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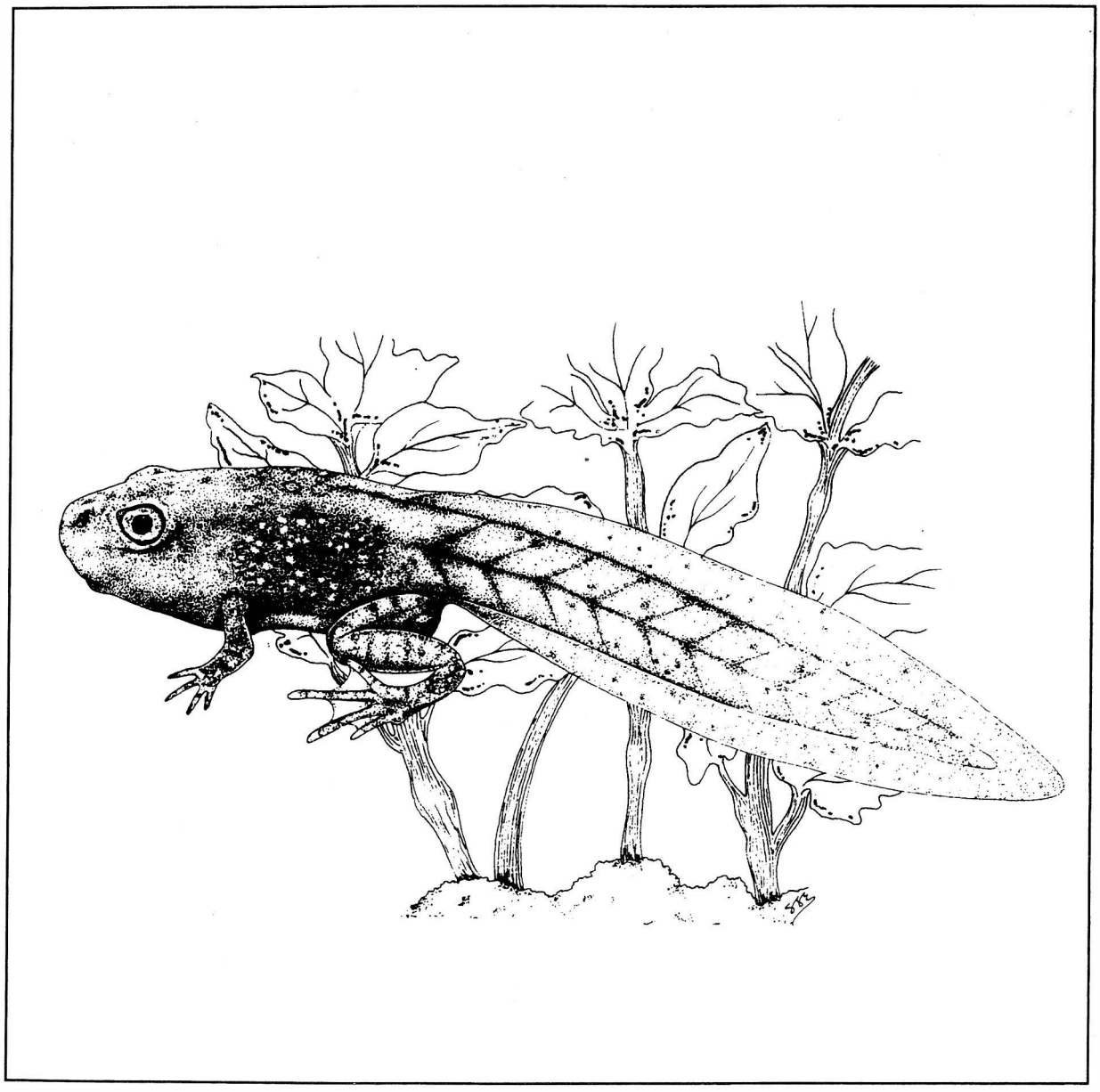

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BRITISH HERPETOLOGICAL SOCIETY

FRONT COVER: Metamorphosing tadpole of the Common Frog, *Rana temporaria* (S. Elmhurst)

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REVIEW:

BRITISH QUATERNARY HERPETOFAUNAS: A HISTORY OF ADAPTATIONS TO PLEISTOCENE DISRUPTIONS

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ABSTRACT

The British Quaternary herpetofauna and the modern one are the products of adaptations to several disruptive patterns. These include mass habitat loss due to glaciation, alternating cold and temperate climates, and the development of seaways isolating the British Islands. Fossil herpetofaunas are now known from all of the Middle and Upper Pleistocene stages (except the Beestonian) and from the Flandrian. The cold stages have yielded only *Rana temporaria, Lacerta vivipara* and *Natrix natrix*. The temperate stages have been enriched by exotic continental species incuding: *Pelobates fuscus, Pelodytes punctatus, Hyla* sp., *Rana arvalis, Rana esculenta* or *ridibunda, Rana lessonae, Emys orbicularis, Elaphe longissima,* and *Natrix maura* or *tessellata.* Middle Pleistocene Cromerian Interglacial faunas collectively have 38.5% exotic species and Middle Pleistocene Hoxnian Interglacial faunas have 46.5% exotic species. Late Pleistocene Ipswichian (Last Interglacial) faunas have 45.5% exotic species. The only exotic species recorded from the Flandrian (Holocene) is *Emys orbicularis.* The modern British amphibian fauna must have been in place early in the Flandrian (Holocene), as five of the six modern species occur at the Whitemoor Channel Site, East Cheshire, 10,000 to 8,500 BP; and there seems no reason to doubt that the modern reptile fauna was also then in place.

INTRODUCTION

The Pleistocene Epoch is characterised by climatic fluctuations and sea level changes brought on by advancing and retreating continental ice sheets over a period that began almost two million years before the present and that ended only about ten thousand years ago. The Pleistocene saw the rise and spread of *Homo sapiens* throughout the world and a great decrease in the mammalian megafauna by the end of the epoch. The Flandrian (Holocene) saw the eventual domination of the world by humans and their factories, crops and domesticated animals.

In Britain the evidence indicates that there were sharp contrasts in climate between glacial and interglacial stages wrought by shifting polar front positions in the North Atlantic (Stuart, 1982). These changes are reflected sharply by some elements of the mammalian fauna where arctic foxes, reindeer, and arctic voles occur during glacial periods; and African lions, African hippos and macaque monkeys occur in the interglacial ones.

For many years, the British Pleistocene herpetofauna has been neglected by vertebrate paleontologists. But in the last decade, interest has revived, and several articles (see references in this paper) have been written about the herpetofaunas of interglacial, and to a lesser extent, glacial sites. The purpose of this paper is to synthesize these works.

Significant Pleistocene faunas in Britain (Stuart, 1982) are mainly restricted to two interglacial stages (Cromerian and Hoxnian) in the Middle Pleistocene and one interglacial (Ipswichian) and one glacial stage (Devensian) in the Upper Pleistocene (Table 1). The Cromerian Middle Pleistocene Interglacial Stage is believed to have begun about 350,000 to 500,000 years before the present (BP) and the Hoxnian Middle Pleistocene Interglacial Stage is thought to have begun about 200,000 to about 250,000 BP.

