deposited during the first part of a climatic deterioration that began 30,000 years ago and that culminated in the glacial maximum in North America about 18,000 years ago (Watts, 1983). Of the 13 species identified from Zone 4, two are extralimital: *Desmognathus ochrophaeus* and *Lampropeltis t. triangulum*, both occur only in the tip of northwestern Alabama today. Again, the fauna does not suggest a climate much different than occurs in the area of the cave today.

Also, the presence of egg-laying reptiles (*Chrysemys picta*, *Anolis carolinensis*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis getulus* and *Lampropeltis t. triangulum*) and especially *Anolis carolinensis*, a species very vulnerable to cold (Mount, 1975) negates the possibility of a Tundra-like or Boreal-like climate during the deposition of the bones in Zone 4.

CONCLUSIONS

Late Wisconsinan herpetofaunas from the middle latitudes of North America usually are very similar to the herpetofaunas that occur in the vicinity of the fossil localities today, whereas the fossil mammalian faunas from these localities usually have many extralimital and extinct taxa. The Bell Cave herpetofauna fits this pattern. Many of the fossil amphibian and reptile bones were badly damaged by predators and scavengers, and the wide variety of habitats represented by the amphibian and reptile species is attributed to transportation by palaeopredators. It is difficult to suggest a palaeoclimate much different from the climate of the area today based on the herpetologic remains from any of the stratigraphic units in Bell Cave. Certainly, the presence of many egg-laying turtles, lizards and snakes in all units negates a Tundra-like or Boreal-like interpretation of the palaeoclimate.

ACKNOWLEDGEMENTS

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REFERENCES

- Auffenberg, W. (1963). The fossil snakes of Florida. *Tulane Studies in Biology*, **10**, 131-216.
- Brattstrom, B. H. (1967). A succession of Pliocene and Pleistocene snake faunas from the High Plains of the United States. *Copeia*, (1967) **1**, 188-202.
- Conant, R. (1975). *A Field Guide to the Reptiles and Amphibians of Eastern and Central North America*. Houghton Mifflin, Boston.
- Emmons, L. H. (1989). Jaguar predation on chelonians. *Journal of Herpetology*, **23**, 311-314.
- Fay, L. P. (1984). Late Wisconsinan Appalachian herpetofaunas: stability in the midst of change. *Ph.D. Dissertation, Michigan State University, East Lansing*.
- Fay, L. P. (1986). Wisconsinan herpetofaunas of the central Appalachians. *Virginia Division of Mineral Resources Publication*, **75**, 126-128.
- Fay, L. P. (1988). Late Wisconsinan Appalachian herpetofaunas: relative stability in the midst of change. *Annals of the Carnegie Museum*, **57**, 189-220.
- Hibbard, C. W. (1949). Techniques of collecting microvertebrate fossils. *Contributions of the Museum of Paleontology, University of Michigan*, **8**, 7-19.
- Holman, J. A. (1967). A Pleistocene herpetofauna from Ladds, Georgia. *Bulletin of the Georgia Academy of Science*, **25**, 154-166.
- Holman, J. A. (1977). The Pleistocene (Kansan) herpetofauna of Cumberland Cave, Maryland. *Annals of the Carnegie Museum*, **46**, 157-172.
- Holman, J. A. (1981). A review of North American Pleistocene snakes. *Publications of the Museum, Michigan State University, Paleontological Series*, **1**, 261-306.
- Holman, J. A. (1982a). A fossil snake (*Elaphe vulpina*) from a Pliocene ash bed in Nebraska. *Transactions of the Nebraska Academy of Sciences*, **10**, 37-42.
- Holman, J. A. (1982b). The Pleistocene (Kansan) herpetofauna of Trout Cave, West Virginia. *Annals of the Carnegie Museum*, **51**, 391-404.
- Holman, J. A. (1984). Herpetofauna of the Duck Creek and Williams local faunas (Pleistocene/Illinoian) of Kansas. *Special Publication of the Carnegie Museum of Natural History*, **8**, 20-38.
- Holman, J. A. (1985a). Herpetofauna of Ladds Quarry. *National Geographic Research*, **1**, 423-436.
- Holman, J. A. (1985b). New evidence for the status of Ladds Quarry. *National Geographic Research*, **1**, 569-570.
- Holman, J. A. (1986). The known herpetofauna of the late Quaternary of Virginia poses a dilemma. *Virginia Division of Mineral Resources Publication*, **75**, 36-42.
- Holman, J. A. (1989). Pleistocene herpetofaunas and their impact on the interpretation of recent faunas, a synthesis. *First World Congress of Herpetology Abstracts*, Kent, United Kingdom, p. 146.
- Holman, J. A. and Grady, F. (1987). Herpetofauna of New Trout Cave. *National Geographic Research*, **3**, 305-317.
- Holman, J. A. and Richards, R. (1981). Late Pleistocene occurrence in southern Indiana of the smooth green snake, *Ophedrys vernalis*. *Journal of Herpetology*, **15**, 123-125.
- Mount, R. H. (1975). *The Reptiles and Amphibians of Alabama*. Auburn University Agricultural Station, Auburn.
- Romer, A. S. (1956). *Osteology of the Reptiles*. University of Chicago Press, Chicago.
- Tihen, J. A. (1958). Comments on the osteology and phylogeny of ambystomatid salamanders. *Florida State Museum Bulletin, Biological Sciences*, **3**, 1-50.
- Watts, W. A. (1983). Vegetational history of eastern United States 25,000 to 10,000 years ago. In: Wright, H. E. and Porter, S. C., editors; *Late Quaternary Environments of the United States*, Volume 1: *The Late Pleistocene*. University of Minnesota Press, Minneapolis (pp. 294-310, within).
- Wilson, V. V. (1975). The systematics and paleoecology of two late Pleistocene herpetofaunas from the southeastern United States. *Ph.D. Dissertation, Michigan State University, East Lansing*.

SHORT NOTE: A SIMPLE CONSISTENT TERMINOLOGY FOR THE BASIC COLOUR PATTERNS OF THE VENOMOUS CORAL SNAKES AND THEIR MIMICS

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In the course of our studies on the venomous New World coral snakes (Family Elapidae) and their less toxic or harmless mimics it has become clear that a barrier to accurate description of models and mimics is the absence of a consistent terminology for the various colour patterns exhibited by these reptiles. The lack of uniformity in terminology hampers the analysis of evolutionary trends and geographic variation within genera and species and also creates confusion in documenting concordant geographic variation between models and presumed mimics. Consequently, we present below a simple and concise set of terms that standardises description of the principal colour patterns for these snakes. It is our intention to prepare a more comprehensive description of variation within the basic types defined here and to provide a taxonomic review of their occurrence in New World species in a subsequent paper.