The Ipswichian Late Pleistocene Interglacial Stage is thought to have begun about 120,000 BP and the Devensian Late Pleistocene Glacial Stage is believe to have begun about 110,000 BP. The Devensian is generally equated with the North American Wisconsinan and is thought to have ended about 10,000 BP.

The Flandrian (Holocene on a Worldwide basis) lasted from about 10,000 BP to the present, and is considered here not to have been part of the Pleistocene. The Flandrian also has significant British vertebrate fossil faunas.

Recently, it has been suggested that some sites yielding vertebrate fossils represent unnamed interglacial stages between the Cromerian and the Anglian and between the Hoxnian and the Ipswichian. Some of these faunas will be noted later.

PLEISTOCENE BARRIERS TO HERPETOLOGICAL DISPERSAL

Disruptions of British herpetological communities in the Pleistocene include (1) massive glacial ice sheets that obliterated herpetological habitats, (2) alternating cold and temperate climates, and (3) the seaways that formed, isolating the British Islands.

ICE SHEETS

Ice sheets eliminated herpetological habitats in vast portions of Britain during Middle and Upper Pleistocene times. It is believed that the last glacial stage (Devensian) lasted about 100,000 years (110,000 - 10,000 BP), whereas the last interglacial (Ipswichian) lasted only about 10,000 years (120,000 - 110,000 BP) (Stuart, 1982). The chronology of the other glacial and interglacial stages (Table 1) are not well documented.

During the Anglian Glacial Stage, the ice advanced as far south as Finchley, North London, and across to the Severn Estuary leaving only the southern counties as possible

Fig. 1 Approximate distribution of the ice (areas enclosed by broken line) during the time of the Devensian glacial expansion about 18,000 BP. Britain and Ireland appear as they are today. (Modified from Sutcliffe, 1985).

herpetological habitats. During the succeeding Wolstonian glaciation possible herpetological habitats were again greatly restricted, but not to the extent as in the Anglian.

The last significant glaciation of the British Isles occurred in the later part of the Devensian when the ice advanced from about 18,000 to 15,000 BP (Fig. 1). This advance did not move as far south as the preceding ones, and left much of central and southern Britain as possible herpetological habitats.

Low Temperatures

As ice sheets obliterated herpetological habitats, one would expect that very cold temperatures existed south of the glacial boundaries, and that these low temperatures would have excluded all but the most cold-tolerant amphibians and reptiles.

The northern parts of the seas surrounding the British Isles were completely frozen over during the height of glacial times (Sutcliffe, 1985) and this would diminish the ameliorating climatic effects normally afforded by such large bodies of water.

Tundra vole *(Microtus gregalis)*, wooly rhino (*Coelodonta antiquitatus*) and reindeer (*Rangifer tarandus*) occured during Anglian glacial times and the latter two occurred in the Wolstonian glacial stage. Arctic lemming (*Dicrostonyx torquatus*), tundra vole (*Microtus gregalis*), arctic fox (*Alopex lagopus*), woolly rhino (*Coelodonta antiquitatus*, reindeer (*Rangifer tarandus*), and musk ox (*Ovibos moschatus*) occurred in the Devensian glacial stage (Stuart, 1982). These tundra and arctic mammals attest to the fact that temperatures must have been too low for all but the most cold-tolerant amphibians and reptiles.

Seaways

During most of the Pleistocene the British Islands were connected to the European continent. Sea level changes in the British Late Pleistocene are a subject of some controversy (Stuart, 1982), but it is generally agreed that Britain first separated from Ireland and then from the continent early in the Flandrian (Holocene). The classic idea is that a very depauperate Devensian British herpetofauna became enriched from the continent during a warming trend that began about 10,000 years ago, and lasted until about 8,500 BP. Ireland has a smaller herpetofauna than Britain as a result of having been cut off earlier.

LAST 120,000 YEARS: YEARS BP AT START OF STAGE	STAGE
10,000	Flandrian Postglacial
20,000 30,000 40,000 50,000 60,000 70,000 80,000 90,000 100,000 110,000	Devensian Glacial
120,000	Ipswichian Interglacial
EARLIER STAGES: YEARS BP AT START OF STAGE	**STAGE**
?	Wolstonian Glacial
200-250,000	Hoxnian Interglacial
?	Anglian Glacial
350-500,000	Cromerian Interglacial

TABLE I. British Pleistocene Stages Referred to in Text

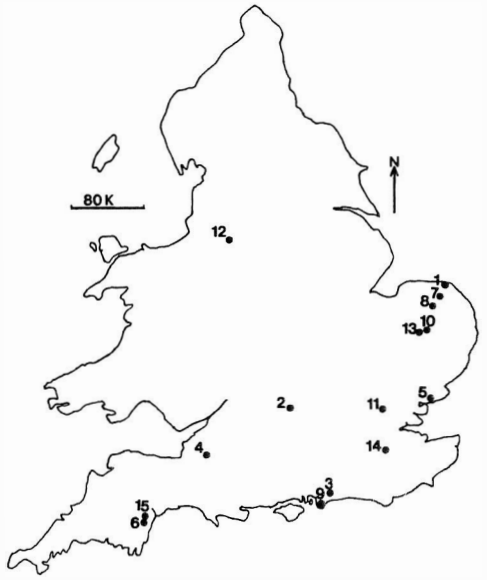

Fig. 2 Major British Pleistocene localities (closed circles) that have yielded fossil amphibians and/or reptiles. CROMERIAN INTERGLACIAL: (1) West Runton, Norfolk; (2) Sugworth, Berkshire; (3) Boxgrove, West Sussex; (4) Westbury-Sub-Mendip Cave, Somerset. HOXNIAN INTERGLACIAL: (5) Cudmore Grove, Essex. WOLSTONIAN GLACIAL: (6) Tornewton Cave, Devon. IPSWICHIAN GLACIAL: (7) Itteringham, Norfolk; (8) Swanton Morley, Norfolk; (9) Selsey, West Sussex; (10) Shropham (I), Norfolk. DEVENSIAN GLACIAL: (10) Shropham (D), Norfolk; (11) Nazeing, Essex. FLANDRIAN (HOLOCENE): (12) Whitemoor Channel, Cheshire; (13) East Wretham, Norfolk; (14) Ightham Fissures, Kent; (15) Cow Cave, Devon.

CHRONOLOGY OF BRITISH PLEISTOCENE HERPETOFAUNAS

The following chronological accounts are based mainly on interpretations made by Stuart (1982) and Kolfschoten, (1985, 1990). These reports indicate that the type section of the Cromerian (first glacial stage of the Middle Pleistocene) at West Runton, Norfolk, is older than the Little Oakley, Essex; Boxgrove, Sussex and Westbury, Somerset, sites and is roughly equivalent to the Sugworth, Berkshire, site. Moreover, it is possible that the Boxgrove and Westbury sites represent an unnamed stage between the "Cromerian" and the following Anglian glacial stage. Moreover, there is the strong possibility that the Stutton/Harkstead, Suffolk and Stoke Tunnel, Suffolk, Ipswichian sites may form a distinct stage from the later Itteringham, Norfolk; Swanton Morely, Norfolk and Shorpham, Norfolk, sites.