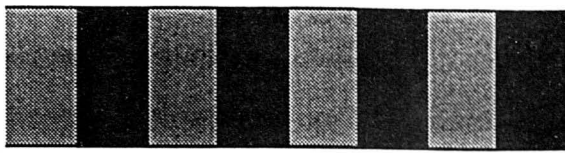
The system that we propose is derived from the descriptors for the dorsal colour patterns of the venomous coral snakes (*Micrurus* and *Micruroides*) developed by Schmidt (1936) and Dunn (1954) based upon the number of different colours forming individual rings and the number of black rings separating the red ones. Their system made a distinction between those patterns characterised by alternating rings of black and a lighter colour (usually red, but sometimes white or yellow) and those having black rings, red rings and rings of a light colour (usually yellow but sometimes white). The former were termed **bicolor** and the latter **tricolor** in conformance with general usage for other snakes. Schmidt (1936) pointed out that the tricolor forms could be divided into two subgroups, those in which each red ring is separated from the next by an alternating light-black-light sequence of rings and those with a more complex pattern where the red rings are separated from one another by an alternating black-light-black-light-black sequence of rings. Schmidt referred to the latter pattern as the **triad** type because there were three black rings between each red one. Dunn (1954) refined this terminology further and grouped coral snakes into three pattern categories: bicolor, tricolor and tricolor triad.

Presumed coral snake mimics of a number of genera of harmless and rear-fanged snakes have been recorded as having bicolor, tricolor or tricolor triad dorsal patterns. These patterns may be of bands or rings (a few coral snakes are also banded, not ringed). In addition, several non-elapid tricolor species exhibit a

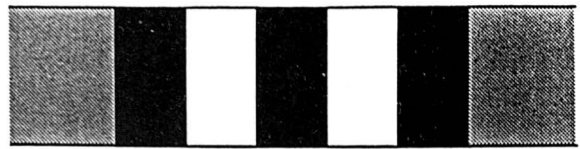
pattern not found in any coral snake. In these forms each red band or ring is separated from the next red one by a simple alternation of black-light-black rings (or bands). Unfortunately a number of authors, most notably Klauber (1943) for *Lampropeltis* and Taylor and Smith (1943) for *Scaphiodontophis*, have referred to components of this pattern as 'triads'. In *Lampropeltis* the black-red-black component was called a 'triad'. In *Scaphiodontophis* 'triad' was used in exactly the opposite sense for the black-light-black component. These usages, which have been followed in several subsequent studies of these genera, create considerable confusion since the term triad has been utilised by Schmidt (1936), Dunn (1954) and most recent students of coral snakes for the black-light-black-light-black sequence of rings in coral snakes (i.e. for three black rings).

Two other tricolor patterns also occur in non-elapid snakes (Mertens, 1956). In one geographic subdivision of the rear-fanged *Erythrolamprus aesculapii* and some *Atractus*, the red-rings are separated from one another by a black-light-black-light-black-light-black sequence of rings. One geographic unit within the harmless species *Simophis rhinostoma* has the red rings separated from one another by an alternating black-light-black-light-black-light-black-light-black sequence of rings. This same pattern is also typical of the Mexican and Guatemalan coral snake, *Micrurus elegans*.

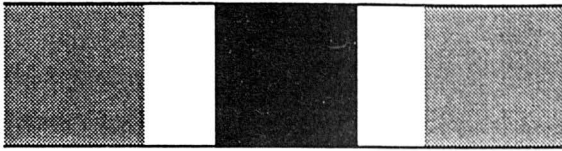
As may be seen from the above review several different tricolor patterns are found in these snakes and two very different patterns types and two different sequences in the same pattern type have been called triads. Consequently, we propose the following revised and standardised terminology to describe the various dorsal (banded or ringed) patterns found in these snakes (Fig. 1). For tricolor species this system emphasises the number of black bands or rings separating the red rings from one another. Following the implication of the use of the term tricolor triad (i.e. three intervening black bands or rings separating the red ones from one another) as originally applied to coral snakes, it uses a newly coined set of descriptors to designate the condition of one (**monad**), two (**dyad**), four (**tetrad**) or five (**pentad**) black bands or rings separating the red ones. This eliminates the confusion caused by Klauber (1943) and Taylor and Smith (1943) and others in their usage of 'triad' for different components of the pattern of snakes having what is here called a dyad pattern.



BI



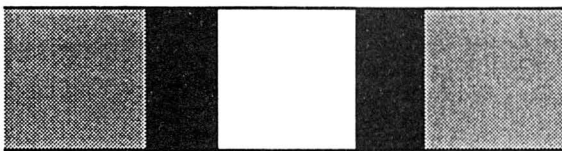
TT



TM



TTE



TD



TP

Fig. 1 A schematic representation of the major pattern types occurring in the venomous coral snakes and their mimics. The stippled areas represent red; the white areas represent yellow or white; the black areas are black. BI = bicolored, TM = tricolor monad, TD = tricolor dyad, TT = tricolor triad, TTE = tricolor tetrad, TP = tricolor pentad.

A. **Unicolor** — essentially a uniform red dorsum (e.g. some Yucatan Peninsula *Micrurus diastema*).

B. **Bicolor** — alternating bands or rings of black and light (red, yellow or white), frequently red in the venomous coral snakes (e.g. *Micrurus mipartitus*, *Urotheca euryzona*).

C. **Tricolor** — alternating bands or rings of black, red and light (usually yellow, sometimes white).

1. **Tricolor monads** — red bands or rings separated from one another by a sequence of alternating bands or rings of light-black-light; one black ring between red rings (e.g. *Micrurus fulvis*, *Rhinobothryum*).

2. **Tricolor dyads** — red bands or rings separated from one another by a sequence of alternating bands or rings of black-light-black; two black rings between red rings (e.g. some *Scaphiodontophis*, *Lampropeltis pyromelana*, most *Lampropeltis zonata*).

3. **Tricolor triads** — red bands or rings separated from one another by a sequence of alternating bands or rings of black-light-black-light-black; three black rings between red rings (e.g. *Micrurus isozenus*, some *Atractus elaps*).

4. **Tricolor tetrads** — red bands or rings separated from one another by a sequence of alternating bands or rings of black-light-black-light-black-light-black; four black rings between red rings (e.g. some *Atractus elaps*, some *Atractus latifrons*).

5. **Tricolor pentads** — red bands or rings separated from one another by a sequence of alternating bands or rings of black-light-black-light-black-light-black-light-black (e.g. *Micrurus elegans*, some *Simophis rhinostoma*).

Snakes having bicolor, tricolor dyad, tricolor triad, tricolor tetrad or tricolor pentad patterns have the red bands or rings bordering black ones. In the tricolor monad pattern the red bands or rings are separated from the black bands or rings by a yellow or white band or ring.

Most species of coral snakes and members of the coral snake mimic guild possess only a single pattern type. However, as indicated above, some taxa exhibit geographic variation in pattern while a few species may have different patterns present on different parts of the body (e.g. some *Scaphiodontophis*). These and other variants will be more fully discussed in our forthcoming review of variation and the taxonomic occurrence of coral snake patterns.

REFERENCES

- Dunn, E. R. (1954). The coral snake 'mimic' problem in Panama. *Evolution*, **8**, 97-102.
- Klauber, L. M. (1943). The coral king snakes of the Pacific coast. *Transactions of the San Diego Society of Natural History*, **10**, 75-82.

- Mertens, R. (1956). Das Problem der Mimikry bei Korallenschlangen. *Zoologische Jahrbucher (Systematik)*. **84**, 541-576.
- Schmidt, K. P. (1936). Preliminary account of coral snakes of South America. *Zoological Series of the Field Museum of Natural History*. **20**, 189-203.

- Taylor, E. H. and H. M. Smith (1943). A review of American sibynophine snakes, with a proposal of a new genus. *University of Kansas Science Bulletin*. **29**, 301-327.

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SHORT NOTE: A NOTE ON THE FEEDING HABITS OF *AMEIVA FUSCATA* FROM DOMINICA, LESSER ANTILLES

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INTRODUCTION

All but one of the Lesser Antillean islands or island groups, has (or once had) its own species of macroteiid 'ground lizard' (*Cnemidophorus* or *Ameiva*) (Baskins and Williams, 1966; Schwartz and Henderson, 1985). Ground lizards favour dry coastal habitats which, in the Lesser Antilles, have been subject to much development for housing, tourism and cultivation. Probably as a result of such habitat destruction, and possibly also due to predation by introduced mongoose (*Herpestes herpestes*), ground lizards are now rare or extinct on several islands (Underwood, 1962; Corke, 1987; Johnson, 1988).

Dominica (15° 25' N, 61° 25' W) is unusual in the Lesser Antilles in having retained between 60 per cent and 75 percent of its original forest cover, including its coastal woodlands (Evans, 1986). The latter support populations of *Ameiva fuscata*, confined to Dominica. There have been few published reports of the diets of *Ameiva*, and none for *A. fuscata* or other Lesser Antillean species. Hirth (1963), Hillman (1969) and Echternacht (1983) described the diet and feeding behaviour of several Costa Rican species and more recently Vega *et al.* (1988) described the diet of *A. ameiva* in Argentina.

As part of a long term study of Dominica's forests, including the reptile and amphibian communities, data were collected on the diet and feeding behaviour of *A. fuscata* in one of the two types of coastal woodland, Dry Scrub Woodland.

STUDY AREA AND METHODS

Fieldwork in the Cabrits Peninsula, north-east Dominica, was conducted in March-April 1988 and December-January 1989; these dates corresponded approximately to dry and wet seasons respectively. More trees were in fruit or flower in the dry season than in the wet season, and the mean litter layer was significantly deeper at that time ($\bar{X} = 2.76\text{cm}$, $N = 5$ composite samples, dry season; $\bar{X} = 0.98\text{cm}$, $N = 5$ composite samples, wet season ($t_{4,4} = 3.98$, $p < 0.02$).

Prey availability at ground level was estimated using pitfall (can) traps (78mm deep, 73mm diameter filled to c.30mm depth with water plus detergent). During both the dry and wet season visits five lines of 10 pitfall traps were set for 48h on two dates separated by at least 14 days. The catch was sorted to order/family and prey length. Pitfall traps do not necessarily provide representative samples of species composition and species diversity (Southwood, 1978). Thus comparison between invertebrate availability and prey taken must be viewed with caution, and only large differences are described here.

A. fuscata, whilst not threatened, is a protected species in Dominica, and large scale destructive sampling principally for stomach contents was undesirable. Non-destructive live capture and stomach flushing (Pietruszka, 1987) proved very difficult with this species and all but seven out of a total of 19 specimens were killed. Thus the sample size for diet analysis was small. Nevertheless, specimens from most

of the size range (maximum snout-vent of c.250mm (D. J. Bullock unpublished)) were represented as follows: seven with snout-vent lengths of ≤ 70 mm; four with snout-vent lengths between 71 and 140mm and eight with snout-vent length ≥ 141 mm. Stomach contents were sorted to order/family and dimensions of prey measured to 0.1mm accuracy.

Quantitative observations of foraging behaviour of *A. fuscata* consisted of timed watches (minimum of 5 minutes duration) of undisturbed focal individuals between 0700h and 1700h in clear, sunny weather, periods when this species was known to be active (D. J. Bullock and P. G. H. Evans unpublished). Attempts at hand capture and sessions of undisturbed observations were incompatible so the former were mainly restricted to the dry season and the latter to the wet season visits respectively. Snout-vent length, initial microhabitat (litter, rock, soil), distance moved (m), number of bask sites and number of prey capture attempts (successful and unsuccessful) were recorded.

RESULTS AND DISCUSSION

Comparison of the prey size distribution in pitfall traps between dry and wet seasons showed that there were more large prey and a fewer number of large prey items available in the dry season than wet season. As the majority of stomach samples were obtained in the dry season, only pitfall data from the dry season were used to compare availability with diet.

One of the stomachs contained only soil and mites (Acari) that had probably been ingested unintentionally, and so was excluded from computations. Oligochaeta, and adult Coleoptera (mainly a large, brown species) were the most abundant prey items. In volumetric terms, adult Coleoptera were by far the most important prey, followed by Oligochaeta (Table 1). Comparison between the percentage volumes of each prey type in pitfall traps and stomachs gave a tentative indication of the degree to which *A. fuscata* selected certain invertebrates. Thus adult Coleoptera and Oligochaeta were selected. Opilionids however were not taken. This apparent avoidance was probably because the species concerned was nocturnally active; during the day it was inactive under rocks where it would have been inaccessible to *A. fuscata*. Dictyoptera and Orthoptera were also apparently avoided, probably again because the most abundant species were nocturnal. The occurrence of a large amount of leaves in the stomach of one individual indicates that *A. fuscata* is not exclusively insectivorous (Table 1). Casual observations revealed that this species also ate carrion and fallen crop fruits such as avocado (*Persea* sp.), soursop (*Annona muricata*) and banana (*Musa* sp.).

Maximum arthropod prey length was positively correlated with lizard head width ($r = 0.708$, $df = 18$, $p < 0.001$) and snout-vent length ($r = 0.573$, $df = 18$, $p < 0.01$). Comparison of the prey length distribution in pitfall traps and stomachs suggested that *A. fuscata* took relatively large (> 5 mm length) prey and tended to

Prey type	Pitfall		Stomach		
	Volume		Volume	Number	
	%	\bar{X}	%	\bar{X}	%
Annelida					
Oligochaeta	0.0	134.9	9.6	4.6	24.9
Arthropoda					
Araneae	1.0	24.8	1.8	0.2	0.9
Opiliones	41.1	0.0	0.0	0.0	0.0
Isopoda	0.0	1.1	0.1	0.7	3.6
Diplopoda	0.4	8.0	0.6	0.1	0.3
Chilopoda	1.2	0.0	0.0	0.0	0.0
Collembola	0.1	0.0	0.0	0.0	0.0
Dermaptera	4.0	21.1	1.5	1.3	7.2
Dictyoptera	22.0	0.0	0.0	0.0	0.0
Orthoptera	18.3	15.5	1.1	0.2	0.9
Psocoptera	tr	0.0	0.0	0.0	0.0
Hemiptera (nymph)	0.1	0.0	0.0	0.0	0.0
Thysanoptera	0.1	0.0	0.0	0.0	0.0
Diptera	2.0	0.1	tr	0.1	0.3
Hymenoptera (Ants)	1.7	2.2	0.2	0.7	3.6
(Others)	0.0	4.9	0.3	0.6	3.0
Coleoptera (Adults)	7.4	526.2	37.5	3.1	16.8
(Larvae)	0.0	15.9	1.1	1.4	7.8
Mollusca					
Gastropoda	0.0	3.1	0.2	0.8	4.5
Others	0.5	5.1	0.4	0.5	2.7
Seed and Vegetation	—	53.9	3.8	3.8	20.7

TABLE 1: Summary of the stomach contents of *Ameiva fuscata*. Volumes measured in mm³. 'Others' includes empty Gastropoda shells, Myrmeleontidae, Acari and unidentified items.

avoid relatively small (<2 mm length) prey ($X^2_1 = 548.07$, $P < 0.001$).