Figure 2 indicates the most important British Pleistocene localities that have thus far yielded amphibian and/or reptile remains.

Middle Pleistocene Sites

Middle Pleistocene sites and their herpetofaunas are listed in Table 2. Exotic species are preceded by an asterisk (*) there and in the following discussion.

Cromerian Interglacial. Vertebrate faunas are well-known from the Cromerian temperate stage, especially the mammalian components (Stuart, 1982). The West Runton Site in Norfolk and the Westbury-sub-Mendip site in Somerset have especially large vertebrate assemblages (Stuart, 1982; Andrews, 1990). These faunas represent conditions somewhat warmer than occur in Britain today.

The combined herpetofaunas of the "earlier Cromerian" sites (West Runton and Sugworth) consist of *Triturus vulgaris, Bufo bufo, *Rana esculenta* or *ridibunda, *Rana arvalis, Rana temporaria, Anguis fragilis, Natrix natrix* and *Vipera berus.* Of the eight identified species, the two exotics form 25% of the combined faunas.

The combined herpetofaunas of the "later Cromerian" sites (Little Oakley, Boxgrove and Westbury) consist of *Triturus vulgaris, *Pelobates fuscus, *Pelodytes punctatus, Bufo bufo, *Rana arvalis, Rana temporaria, *Emys orbicularis, Anguis fragilis, Coronella austriaca* and *Vipera berus.* Of the 10 identified species, the four exotics form 40% of the combined faunas. It is interesting to note that the only British records for the exotic species *Pelobates fuscus* and *Pelodytes punctatus* are from these "later Cromerian" sites, as is the earliest British record of *Emys orbicularis.* Moreover, the earliest record of *Coronella austriaca*, a species occurring only in extreme southern England today, is from Westbury.

A technique used in North America to identify Pleistocene Paleoclimates looks at the closest area to the fossil sites where all of the extant fossil species could be found living together today. This "area of sympatry" concept was mainly developed by C. W. Hibbard in the 1950's. The closest area of sympatry of the Westbury fauna would be at about the Anger area of the Loire Valley in France. This simple method suggests that the Westbury herpetofauna lived in a somewhat warmer climate than did the West Runton one.

Middle Pleistocene

CROMERIAN (I). (12 herpetological species, 41.7% exotic)

	Triturus vulgaris (1,4)
*	*Pelobates fuscus* (4)
*	*Pelodytes punctatus* (5)
	Bufo bufo (1,4)
*	*Rana arvalis* (1,2,3,4)
*	*Rana esculenta* or *ridibunda* (1)
	Rana temporaria (1,4,5)
*	*Emys orbicularis* (3,5)
	Anguis fragilis (1,4,5)
	Coronella austriaca (5)
	Natrix natrix (1,2,3,5)
	Vipera berus (1,5)

Cromerian Herpetological Sites: 1, West Runton, Norfolk (Holman *et al.*, 1988; Holman, 1989). 2, Sugworth, Berkshire (Stuart, 1980; Holman, 1987*c*). 3, Little Oakley, Essex (Lister *et al.*, 1990). 4, Boxgrove, Sussex (Holman, 1992*d*). 5, Westbury-sub-Mendip, Somerset (Stuart, 1979; Holman, 1992*e*).

ANGLIAN (G) (indefinite herpetological species, 0.0% exotic)

Bufo sp. and/or *Rana* sp.

Anglian Herpetological Site: Halls Pit, Oxfordshire (Stuart, 1982).

HOXNIAN (I) (15 herpetological species, 46.7% exotic)

	Triturus cristatus (1)
	Triturus vulgaris (1)
*	*Hyla sp.* (1)
	Bufo bufo (1,2,3)
*	*Rana arvalis* (1,3)
*	*Rana esculenta* or *ridibunda* (1)
*	*Rana lessonae* (1)
	Rana temporaria (3)
*	*Emys orbicularis* (1,4)
	Anguis fragilis (1,3)
	Lacerta sp. (1)
*	*Elaphe longissima* (1)
*	*Natrix maura* or *tessellata* (1)
	Natrix natrix (1,3,4)
	Vipera berus (1)

Hoxnian Herpetological Sites. 1, Cudmore Grove, Essex (Holman *et al.*, 1990). 2. Barnfield Pit, Swanscombe, Kent (Holman, 1987*a*). 3, Greenlands Pit, Essex (Holman & Clayden, 1988). 4, Ingress Vale, Swanscombe, Kent (Stuart, 1982; Holman, 1987*a*).

Upper Pleistocene

WOLSTONIAN (G) (one herpetological species, 0.0% exotic)

Bufo sp. and/or *Rana* sp. (2)
Rana temporaria (1)

Wolstonian Herpetological Sites: 1, Tornewton Cave, Devonshire (Holman, 1990). 2, Waterhall Farm, Hertfordshire (Holman, 1990).

IPSWICHIAN (I) (11 herpetological species, 45.5% exotic)

	Triturus vulgaris (6)
*	*Hyla* sp. (3)
	Bufo calamita (5)
	Bufo bufo (3,5,6,8).
*	*Rana arvalis* (6,8)
*	*Rana esculenta* or *ridibunda* (3)
	Rana temporaria (3,6,8)
	Lacerta cf. *Lacerta vivipara* (6)
*	*Emys orbicularis* (1,2,3,4,5,6,7,8)
*	*Natrix maura* or *tessellata* (6)
	Natrix natrix (3,5,6,8)

Ipswichian Herpetological Sites: 1, Bobbitshole, Suffolk (Stuart, 1979). 2, Harkstead, Suffolk (Stuart, 1979). 3, Itteringham, Norfolk (Hallock *et al.*, 1990). 4, Mudesley, Norfolk (Stuart, 1979). 5, Selsey, Sussex (Holman, 1992*a*). 6, Shropham (I), Norfolk (Holman & Clayden, 1990). 7, Stoke Tunnel, Suffolk (Stuart, 1979). 8, Swanton Morley, Norfolk (Stuart, 1979; Holman, 1987*b*).

DEVENSIAN (G) (four herpetological species, 0.0% exotic)

"amphibians" (5)
Bufo sp. and/or *Rana* sp. (1)
Bufo sp. (2)
Rana sp. (2)
Rana temporaria (3,4)
Lacerta vivipara (2)
Natrix natrix (3)

Devensian Herpetological Sites: 1, Coston, Norfolk (Stuart, 1982). 2, Nazeing, Essex (Stuart, 1982). 3, Shropham (D), Norfolk (Holman, 1992*c*). 4, Upton Warren, Worcestershire (Stuart, 1982). 5, Wilments Pit, Middlesex (Stuart, 1982).

FLANDRIAN (I) (10 herpetological species, 10.0% exotic)

Note - The Flandrian is equivalent to the "Holocene" on a worldwide basis. Site 8 is from the early Flandrian; Site 4 is from middle Flandrian; and the other sites have poor stratigraphic control.

Triturus helveticus (5,8)
Triturus vulgaris (8)
Bufo Bufo (1,2,3,5,6,8)
Bufo calamita (2,5,8)
Rana temporaria (1,2,3,5,6,7,8)
Emys orbicularis (4)
Anguis fragilis (2,3,5)
Coronella austriaca (5)
Natrix natrix (3,5,6)
Vipera berus (2,5)

Flandrian Herpetological Sites: 1, Bathford, Somerset (Holman, 1987*a*). 2, Cow Cave, Devonshire (Holman, 1988). 3, Dog Holes, Lancashire (Holman, 1987*a*). 4, East Wretham, Norfolk (Stuart, 1979). 5, Ightham Fissures, Kent (Holman, 1985; 1987*a*). 6, Happaway Cave, Torquay, Devon (Holman, 1987*a*). 7, Netteswell, Essex (Holman, 1987*a*). 8, Whitemoor Channel, East Cheshire (Holman & Stuart, 1991).

TABLE 2. The British Pleistocene herpetofauna. * = exotic taxa; I = glacial stage; G = interglacial stage.

THE NATIVE HERPETOFAUNA IN BRITAIN TODAY (Only *Lacerta agilis* is not known as a British Pleistocene Fossil)
Triturus cristatus
Tirturus helveticus
Triturus vulgaris
Bufo bufo
Bufo calamita
Rana temporaria
Lacerta agilis
Lacerta vivipara
Anguis fragilis
Natrix natrix
Coronella austriaca
Vipera berus

TABLE 2. (Continued) The British Pleistocene herpetofauna.

Anglian Glacial. During the Anglian cold-stage, which possibly lasted about 100,000 years (Table 1), the ice advanced well into southern England leaving only a few southern counties as possible herpetological habitat. Vertebrate faunas are not nearly as abundant as in the Cromerian, and consist mainly of mammals, some of which are quite cold-adapted (eg. tundra vole, *Microtus gregalis* and reindeer, *Rangifer tarandus*). Anuran remains were found in association with several mammals (including tundra vole and reindeer) at Hall's Pit near Benson, Oxfordshire; but the amphibian remains were identified only as *Rana* sp. and/or *Bufo sp.* (Stuart, 1982). These are the only recorded herpetological remains from the Anglian as far as I am aware.

The meagre pollen data from Anglian sites indicate unwooded, cold conditions (Stuart, 1982). Therefore, the lack of reptilian remains from the Anglian is not surprising; and it would be expected that many of the herpetological species that occur in the succeeding Hoxnian Interglacial had to invade or re-invade formerly uninhabitable areas.

Hoxnian Interglacial. Fossil vertebrates of the Hoxnian temperate stage have been mainly recovered in the process of archaeological investigations. The Cudmore Grove fauna from Mersea island, Essex, however, is an exception. This fauna contains the only substantial herpetofauna from the Hoxnian and is the most important fossil herpetofauna known from Britain.

Pollen from this site indicates a later part of Stage II (Ho IIIb) which had a mixed oak forest with some late immigrating taxa such as *Carpinus betulus* and *Abies* (Holman, Stuart & Clayden, 1990).

Herpetological taxa identified from the Cudmore Grove site are *Triturus vulgaris, Triturus cristatus, Hyla* sp., *Bufo bufo, *Rana arvalis, *Rana esculenta* or *ridibunda, *Rana lessonae, *Emys orbicularis, Anguis fragilis, Lacerta* sp., *Elaphe longissima, *Natrix maura* or *tessellata, Natrix natrix*, and *Vipera berus.* Of the 14 identified taxa; the seven exotic species form 50% of the fauna, the highest percentage of exotics from any single British Pleistocene herpetofauna known.

Oddly, the nearest area of sympatry for the Cudmore Grove herpetofauna would be in the Trieste area near the Adriatic Sea. This is because of the combination of the mainly northern modern occurrence of *Rana arvalis* in western Europe with other largely southern species (see maps in Arnold & Burton, 1978).

The Greenlands Pit, Purfleet, Essex, site is the only other Hoxnian site in Britain with more than two herpetological species including *Bufo bufo, *Rana arvalis, Rana temporaria, Rana* sp., *Anguis fragilis*, and *Natrix* cf. *natrix.* Allen (1977) pointed out the possibility that the deposit was laid down during another interglacial stage between the Hoxnian and the Ipswichian.

Of the five species identified, the one exotic species forms 20% of the fauna.

Upper Pleistocene Sites

Wolstonian Glacial. Vertebrate faunas are rather poorly known from the Wolstonian Cold Stage (Stuart, 1982). Evidence indicates that cold climates existed for much of this stage, and that the landscape was treeless and dominated by herbaceous vegetation. Reindeer, horses, mammoths and wooly rhinos have been recovered from Wolstonian sites (Stuart, 1988), but amphibian remains are scarce and no reptile remains have been reported from this stage.

Rana temporaria has been identified from Tornewton Cave, Devonshire, by Holman (1990) and *Bufo* sp. and/or *Rana* sp. have been identified from the Waterhall Farm Site, Hertfordshire (Stuart, 1982; Holman, 1990).

Ipswichian Interglacial. Vertebrate faunas from the Ipswichian/Last Interglacial may actually represent two temperate stages (e.g. Sutcliffe & Kowalski, 1976; contra Stuart, 1976, 1982). Herpetological evidence does little to reflect upon this as only two Ipswichian herpetofaunas are substantial, and both of these appear to represent the same temporal period within the Ipswichian (A. J. Stuart pers. comm.). All eight Ipswichian sites that contain herpetological remains contain the exotic European pond tortoise, *Emys orbicularis.* This species is important as it indicates a somewhat warmer summer climate than occurs in Britain today (Stuart, 1979, 1982).

The two substantial Ipswichian herpetofaunas are the Itteringham Site, Norfolk, and the Shropham Site, Norfolk. The combined herpetofaunas of these sites (considered to represent the same temporal stage of the Ipswichian, as presently conceived) include *Triturus vulgaris, *Hyla* sp., *Bufo bufo, *Rana arvalis, *Rana esculenta* or *ridibunda, Rana temporaria, *Emys orbicularis, Lacerta* cf. *L. vivipara, *Natrix maura* or *tessellata* and *Natrix natrix.*

Of the 10 identified taxa, the five exotic species form 50% of the fauna, the same percentage as in the rich Hoxnian Cudmore Grove herpetofauna. But the closest area of modern sympatry would be in the eastern Baltic countries (see maps in Anrold & Burton, 1978).

Of additional Ipswichian interest is the natterjack toad, *Bufo calamita*, from the Selsey, Sussex Site (Holman, 1992*a*), as this is the earliest fossil record in Britain of this presently endangered species.

Devensian Glacial. The Devensian Cold Stage/Last Glacial is a critical unit of time to consider with respect to the depauperate nature of the modern British herpetofauna. The preceding Ipswichian Interglacial with its temperate herpetofauna consisting of about 46% exotic species (Table 2) lasted about 10,000 years. The Devensian that followed lasted about 100,000 years and had cold, sometimes savage, climates. Moreover, for most of the Devensian, a mixed savanna/tundra type flora occurred in the non-glaciated areas of Britain. There is no modern analog for this vegetation.