A. fuscata were invariably wary and very difficult to observe undisturbed. The majority of individuals (89 per cent) were observed foraging amongst litter, in a grubbing fashion as do other members of the genus (Hirth, 1963), poking their snouts into cavities or holes, or under litter. The large forked tongue was flicked constantly and, occasionally, one or both forefeet were used to remove litter or loosen surface soil to expose a prey item. Mean rate of movement was 7.1 m per 10 minutes ($SD = 7.65$, $N = 29$) during which time a mean of 3.4 bask sites ($SD = 2.68$, $N = 29$) were used. Of 58 prey capture attempts, 19 (22 per cent) were successful. One large lizard ($SVL = 180$ mm) was observed for 20 minutes feeding on a land crab (*Gegarcinus* sp.) that it had apparently killed in its burrow; it withdrew parts of the crab's body to devour above ground.

On basis of our limited observations and analyses, it is clear that *A. fuscata* is predominantly insectivorous, but that some individuals (1 in 19 sampled) ingest large quantities of vegetation. Janzen (1973) suggested that island *Ameiva* species may ingest more vegetation than mainland counterparts and that this is related to a dearth of both large insects and native terrestrial predators. Island *Ameiva* could thus spend more time basking and fermenting vegetation, than those on the mainland. Pough (1973) argued that for scincid and iguanid lizards adoption of herbivory was more likely to occur above a mass of 100 g, provided that sufficient time was devoted to basking. Within the genus *Ameiva*, *A. fuscata* is exceptionally large, reaching 250 mm snout-vent length and a mass of 600 g. In censuses approximately 44 per cent of *A. fuscata* had a snout-vent length of >140 mm and a corresponding mass of >100 g (D. J. Bullock unpublished). Thus on the basis of lizard size and island location, *A. fuscata* could be expected to be at least partly herbivorous. However, basking times were short and clearly more related to maintenance of active body temperature (several degrees above air temperature) (Brooks, 1968) than to fermenting vegetation.

Highest densities of *A. fuscata* are in coastal woodland (D. J. Bullock and P. G. H. Evans unpublished), in the litter layer of which most of its prey are located. With the exception of in coconut plantations, the litter layer is typically absent from areas which were previously of coastal woodland but now have been replaced by cultivation or pasture. Observed lower densities of *A. fuscata* in many cultivated areas may be related to the reduced litter layer and consequent reduction in food supply. In the face of continued and escalating development of coastal woodlands in Dominica, we may therefore

expect the population to decline and become more fragmented.

ACKNOWLEDGEMENTS

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REFERENCES

- Baskin, J. W. and E. E. Williams (1966). The Lesser Antillean *Ameiva* (Sauria, Teiidae). *Studies on the fauna of Curacao and other Caribbean islands* No. 89, 23, 144-175.
- Brooks, G. R. (1968). Body temperatures of three lizards from Dominica, West Indies. *Herpetologica*, 24, 209-214.
- Corke, D. (1987). Reptile conservation on the Maria Islands (St. Lucia, West Indies). *Biological Conservation*, 40, 263-279.
- Echternacht, A. C. (1983). *Ameiva* and *Cnemidophorus*. In: *Costa Rican Natural History*, 375-379. D. H. Janzen (Ed.) Chicago: University of Chicago Press.
- Evans, P. G. H. (1986). Dominica Multiple Land Use Project. *Ambio*, 15, 82-89.
- Hillman, P. E. (1969). Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology*, 50, 476-481.
- Hirth, H. F. (1963). The ecology of two lizards on a tropical beach. *Ecological Monographs*, 33, 83-112.
- Janzen, D. H. (1973). Sweep samples of tropical foliage insects: effect of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, 54, 687-701.
- Johnson, T. H. (1988). *Biodiversity and conservation in the Caribbean: Profiles of selected islands*. Monograph No. 1. Cambridge: I.C.B.P.
- Pietruszka, R. D. (1987). On the application of stomach flushing to Namib Desert lizards. *Madoqua*, 15, 73-78.
- Pough, F. H. (1973). Lizard energetics and diet. *Ecology*, 54, 836-844.
- Schwartz, A. and Henderson, R. W. (1985). *A guide to the identification of the amphibians and reptiles of the West Indies exclusive of Hispaniola*. Milwaukee: Milwaukee Public Museum.
- Southwood, T. R. E. (1978). *Ecological methods*. London: Chapman and Hall.
- Underwood, G. (1962). Reptiles of the Eastern Caribbean. *Caribbean Affairs* (New ser.) (Jamaica), 1, 1-191.
- Vega, L. E., Chani, J. M. and Trivi de Mandi, M. (1988). Observations on the feeding habits of *Ameiva ameiva*. *Herpetological Review*, 19, 53-55.

SHORT NOTE: **NOTES ON THE OCCURRENCE AND DISTRIBUTION OF *LACERTA HORVATHI*** **MÉHELY, 1904 IN FEDERAL REPUBLIC OF GERMANY**

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During herpetological investigations in the F.R. Germany province of Munich we gathered new interesting distributional data on *Lacerta horvathi* Méhely, a lacertid lizard whose occurrence has never before been reported in F.R. Germany (Blauscheck, 1985). The investigations took place in the southernmost territory of the Munich province, in a study area of about 20km (see Fig. 1), which was sampled in the periods July-August 1989.

Lacerta horvathi is a relatively poorly known species assigned to a problematic group of lacertid lizards, i.e. *Archaeolacerta*, considered either as a distinct genus (Lanza, Cei and Crespo, 1977; Guillaume and Lanza, 1982), or as a subgenus (Mayer and Tiedemann, 1982; Lutz and Mayer, 1985; Lutz, Bischoff and Mayer, 1986). The phylogenetic relationships of this species are not clear: on one hand karyological and histological data would indicate that *L. horvathi* belongs to the same species group of *L. vivipara*, as these lacertid lizards have similar karyotypes (2n = 36, with 36 acrocentric macrochromosomes and no microchromosomes) (De Luca and Dulić, 1988; Capula, Lapini and Capanna, 1989) and present a similar structure of the spiny epithelium of the hemipenis (Böhme, 1971); on the other, protein electrophoresis and micro-complement fixation analysis would suggest that *L. horvathi* is closely related to *L. bedriagae* and *L. oxycephala*, as pointed out by Mayer and Tiedemann (1982) and Lutz and Mayer (1985).