Vertebrate faunas are more abundant in the Devensian than in any other British Pleistocene cold stage and in general, mammalian faunas are well represented. But as might be expected, the few herpetological species recorded are cold-tolerant ones that today are able to adjust to conditions within or near the arctic circle (Holman, 1990).

The North American Wisconsinan glacial stage is temporally equivalent to the Devensian (Sutcliffe, 1985). During the Wisconsinan, especially during the last 25,000 years, disharmonious vertebrate communities with no modern analogs existed south of proglacial regions (Lundelius *et al.*, 1983). These communities consisted of mixtures of "northern" and "southern" species and they existed in the equable climates that occurred in these regions.

The model that was proposed to explain these mixed faunas was that many species forced southward by advancing glaciation were able to mix with the resident faunas because of the cool summer climates that occurred as part of the equable climates of the region. Thus, North America and Britain were very different in the problems confronting their respective vertebrate faunas. North America had a vast southern refugium where climates were equable and with summers that were cool enough to accommodate many species of northern immigrants and from which herpetological species could re-invade formerly glaciated area (Holman, 1992*b*). Britain's reinvasions however, came from a cool continental western Europe which was cut off from any large warm refugia by mountains.

Flandrian (Holocene on a Worldwide Basis). As the Flandrian climate warmed, the modern British herpetofauna plus *Emys orbicularis* reinvaded areas from which they were previously displaced by glaciers, cold climates and inhospitable ecological communities. The earlier separation of Ireland left it with a very depauperate herpetofauna. The later separation of Britain from the continent allowed it to accumulate a less depauperate herpetofauna of at least 13 species (counting the now absent *Emys orbicularis*).

Unfortunately there is poor stratigraphic control in most Flandrian herpetological sites because so many of them are from unstratified caves or fissures. The largest Flandrian herpetofauna comes from the Ightham Fissures Site near Sevenoaks, Kent and includes eight species: *Triturus helveticus, Bufo bufo, Bufo calamita, Rana temporaria, Anguis fragilis, Coronella austriaca, Natrix natrix*, and *Vipera berus.* Holman (1985) postulated that this site might represent a time in the early Flandrian when the climate of Britain had become about as warm as it is today. But Stuart (in Holman & Stuart, 1991) cautions that the Ightham site could represent any time within the Flandrian from 10.000 years ago to a few hundred years ago.

Only two sites within the Flandrian have precise pollen dates. The first, the Whitemore Channel Early Flandrian site near Bosley, East Cheshire, representing a period of 10,000 to 8,800 years BP (Holman & Stuart, 1991); contained five of the six native amphibian species *Triturus vulgaris, Triturus helveticus, Bufo calamita, Bufo bufo*, and *Rana temporaria.* This indicates that the modern amphibian fauna was in place in Britain early in the Flandrian, and there seems no reason to doubt that the modern reptile fauna was also then in place.

The second site, East Wretham, Norfolk, contains the only record of the European pond tortoise, *Emys orbicularis*, from the Flandrian of Britain. This site was pollen-dated to a warm period within the middle part of the Flandrian (Zone VIIa, F1 11d, Stuart, 1982).

SUMMARY

The modern British herpetofauna (Table 2) intimately reflects the Quarternary glaciology, climatology, ecology and geography of what is now the British Isles. The modern herpetofauna of Britain is clearly derived from adjacent areas in northwestern Europe. But during interglacial stages of the Pleistocene, several exotic continental species took advantage of somewhat warmer temperatures than occur in Britain today.

Until early in the Flandrian (Holocene) Britain and Ireland were connected to the European continent. From time to time in previous Pleistocene stages, ice sheets thrust southward over what are now these islands. The glaciers obliterated herpetological habitats. Moreover, cold climates and disturbed communities occurred in the proglacial areas. During these times only three species have been recorded in Britain, two of which (*Rana temporaria* and *Lacerta vivipara*) are probably the most cold-tolerant ones that exist in Europe today.

During the interglacial stages when the glaciers withdrew and climates became as warm or warmer than today, herpetological species reinvaded Britain and Ireland, presumably mainly from limited western European refugia north of the Pyrenees and Alps. Amongst these invaders were continental species that do not occur as natives in Britain today. These exotics (Table 2) are: *Pelobates fuscus, Pelodytes punctatus, Hyla* sp., *Rana arvalis, Rana esculenta* or *ridibunda, Rana lessonae, Emys orbicularis, Elaphe longissima*, and *Natrix maura* or *tessellata.* Of these forms, *Pelodytes punctatus, Elaphe longissima*, and *Natrix maura/tessellata* occur wholly south of the British Islands today; and with the exception of *Rana arvalis*, the others occur mainly south of Great Britain (Arnold & Burton, 1978).

The Cudmore Grove, Essex, fauna of the Hoxnian Interglacial Stage had the richest and most exotic Pleistocene herpetofauna in Great Britain with 14 species, half of which were exotic.

Ireland was cut off from the mainland first, and has a very depauperate modern herpetofauna of at most four species. Britain was cut off later, and its 12 modern species (Table 2) are several fewer than in adjacent continental areas.

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A REVIEW OF THE GENUS *LYCOPHIDION* (SERPENTES: COLUBRIDAE) IN NORTHEASTERN AFRICA

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ABSTRACT

Variation in *Lycophidion* populations of the southern Sudan, Somalia, Ethiopia, Uganda and Kenya is analysed. Five species occur in this area: *L. irroratum* and *L. ornatum* are restricted to forests, *L. depressirostre* and *L. taylori* sp. nov. inhabit dry savannas, *L. capense jacksoni* is found in the moister savannas of the highlands and plateau areas, while *L. capense loveridgei* occurs in both forest and savanna of the coastal strip. *L. irroratum* is readily distinguished by the paired apical pits on the dorsal scales. *L. depressirostre* and *L. taylori* both have lower ventral and subcaudal counts than the other taxa, but *L. depressirostre* can be distinguished from all other species by its more numerous maxillary teeth (8 to 9 + 19 to 24 compared with 7 to 8 + 11 to 18) and usually one colour pattern. *L. taylori* is very variable in colouration, but most specimens have a white blotch or collar on the nape and white dorsal stippling may be very extensive. The type series of *L. taylori* comes from the border between northern Somalia and Ethiopia, but there are isolated specimens from northern Kenya (Turkana District), Chad and Senegal.

INTRODUCTION

The last overall review of the African snake genus *Lycophidion* Duméril & Bibron was provided by Laurent (1968), but the material that he examined was mainly from East Africa. Unaware of Laurent's study, Hughes was working on the genus in West Africa and Zaire, while Broadley was investigating the genus in southern and eastern Africa. While working on the collections in the British Museum early in 1968, Broadley identified three new taxa of *Lycophidion*, but two of them were described by Laurent (1968, *L. depressirostre* and *L. capense pembanum*). The third was not named by Laurent, but Broadley held up description in the hope of obtaining additional material: the taxon is finally described in the present paper.

A small wolf snake from central Mozambique proved to represent a new genus and species - *Cryptolycus nanus* (Broadley, 1968), apparently derived from *Lycophidion semiannule*. Analysis of variation in Zimbabwean material of *L. capense* showed that it should be referred to the typical form rather than *L. c. multimaculatum* Boettger, 1888, as indicated by Laurent (1968): it also revealed the presence of a cryptic species - *L. variegatum* (Broadley, 1969).