L. horvathi is present, with scattered populations, in northern and western Yugoslavia, in northeastern Italy, and in southwestern Austria. In Yugoslavia this lizard inhabits the mountain regions of Dalmatia (Velebit and Kapela Mountains), Istria (Učka Mount), and Slovenia (Julian Alps) (Brelj and Džukić, 1974; Bischoff, 1984). In Italy, where it occurs up to an altitude of 2000m a.s.l. (Darsa, 1972), *L. horvathi* has been till now encountered in few localities of the Carnic and Julian Alps (Lapini and Dolce, 1983; Lapini, 1988). In Austria, where the species was discovered only recently by Grillitsch and Tiedemann (1986), it occurs in at least nine localities of the Carinthia Region (Eggenberger, quoted by Lapini, 1988).

Up to now it was thought that both northern and western limits of this lizard's range were the Carnic Alps (Forni Avoltri, Udine, NE Italy) (Lapini and Dolce, 1983). In this note we report three new locality records of *L. horvathi* which extend the known range of this species to southern F.R. Germany. Fig. 1 shows the approximate locations of the sites in which

specimens of *L. horvathi* were encountered and collected. These specimens were given to the Natural History Museum (Zoological Section) of the University of Florence, and are now preserved in the Herpetological Collection of this Institute. In the localities 1 and 2 (numbers refer to Fig. 1), which are sited 5km E of Mittenwald, were collected four (2 males, 2 females) and two (1 female, 1 juvenile) specimens respectively. In the locality 3, which is sited 6km SE of Vorderriss, was collected only an adult female. In all these sites *L. horvathi* apparently does not coexist with any other lacertid lizard. The specimens captured were encountered only on the rock slopes lacking in vegetation of the northern side of the Karwendel Mountains (Karwendelgebirge), at an altitude of about 800m a.s.l., close to the border between F.R. Germany and Austria. Morphometric and meristic characters of the adult specimens collected (reported in Table 1), together with colouration features and other morphological characters examined, are very similar to those reported by Lapini and Dolce (1983) for Italian and Jugoslavian specimens.

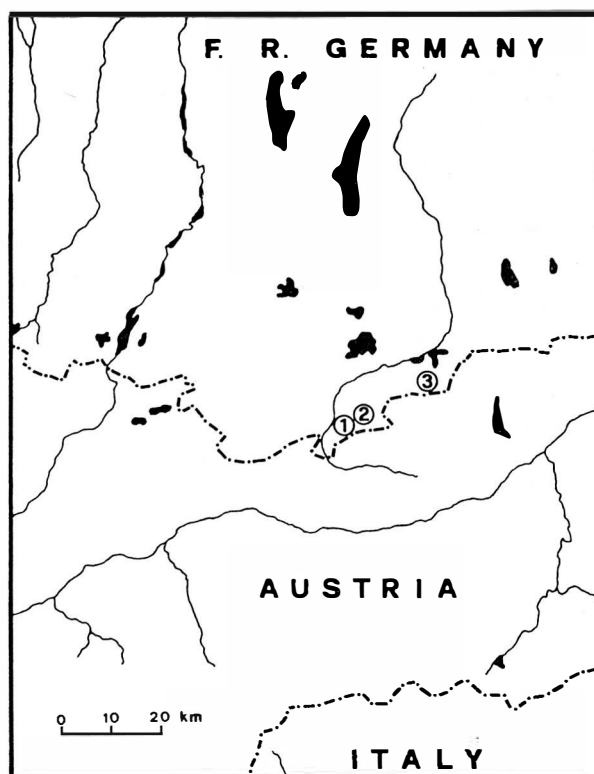


Fig. 1: 1, 2, 3: Locality records of *Lacerta horvathi* in Federal Republic of Germany.

	♂	♂	♀	♀	♀	♀
Head length	12.6	11.9	13.0	11.7	10.4	10.9
Head width	8.6	7.1	8.1	7.1	6.5	7.6
Head depth	5.0	4.0	4.9	4.0	4.0	3.7
Body length	39.8	35.4	46.3	38.1	32.0	44.0
Tail length	42.6(b)	87.2(i)	86.2(r)	84.7(i)	74.1(i)	57.2(b)
Foreleg length	17.3	16.4	18.1	15.0	14.2	16.3
Hindlimb length	27.0	26.3	28.8	23.5	21.4	24.5
Dorsal scales in a series at midbody	44	43	42	44	47	45

TABLE 1: Morphometric and meristic characters of 2 males and 4 females of *L. horvathi* from the study area. Measurements are in mm. (b) = broken tail; (i) = intact tail; (r) = regenerated tail.

Our observations establish that *L. horvathi* has a far more widespread occurrence in the Alps than is indicated by the existing distribution accounts on the species (Lapini and Dolce, 1983; Bischoff, 1984; Grillitsch and Tiedemann, 1986). *Lacerta horvathi* is a new species to the F.R. Germany fauna, and the new localities discovered in this country extend the known species range from NE Italy approximately 100km to north and 110km to west. Since *L. horvathi* occurs on the northern side of the Karwendel Mountains, we can infer that the species is also present in western Austria, on the southern side of this Massif, and, possibly, in other alpine localities of Austria and southern F.R. Germany.

REFERENCES

- Bischoff, W. (1984). *Lacerta horvathi* Mähely 1904 — Kroatische Gebirgseidechse. In: *Handbuch der Reptilien und Amphibien Europas*, Band 2/I Echten (Sauria) II. (Lacertidae II: *Lacerta*), 265-275. Böhme, W. (Editor). Wiesbaden: AULA Verlag.
- Blauscheck, R. (1985). *Amphibien und Reptilien Deutschlands*. Hannover: Landbuch-Verlag GmbH.
- Böhme, W. (1971). Über das Stachlepitel am Hemipenis lacertider Eidechsen und seine systematische Bedeutung. *Z. zool. Syst. Evol.-forsch.* **9**, 187-223.
- Brelih, S. and Džukić, G. (1974). Catalogus faunae Jugoslaviae. IV/2. Reptilia. *Con. Acad. Sci. Rep. Slov.*, Ljubljana, **4**(2), 1-33.
- Capula, M., Lapini L. and Capanna, E. (1989). The karyotype of *Lacerta horváthi* Mähely, 1904 (Reptilia, Sauria, Lacertidae). *Genetica*, **79**, 11-16.
- Darsa, M. (1972). Anfibi e Rettili di Fusine. *Hyta. Notiz. U.E.I.* **2**(1), 3-13.
- De Luca, N. and Dulić, B. (1988). Karyotype of horvath's rock lizard *Lacerta (Archaeolacerta) horvathi* Mähely, 1904 (Reptilia: Lacertidae). *Amphibia-Reptilia*, **9**, 353-356.
- Grillitsch, H. and Tiedemann, F. (1986). *Lacerta horvathi* Mähely, 1904 — Erstnachweis für Österreich. *Ann. Naturhist. Mus. Wien.* **88/89** B, 357-359.
- Guillaume, C.-P. and Lanza, B. (1982). Comparaison électrophorétique de quelques espèces de Lacertidés méditerranéens. Genes *Podarcis* et *Archaeolacerta*. *Amphibia-Reptilia*, **4**, 361-375.
- Lanza, B., Cei, J. M. and Crespo, E. G. (1977). Immunological investigations on the taxonomic status of some Mediterranean lizards (Reptilia, Lacertidae). *Monit. zool. ital.* (N.S.) **11**, 211-221.
- Lapini, L. (1988). Osservazioni sulla fauna erpetologica (Amphibia, Reptilia) dell'alta Val Torre (Italia nord-orientale, Prealpi Giulie). *Gortania. Atti Museo Friul. Storia Nat.* **9** (1987), 201-222.
- Lapini, L. and Dolce, S. (1983). *Lacerta (Archaeolacerta) horváthi* Mähely, 1904 in Italia: nuove stazioni per le Alpi Carniche e Giulie. *Gortania. Atti Museo Friul. Storia Nat.* **4** (1982), 213-225.
- Lutz, D., Bischoff, W. and Mayer, W. (1986). Chemo-systematische Untersuchungen zur Stellung von *Lacerta jayakari* Boulenger, 1887 sowie der Gattungen *Gallotia* Boulenger und *Psammotromus* Fitzinger (Sauria: Lacertidae). *Z. zool. Syst. Evol.-forsch.* **24**, 144-157.
- Lutz, D. and Mayer, W. (1985). Albumin evolution and its phylogenetic and taxonomic implications in several lacertid lizards. *Amphibia-Reptilia*, **6**, 53-61.
- Mayer, W. and Tiedemann, F. (1982). Chemotaxonomical investigations in the collective genus *Lacerta* (Lacertidae: Sauria) by means of protein electrophoresis. *Amphibia-Reptilia*, **2**, 349-355.

BOOK REVIEWS:

(1) *Turtles of the World*. Carl H. Ernst and Roger W. Barbour. Smithsonian Institution. 313 pp. (1989). US\$45.00.

Turtles of the World, which describes the Testudines, includes what are also known as tortoises. It is possibly helpful in the case of the last that the timing of the book's publication, as a complementary volume, should have been 1989 like the IUCN Species Survival Commission's Occasional Paper No. 5, *The conservation biology of tortoises* (timed to coincide with the First World Congress of Herpetology, 11-19 September 1989), which includes a virtually complete bibliography of tortoise literature. Ernst and Barbour's work, moreover, also covers all of the freshwater and marine turtles, effectively anticipating the intention of IUCN/SSC to cover these species also. After a useful general introduction to the order Testudines which gives the terminology for describing the shell scutes and bones, the cranium and head scalation, the authors cover the species making up the families from Pelomedusidae to Testudinidae, each of which also has an introductory section. Each genus then follows and a description of the species making them up is treated under the headings: recognition, distribution, habitat and natural history. A key is included for identification of species when more than one makes up the genus. A black and white photograph illustrates most species if not otherwise included with those depicted in sixteen excellent colour plates. For such a comprehensive work, it is not surprising that a number of papers are not referred to in the bibliography, which apart from some species covered by American authors and publications, and the European journal, *Amphibia-Reptilia*, does not seem to be more up-to-date than about 1986. This is understandable, however, since there is inevitably a lag period before articles on Chelonia published in more esoteric journals get widely circulated. For the genus *Testudo*, with which the reviewer has had most experience, Loveridge and Williams (1957) appears to have been the main reference source for *T. graeca* and *T. kleinmanni*, and Arnold, Burton and Ovenden (1978) for *T. hermanni* and *T. marginata*. I personally feel that it would have been helpful if each of the species sections could have included the authors' prime reference sources (if any). This would not have been too onerous with a comprehensive bibliography given in any case.

The above comments are a description rather than a criticism, for this is a valuable review, undoubtedly useful as a reference source and at the equivalent of approximately £28 makes a fine contribution to chelonian literature. It is splendidly produced and would make a durable addition for the enthusiast's bookshelf.

REFERENCES

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

Loveridge, A. and Williams, E. E. (1957). Revision of the African tortoises and turtles of the suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 115, 163-557.

M. R. K. Lambert

(2) *The Isle of Sea Lizards*. Angus Bellairs. 299pp. Durrell Institute of Conservation and Ecology, University of Kent at Canterbury. (1989). Paperback. £6 including p & p, from the author. 7 Champion Grove, London, SE5 8BN.

This work can be considered at two levels: as a fictional yarn and as an insight into the biography, mind and dreams of one of our most liked and respected herpetologists. The chief character, Adrian Barnard, is Angus Bellairs himself with his love of nature (including beautiful women), his tolerance, his admiration for the military virtues and his liberal views of English life. He has his hatreds, too, of cruel animal experiments, of commercialism in education and, most of all, of turning biology into 'cells, nerves and chemicals'. 'Zoology is about animals' he says. Indeed, there are Professors of Zoology who appear to know nothing about animals, their differences and relationships. It has gone too far: soon we must return to proper respect for the zoologist and botanist who know what they are talking about. If the day comes when all we need is a DNA sequence and a computer to put a plant or animal in its exact place on the family tree, we shall all the more want Angus and his like for their ability to write so clearly in conveying to us all the beauty and diversity of the forms we may still have with us. How many remain depends on conservation efforts, which Angus strongly supports.

Angus has a vivid turn of phrase, as when he describes the defeated Malaysian communist guerillas as 'retaining like decapitated wasps a hopeless, deadly stinging reflex'. In the story, Adrian is commissioned to go with an attractive aggressive female US centipede expert to search a remote Pacific island for living examples of a marine reptilian relic of the Cretaceous period. The sequel includes adventure, sex and violence, though not so nasty as the kind favoured by many thriller writers. There is humour and philosophy and plenty of true and partly true zoological stories of great interest to naturalists, as well as campus politics, tales of Shelley's time, and of the Third Reich. It's a strong mixture and, perhaps the truest test of fiction, hard to put down. John Robertson in illustrating the cover has made a chiral error. This is an informative and enjoyable read.

G. A. D. Haslewood

(3) *Snakes of the Arabian Gulf and Oman*. Michael Gallagher. (Privately printed: R.O.2 post free from P.O. Box 668 Muscat, Sultanate of Oman). 16pp. (1990).

Nine of the 21 species of land snakes found in eastern Arabia are dangerous, but some of these have only a

limited distribution. Thus, the black desert cobra (*Walterinnesia aegyptia*) is not found in the south or south east of the Arabian peninsula; one species of saw-scaled viper (*Echis coloratus*) occurs only near water and in mountainous regions from Musandam to central Oman; the horned viper (*Cerastes cerastes*) is restricted to sandy habitats; while the false horned viper (*Pseudocerastes persicus*) is confined to high mountains. The nine sea snakes described are also dangerous, but only the yellow-bellied sea snake (*Pelamis platurus*) is widely dispersed. The others are restricted to the warm shallow parts of the Arabian Gulf and the Gulf of Oman.

Sections of the pamphlet under review that are concerned with dangerously poisonous snakes are marked red or orange, those devoted to mildly toxic back-fanged colubrid species — the hooded malpolon (*Malpolon moileensis*), the sand snake (*Psammophis schokari*) and the cat snake (*Telescopus dhara*) — are yellow, while those related to harmless species (among which is included the amphisbaenid *Diplometopon zarudnyi*) are green. Major Gallagher's attractive booklet includes excellent colour photographs of most of the species described, and contains details of their distribution, characteristics and size so that readers can identify the common species with reasonable confidence. There is a useful index, and the back cover gives helpful instructions about the prevention of snakebite and first aid treatment if required. This consists of reassuring the victim, restraining movement, and cleaning the wound. If a doctor or hospital cannot be reached within 30 minutes, affected limbs should be bandaged and immobilised but the wound should *not* be cut or sucked, nor should a tourniquet be applied or aspirin or spirits given. Anti-venoms should only be administered by a doctor.