Leston & Hughes (1968) revived *L. nigromaculatum* (Peters) as a full species and then Guibé & Roux-Estève (1972) reviewed the West African species and resurrected *albomaculatum* Steindachner as a western race of *L. semicinctum*.

Branch (1976) reviewed the genus in Southern Africa, extending the range of *L. variegatum* south to Natal and describing the distinctive trilobate hemipenis of this species. In the revision of "FitzSimons' snakes of Southern Africa" (Broadley, 1983), the distributions of the southern African taxa were mapped and showed that *L. capense multimaculatum* reaches its southern limit in the extreme north of Namibia and the Caprivi. Further study of Namibian material revealed the presence of an undescribed species which had been confused with *L. hellmichi* Laurent (Broadley, 1991*b*): *L. multimaculatum* has also been identified as a valid species (Broadley, 1991*a*).

There remain some problems with regard to the genus *Lycophidion* in southeastern Africa: *L. semiannule* (Peters, 1854) may be composite and *L. capense vermiculatum* Laurent, 1968, is doubtfully distinct from the typical form. In the circumstances, it seemed desirable to collaborate and publish our findings for northeastern Africa. Broadley will subsequently review the southern African taxa and Hughes will finalise his investigation of the situation in West Africa and Zaire.

MATERIAL AND METHODS

This study is based on the examination of 348 specimens from southern Sudan, Somalia, Ethiopia, Uganda, and Kenya, with additional data for four specimens supplied by Malcolm Largen. Data for the Tanzanian specimens plotted on the distribution maps will be included in the forthcoming paper covering southern Africa.

Two meristic characters (counts of ventrals and subcaudals) have been utilised for statistical analysis and the mean, standard deviation and standard error calculated, the sexes being treated separately.

Ventrals were counted by the Dowling (1951) method. The subcaudal count begins with the first scute in contact with its fellow on the midline and excludes the terminal spine. Dorsal scales were counted one head length posterior to the nape, at midbody and one head length anterior to the vent.

Under "Localities" for each form, literature citations are listed alongside the museum catalogue numbers for the specimens examined. Some authors' names are abbreviated as follows: Blgr = G.A. Boulenger; Laur. = R.F. Laurent; Lov. = A. Loveridge; Park. = H.W. Parker; Scor. = G. Scortecci.

The specimens examined belong to the following institutions (identified by the acronyms throughout the text):

AAM = Addis Ababa Museum, Ethiopia.

AMNH = American Museum of Natural History, New

York, U.S.A.

ANSP = Academy of Natural Sciences, Philadelphia, U.S.A.

BH = Barry Hughes Collection, Wanstead, U.K.

BM = Natural History Museum, London, U.K.

CAS = California Academy of Sciences, San Francisco, U.S.A.

FMNH = Field Museum of Natural History, Chicago, U.S.A.

IRScNB = Insitut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

LACM = Los Angeles County Museum, U.S.A.

MCZ = Museum of Comparative Zoology, Harvard, U.S.A.

MF = Museo Zoologico de "La Specola", Florence, Italy.

MNHN = Museum National d'Histoire Naturelle, Paris, France.

MSNG = Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.

MSNM = Museo Civico di Storia Naturale, Milan, Italy.

NMK = National Museum of Kenya, Nairobi, Kenya.

NMW = Naturhistorisches Museum, Vienna, Austria.

NMZB = Natural History Museum, Bulawayo, Zimbabwe.

SMW = Senckenbergische naturforschende Gesellschaft, Frankfurt-am- Main, Germany.

UMNZ = University of Michigan Museum of Zoology, Ann Arbor, U.S.A.

USNM = National Museum of Natural History, Washington, U.S.A.

ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

ZMB = Zoologisches Museum der Universitat, Berlin, Germany.

ZMUC = Zoological Museum, Copenhagen, Denmark.

CHARACTER ANALYSIS

1. Number of apical pits on dorsal scales. *L. irroratum* has two (rarely three) pits on each scale, all other local species have single pits.

2. Dorsal scale rows. *L. irroratum* and *L. ornatum* differ from the other three species in having no reduction from 17 rows to 15 posteriorly.

3. Ventral plates. The variation in number of ventrals is shown in Table 1. There is no sexual dimorphism in *L. irroratum* (Guibé & Roux-Estève, 1972): in most taxa female counts average 5-7 higher than those of males, but in *L. c. loveridgei* the difference exceeds ten. Counts for *L. taylori* fall in between the ranges of *L. depressirostre* and *L. c. jacksoni*.

4. Subcaudal plates. The variation in number of subcaudals is shown in Table 1. The sexual dimorphism in the first five forms is constant, males averaging six higher than females, but the difference increases to eleven in *L. c. loveridgei*. The latter taxon is readily distinguished from all others by its high subcaudal counts.

5. Head shields. *L. ornatum* consistently differs from *L. depressirostre*, *taylori* and *capense* in having the postnasal separated from the first labial. This character is variable in *L. irroratum*.

6. Colour pattern of head. *L. irroratum* and *L. ornatum* have the most distinct head markings, consisting of a well-defined pale band round the snout, extending through the eye to the temporal region and a stripe extending diagonally from the eye to the angulus oris.

In *L. depressirostre* the pale snout band is ill-defined and breaks up behind the eye, there may be some pale speckling on top of the head. The markings are similar in *L. capense jacksoni*, except that the top of the head is usually immaculate.

In *L. capense loveridgei* there is no pale snout band, but all the dorsal head shields have light speckling or vermiculation.

L. taylori is very variable, there may be a reticulate pattern in white restricted to the snout and sides of the head, or all the dorsal head shields may be heavily stippled with white.

7. Colour pattern of dorsum. In *L. c. jacksoni* and *L. c. loveridgei* each dorsal scale is tipped with white. In *L. depressirostre* there is white stippling on the distal half of each scale, but not on the apex. In *L. irroratum* and *L. ornatum* fine white stippling covers almost the entire scale, although occasional scales show dark spots which are free of stipple. *L. taylori* is variable, there may be only a white mark on the upper distal edge of each scale, more often the entire scale is heavily stippled with white, increasing on the lower lateral rows so that the outer row or two may be uniform white. In 75% of specimens there is a broad white collar or a nuchal blotch, a feature not found in any other taxon.

8. Colour pattern of ventrum. In *L. irroratum* and *L. ornatum* the ventrum is apparently dark throughout life, apart from white stippling on the chin and throat and a narrow pale free edge to the ventrals and subcaudals. *L. depressirostre* is similar, except that the white stippling is very meagre. In *L. taylori* the ventrum appears to be dark throughout life apart from white stipple on the chin, sometimes the white collar extending across the ventrals, and usually the ends of the ventrals are white.

In *L. capense*, juveniles have the ventrum white, but dark stippling develops posteriorly and rapidly extends forwards until adults are unformly dark except for a light patch on the throat and a pale free edge to each ventral.

9. Skull. Bourgeois (1968) described and illustrated the skulls of *L. capense jacksoni* and *L. ornatum* from the Kivu Province of Zaire and drew attention to various differences between them.