J. L. Cloudsley-Thompson

(4) *Reptile Egg-Shell SEM Atlas*. H. Hermann Schleich and Werner Kästle. Gustav Fisher Verlag, Stuttgart and New York, 123pp. (1988). \$44.50.

One major lie which schoolchildren and biology freshmen are told by their teachers and textbooks, concerns the reptile egg: This is eulogised as being cleidoic, its shell isolating it from the environment and liberating it from the ancestral dependence on water. While this is probably true in a historical sense, the everyday facts differ. As herpetologists know only too well, the vast majority of living reptiles lay eggs with pliable shells, which depend on environmental moisture for their healthy development. Sometimes eggs imbibe so much water during development, that their final weight becomes several times the initial one. True, some species do lay calcareous hard shelled eggs, isolated from environmental moisture or drought. The structural, chemical and functional variation of eggshells, among and within taxonomic groups of reptiles, is thus of interest. This specialised branch of herpetology is the subject of Schleich's and Kästle's monograph.

This monograph is an atlas of 45 plates, mostly each comprising eight scanning electron microscope (SEM) photographs. Pictured are various views of the

eggshells of 70 recent species of reptiles and also of some fossil ones. Both the major merits and some of the demerits of this work spring from its monographic nature (only some of the latter will be listed here).

Perhaps the greatest merit of the book is that it is so permeated by the love of the authors for their subject matter. Even readers without personal experience of the logistic, technical and intellectual activities necessary for the creation of such a report, will perceive the efforts, resourcefulness and stick-to-it-ness that had been required for assembling, processing and presenting the material. Indeed, in the case of the turtles alone, the best studied group concerning eggshells, the authors have doubled the available information: Previously, eggshell structure as seen by SEM had been reported for 17 species (Ewert, 1985; Packard, Thompson, Goldie and Voss, 1988). Schleich and Kästle, too, bring data on 17 species, only three of which had been studied before. Presumably their proportional contribution to the knowledge of squamate eggs is even greater.

The worst weaknesses of the book are those that run against the grain of the educator and alienate the beginner. That a personal monograph on some specialised herpetological offshoot can nevertheless be totally educational and self-explanatory, has been demonstrated (among others) by Wever (1978). The present book is almost the polar opposite.

The 45 plates are accompanied by specific explanatory pages, and are preceded by some 20 introductory pages surveying the literature and reviewing the principles and variation of the structure and function of reptile eggshells. The concept of function is invoked repeatedly but is applied to neither the effect of egg shape (continually mentioned) on the shell's mechanical strength (briefly reviewed in Werner, 1972), nor the relation of egg shape to material body shape.

Moreover, despite the interest in function, neither the dynamics of the production of the shell, nor the dynamics of its erosion from within due to calcium exploitation by the embryo (in some species) are properly treated. Worse, although the authors briefly mention the latter issue, of the 70 recent species presented, in 55 cases it is unknown, whether the eggshells depicted were from the beginning, middle or end of the incubation period. Only in 15 species is the stage defined, unfortunately always as 'hatched'. In no single case are comparative pictures available from the beginning and end of the incubation period. A related omission concerns the crocodiles: although four of these are included, there is no mention of the suspected microbial degradation of the eggshell during incubation (Ferguson, 1981, 1985). Thus the quest for interspecific variation in shell structure is largely undermined by the disregard of temporal intraspecific variation.

The reader's efforts to compare between species on the basis of the SEM pictures are further defeated by two petty editorial faults: the various shell views (outer surface, inner surface, complete section ('edge'), partial enlargements) are not uniformly presented in the same order; and magnifications are totally inconsistent across species. Each photograph properly

includes a bar scale; but inexplicably the original magnifications, from which the photographs were variously reduced, are also listed. Another oddity: the X-ray pictures of fossil eggs (pl. 42) are reversed, presented black-on-white, as if radiographs were photographic negatives.

Terms and concepts are sprung on the reader without, or before, being explained: thus fibers in the eggshell are mentioned in sections 1.2.1.1 and 1.2.1.2 but only in 1.2.1.3 are they revealed as consisting of protein (if fibers and fibrils are synonyms); what kind of protein is not disclosed. Or the 'subsurface layer' in 3.2.2 which remains mysterious. Numerous details remain unclear: What should the reader do with the codes accompanying species names in 3.2.1? Was fixation actually effected in formaldehyde gas (section 5.1)? Was a single fragment of *Chelonoidis elephantopus* egg really donated by two sources (p. 34)?

Taxonomy and nomenclature are inconsistent: The authors retained the comprehensive genus *Lacerta* for the readers' convenience, but split *Testudo* without telling the reader that *Chelonoidis* used to belong here. The proposed system of pseudoscientific species names for unidentifiable fossil shells is simply deplorable.

The literature review is refreshing in that, deviating from lamentable common practice, it covers sources in six languages. It indeed enriched the text with various interesting bits of information. Some of the omissions are natural and condonable. Thus the statement that 'sand-gluing gecko egg-shells . . . have only been observed in . . . *Tarentola*' (1.2.1.3) understandably ignores their detailed description in *Pachydactylus laevigatus* (Werner, 1977). Other omissions are worse: On eublepharine eggs (1.2.1.3) it would have been useful to quote Werner (1972): for 'the usual gold stain method' (3.1/4) it would have been kind to refer the reader to any source. But worse is the paucity of reference to the similar work of others, particularly when they had examined the same species: *Careta* had been studied also by Packard, Packard and Boardman (1982); *Terrapene carolina* and *Chelonoidis elephantopus* had been also reported resp., by Erben and by Hirsch in papers actually quoted but without proper comment in the text. One wonders whether the papers of Ewert (1985) and of Packard and Hirsch (1986) really came too late for inclusion.

The listing of Literature is less pedantic than could have been expected. Diacritical marks, correct for Spanish, are misleadingly absent from Turkish. For de Rooij no volume number is given, for Kopec no title is given, and in Stemmler italics are not indicated. The text of the book, too, contains numerous linguistic and editorial blemishes, which require no discussion here.

This is a typical book definable as a 'must' for institutional libraries catering to reptile-minded or embryology-minded scientists. Others, however, would be better advised to await the authors' next output, which they indicate is being prepared.