Skulls were prepared of the five species recorded from northeastern Africa and some striking differences were noted in the proportions of the skull bones and the development of parietal crests.

VENTRALS

TAXON	MALES				FEMALES			
	N	RANGE	MEAN	S.D.	*N*	RANGE	MEAN	S.D.
irroratum	1	164	-	-				
ornatum	16	190-205	198.5	4.3	32	186-212	210.0	6.2
taylori	14	158-176	166.5	5.8	11	165-184	173.3	6.9
depressirostre	29	153-176	162.6	6.7	34	158-180	168.9	5.0
c. jacksoni								
"south"	72	173-198	183.4	5.6	93	177-209	190.1	6.5
"north"	10	176-210	194.0	10.7	22	188-216	203.5	8.6
c. loveridgei	3	196-201	198.0	2.6	3	204-212	208.3	4.0

SUBCAUDALS

TAXON	MALES				FEMALES			
	N	RANGE	MEAN	S.D.	*N*	RANGE	MEAN	S.D.
irroratum	1	38	-	-				
ornatum	16	41-50	44.0	2.6	32	32-42	37.8	2.6
taylori	14	30-38	35.0	2.7	11	26-30	28.0	1.4
depressirostre	28	31-40	34.9	1.9	34	26-34	28.4	1.6
c. jacksoni								
"south"	71	33-48	39.0	2.6	94	27-37	33.2	2.0
"north"	10	33-51	39.4	5.0	21	30-37	33.2	2.0
c. loveridgei	3	51-57	54.0	3.0	3	42-45	43.3	1.5

TABLE 1. *Lycophidion* in northeastern Africa: variation in ventral and subcaudal counts. Note: *L. c. jacksoni* is split into two groups: "south" includes specimens from southern Sudan, Uganda and Kenya. "north" includes specimens from central Sudan, Ethiopia and Somalia.

The short and broad skull of *L. ornatum* (Fig. 1A) seems to represent the ancestral condition, unless this is due to neoteny. In this skull the ratio of parietal maximum length/breadth is 1.12 and there are no indications of parietal crests.

The western species *L. irroratum* (Fig. 1B) has a slightly more elongate skull (parietal L/B 1.26) and has moderately developed parietal crests which are well separated posteriorly.

L. taylori sp. nov. (Fig. 1C) has a moderately elongate skull (parietal L/B 1.39), but only a trace of well separated parietal crests posteriorly.

L. depressirostre (Fig. 1D) has a very elongate skull (parietal L/B 1.95) with strongly developed smoothly curved parietal crests which merge posteriorly.

L. capense jacksoni (Fig. 1E) also has a very elongate skull (parietal L/B 1.88) with strongly developed angular parietal crests which merge posteriorly.

10. Dentition. Hughes has counted the teeth of a series of 40 *L. irroratum* from West Africa and recorded postmaxillary 13-17; palatine 12-16; pterygoid 18-24 and postmandibular 16-20 (unpublished data).

Bourgeois (1968) illustrated the skull of *L. ornatum*, but unfortunately the posterior portions of the maxillae were broken: there are 7 anterior maxillary teeth, 14 palatine and 18-21 pterygoid.

Underwood (pers. comm.) has examined the dentition of a *L. depressirostre* from Aware Melka, Ethiopia (BM 1916.6.24.5)

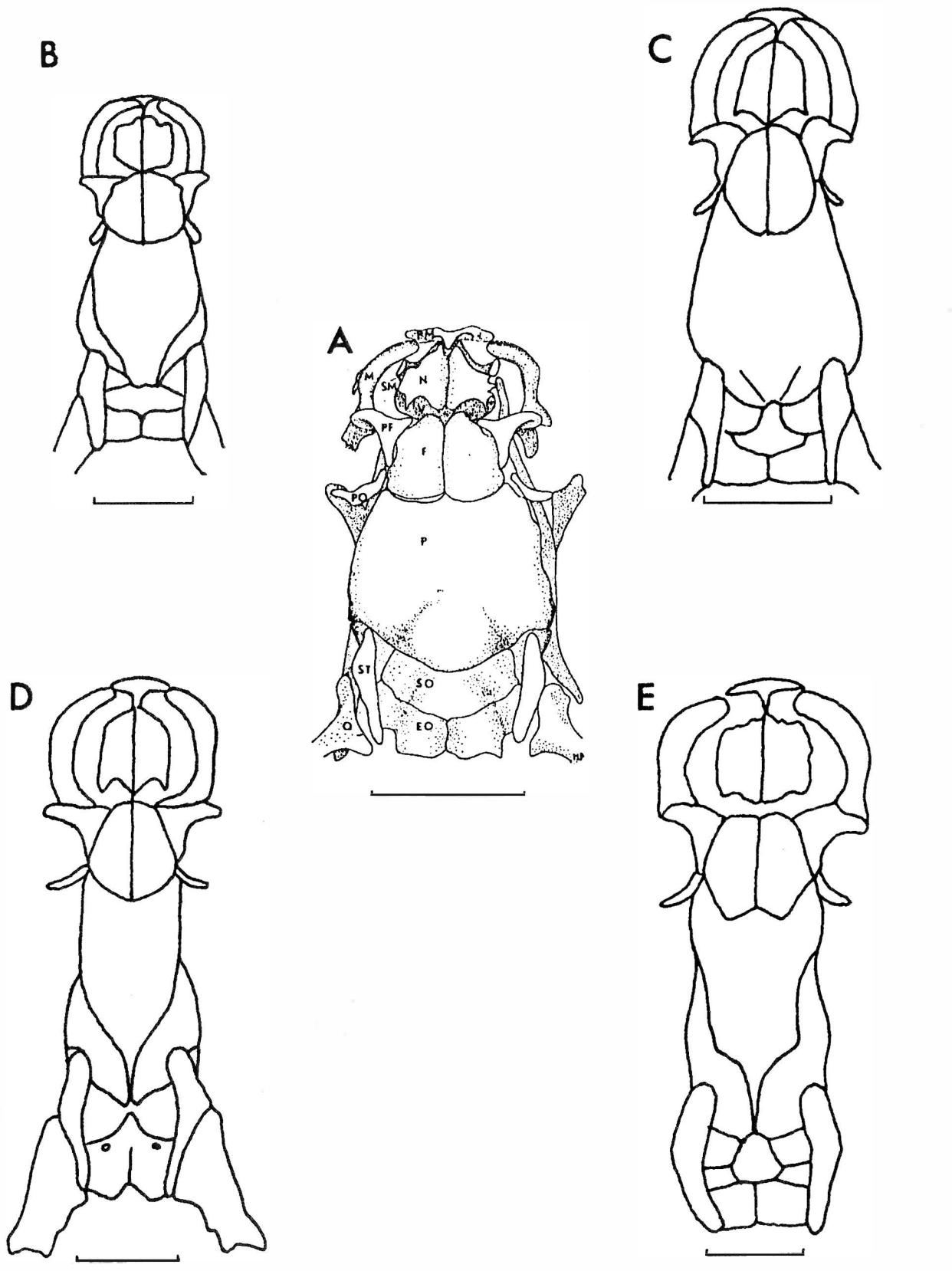

Fig. 1. Dorsal views of skulls of *Lycophidion*: A. *L. ornatum* (MRAC RG. 20950 Lwiro, Kivu, Zaire: after Bourgeois, 1968, Fig. 92); B. *L. irroratum* (NMZB 7918 New Tafo, Ghana); C. *L. taylori* (NMZB 10350 Haud, Somalia - paratype); D. *L. depressirostre* (NMZB 7920 Mareri, Somalia); E. *L. capense jacksoni* (NMZB 130 Kaianja, Uganda). Key to abbreviations for bones: EO = exoccipital; F = frontal; M = maxillary; N = nasal; P = parietal; PF = prefrontal; PM = premaxillary; PO = postorbital; Q = quadrate; SM = septomaxillary; SO = supraoccipital; ST = supratemporal. The line indicates 3 mm to scale.