REFERENCES

- Ewert, M. A. (1985). Embryology of turtles. In *Biology of the Reptilia*, vol. 14, Development A. Gans, C., Billett, F. and Maderson, P. F. A. (Eds.), New York: John Wiley and Sons, pp. 75-267.
- Ferguson, M. W. J. (1981). Extrinsic microbial degradation of the alligator eggshell. *Science, N.Y.*, **214**, 1135-1137.
- Ferguson, M. W. J. (1985). Reproductive biology and embryology of the crocodilians. In *Biology of the Reptilia*, vol. 14, Development A. Gans, C., Billett, F. and Maderson, P. F. A. (Eds.), New York: John Wiley and Sons, pp. 329-491.
- Packard, M. J. and Hirsch, K. F. (1986). Scanning electron microscopy of eggshells of contemporary reptiles. *Scanning Electron Microsc.* **4**, 1581-1590.
- Packard, M. J., Packard, G. C. and Boardman, T. J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica*, **38**, 136-155.
- Packard, M. J., Thompson, M. B., Goldie, K. N. and Vos, M. (1988). Aspects of shell formation in eggs of the Tuatara, *Sphenodon punctatus*. *Journal of Morphology*, **197**, 147-157.
- Werner, Y. L. (1972). Observations on eggs of eublepharid lizards, with comments on the evolution of the Gekkonoidea. *Zoologische Mededelingen*, **47**, 211-224, 1 pl.
- Werner, Y. L. (1977). Ecological comments on some gekkonid lizards of the Namib Desert, South West Africa. *Madoqua*, **10**, 157-169.
- Wever, E. G. (1978). *The Reptile Ear, Its Structure and Function*. Princeton, N. J. and Guildford, UK: Princeton University Press.
- Yehudah L. Werner
- (5) *Handbuch der Paläoherpetologie. Teil 17 B/1. Theriodontia I.* Denise Sigogneau-Russell. 127 pp. Gustav Fischer Verlag, Stuttgart and New York. (1989). About £55.60 (DM 158), paper.
- This is another volume of the multi-volume work initiated by Professor Oskar Kuhn and which intends to eventually document all taxa of fossil amphibians and reptiles. This book appears to identically follow the format of the other volumes and it is written in English.
- This work follows the concept that the mammal-like reptiles (synapsids) consist of two orders, Pelycosauria and Therapsida. The therapsids are broken down into two suborders, the carnivorous theriodonts and the herbivorous anamodonts. The authors contribution, *Theriodontia I.* deals only with the four 'primitive' infraorders of this suborder (Phthinosuchia, Biarmosuchia, Eotitanosuchia and Gorgonopsia).
- These are marvellous beasts, with low, long skulls with a massive facial region formed by huge maxillary bones. They also have a pair of very long canine-like teeth that broadly overlap the dentaries. The postcranial skeleton is somewhat dog-like. These infraorders are known only from the late Permian of the USA, the USSR and South Africa.
- The book is well-written and well illustrated. It is a technical work that will be of greatest interest to those who study Permian vertebrates and/or mammal-like reptiles. It will be of general interest to persons in other areas of vertebrate palaeontology. My class in vertebrate palaeontology especially liked the illustrations of the skulls of the various groups.

Neotherpetologists' will be delighted to know about such an interesting group of ancient carnivorous reptiles and that there are people around that write thorough accounts about them, and that argue about their phylogenetic relationships.

Each infraorder comprises a separate section of the volume. Each of these sections is subdivided into osteological and systematic accounts. The accounts are well illustrated with clear drawings. The systematic accounts appear to deal adequately with the data that are presently available.

Following the sections on the infraorders is a section on phylogenetic relationships. This section will be understood by the non-specialist only if that person carefully studies the previous sections. There are some points of general interest in this section such as the statement that some of these animals were '... highly aggressive carnivorous reptiles, relatively active and capable of a mammalian running gait'.

Finally, there is a section on geological and geographic distribution that indicates the spatial and temporal distribution of these taxa in the USA, the USSR and South Africa.

J. Alan Holman

(6) *Contributions to the history of herpetology*. Craig Adler, J. D. Applegarth and R. Altig. 202 pp. Society for Study of Amphibians and Reptiles. (1989). \$20.

This book comprises the biographies of 152 leading herpetologists, together with their pictures and signatures, starting with Gesner four centuries ago and ending with those who died in 1985 and 1987. There is also an index to 2,500 writers on taxonomic herpetology and a list of what are described as Academic Lineages of Doctoral Degrees in Herpetology, i.e. showing how the department head's specialities may rouse similar interests in members of his staff. The whole work was produced to commemorate the First World Congress of Herpetology, held in Canterbury during September 1989, copies being given to all those who attended the congress.

Not being a taxonomist, I had little interest in the index of authors, but I found that the academic lineages gave an entrancing view of the way in which one expert's work in herpetology could lead to a spreading interest that encompassed other places of research.

But I became particularly engrossed in the biographies of those herpetologists who are past and gone. One reads papers or books by many authors, but how seldom does one know much about the great men themselves and their histories — unless one had had the good fortune to know them personally. In some cases one wonders why did X suddenly stop writing while apparently at the peak of his powers. Craig Adler's biographies give a view not only of these

herpetologists that he names, but also of their colleagues and the context of their work. Even those whom one knew may appear in some new light. Among British herpetologists one learns more of Gray, who first described the tuatera as well as developing the herpetological side of the British Museum: Bell, who apart from his publications on British and foreign species was in the chair at the Linnean Society when Darwin and Wallace read their historic papers on natural selection: Annandale of the Indian Museum and his fieldwork throughout Asia: Charles Pitman and his fieldwork in Africa: H. W. Parker of the British Museum: Arthur Loveridge of African fame: and Malcolm Smith, founder of the British Herpetological Society. Did you know that amongst all his herpetological work he even briefly held the post of Curator of Reptiles at the London Zoo?

This volume is full of scraps and larger morsels of information and detail relating to the herpetologist's world, fascinating in themselves but seldom found elsewhere. If they aren't careful, readers are liable to become addicted.

Deryk Frazer

(7) *Two Old Crocs. Steneosaurus, Metriorhynchus and Relatives*. Michael A. Taylor, John G. Martin and Arthur R. I. Cruickshank. 16 pp. Leicester Museums Publication No. 105. (1990). 75p (£1, including post and packing, from 96 New Walk, Leicester LE1 6TD).

Fossil crocodiles from Peterborough are on display in 'The Dinosaur' exhibition at Leicestershire Museum and Art Gallery. The attractive booklet under review was designed by Angela Pope: it traces the evolutionary descent of crocodilians from *Orthosuchus*, one of the earliest protosuchians, through *Alligatorellus* — an agile hunter of mice and insects — the much larger *Prstichampsus* and the marine, fish-like, *Geosaurus* to *Phobosuchus*, the largest crocodile ever and some 15m long. The two genera from the Oxford clay of Peterborough are described and illustrated in greater detail, and speculations made as to their colouration in life.

Despite the large number of authors and small number of pages, the booklet is written extraordinarily badly, while some sentences are ambiguous and misleading. For example, 'And some crocodiles carried on doing what the crocodiles are superbly good at: ambushing hunters living between land and water, like the modern Nile crocodile and alligator'. (p.4), or 'Ichthyosaurs plesiosaurs, crocodiles, fish, ammonites, belemnites, squidlike animals, and shellfish like oysters . . .' (p.6). A brief list is given of British museums in which fossil crocodiles are displayed, and four references are listed.

J. L. Cloudsley-Thompson

THE HERPETOLOGICAL JOURNAL

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1. The *Herpetological Journal* publishes a range of features concerned with scientific herpetology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by the editor); short notes (with a single data set); controversies, under 'Forum' (details available from editor); and book reviews. Faunistic lists and letters are not published.
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Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206-210.

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

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995-1002.
9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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