and recorded 9+20 maxillary, 15 palatine, 24 pterygoid and 6+21 dentary teeth. The other specimen from this locality has 8+21 maxillary teeth, while Hughes has recorded 19-24 posterior maxillary teeth for BM1949.2.1.80-82 from Haud, Somalia.

Underwood (pers. comm.) has reported the dentition of a *L. taylori* paratype (BM 1949.1.2.83) as maxillary left 7+16, right 8+16; palatine 12; pterygoid 22; dentary 6+21. Two more paratypes (BM 1949.1.2.78-79) have maxillary dentition 8+12 and 7+11 respectively.

Bourgeois (1968) illustrated the skull of a *L. capense jacksoni* from Kivu, Zaire: it has 8+17 maxillary, 12-14 palatine; 20 pterygoid and 7+? dentary teeth. Broadley found 8+17 maxillary teeth in MF 2499 from Adi Ugri, Ethiopia. Underwood found 8+12, 8+14 and 8+16 maxillary teeth in BM 95.12.12. 9-11, and Hughes has recorded a range of 13-19 posterior maxillary teeth (n=32) in this taxon. Three specimens of the typical form from Zimbabwe have 7-8 + 14-17 maxillary, 13 palatine, 20 pterygoid and 7-9 + 19-22 dentary teeth. Hughes has found a range of 14-18 posterior maxillary teeth in *L. c. loveridgei* (n=9).

It does seem that *L. depressirostre* can be reliably distinguished from *L. taylori* and *L. capense* on the number of posterior maxillary teeth (19-24 versus 11-19).

11. Hemipenis. Branch (1976) has described and illustrated the hemipenis of *L. capense capense* from the Transvaal and has pointed out that the description of the retracted organ by Bogert (1940) was based on a Tanzanian specimen of *L. depressirostre*, which differs from *L. capense* in having two enlarged basal spines. Branch (pers. comm.) has examined the retracted hemipenis of an adult male *L. taylori* and finds it indistinguisable from that of *L. capense.*

SYSTEMATIC ACCOUNT

LYCOPHIDION IRRORATUM (Leach, 1819)

Coluber irroratus Leach, 1819, in Bowdich, T.E., Mission from Cape Coast Castle to Ashantee: 494 (Fantee, Ghana).

? *Lycophidion ornatum* (part, not Parker) Witte, 1966: 63.

Lycophidion depressirostre (part) Laurent, 1968: 472.

Lycophidion irroratum Hughes, 1983: 472.

The paratype of *L. depressirostre* from Yei, Sudan (FMNH 58321) differs from that species in having two apical pits on the dorsal scales, and is therefore assigned to *L. irroratum.* This specimen is a male with 17-17-17 dorsals, 164 ventrals and 38 subcaudals, the latter counts falling at the lower limits for *L. irroratum.* Hughes (1983) has previously recorded this species from Sudan and the Garamba National Park in north-eastern Zaire (MAC 20125 - Gangala na Bodio).

IRScNB 4768/2 from the Utukuru River in the Garamba National Park (close to the Sudanese border) was identified by Witte (1966) as a *L. ornatum*, but this 290 mm female snake has only 160 ventrals and 32 subcaudals and could be another *L. irroratum.*

LYCOPHIDION ORNATUM Parker 1936

Lycophidion ornatum Parker, 1936, Novit. Zool., 40: 122 (Congulu, Angola); Laurent, 1956: 116 and 1968: 470; Pitman, 1974: 83 (part); Spawls, 1978: 3.

Lycophidion capense capense (not A. Smith) Loveridge, 1936: 241 (part).

Lycophidion capense ornatum Loveridge, 1942: 266.

Diagnosis. Postnasal usually separated from first upper labial. Dorsal scales with single apical pits, in 17-17-17 (rarely 17-17-15) rows; ventral and subcaudal counts, see Table 1. Dark grey-brown stippled with white, except for two rows of dark dorsal spots; a well defined pale band round the snout forks behind the eye, the lower branch terminating at the angulus oris. Skull short, lacking parietal crests.

Size. Largest male (MCZ 40469 - Sipi, Mt. Elgon, Uganda.) 377+66 = 443 mm; largest female (NMK 1842 - Nyambeni Hills, Kenya) ca. 540+50 mm.

Localities. SUDAN. Gilo (Laur., 1968) FMNH 62307. UGANDA. Bugoye (Laur., 1968) MCZ 48191: Bukalasa-Mengo BM 1960.1.6.61; Butoha BM 1969. 2911; Bwamba Forest LACM 121606-7; Gulu (Laur., 1968) MCZ 47827; Inpenetrable (Kayonsa) Forest BM 1934.12.15.557; LACM 35085; Kianja BM 1960.1.6.60; Kigezi District (Laur., 1968) MCZ 39966; Mabira Forest BM 1960.1.6.59; Muko (Laur., 1968) MCZ 42686; Mushongero MCZ 48192; Nyakabande (Laur., 1968) MCZ 48303; Nyarusiza BM 1960.1.6.78; Rukaraba BM 1960. 1.3.47; Rutoma BM 1969.2910; Sango Bay Forest LACM 39223, 39225-6; Sipi, Mt. Elgon (Laur., 1968) MCZ 40468-70. KENYA. Chuka CAS 122286, 122314-5; NMK 1664, 1666, 1826; Kakamega Forest (Laur., 1968) BM 1962.819; MCZ 40471-3; Karura Forest NMK 1907; Nairobi NMK 1930; Nyambeni Hills NMK 1708, 1710-11, 1714, 1717, 1842-3, 1845.

LYCOPHIDION TAYLORI sp. nov.

Lycophidium capense capense (not A. Smith) Scortecci, 1939: 272.

Lycophidion capense (not A. Smith) Parker, 1949: 54 (part); Lanza, 1972:177.

Lycophidion capense subsp. Laurent, 1968: 476.

Holotype. BM 1949.2.1.76, an adult male from Borama District (43°E:10°N) at ca. 1375 metres. Collected by Col. R.H.R. Taylor, 1932-33 (Fig. 2).

Paratypes. BM 1949.2.1.73, 74, 75, 77, 84 and BM 1955.1.11.39 from Borama District; BM 1949.2.1.72, 79, 83 and NMZB 10350 from Haud; from altitudes between 825 m and 1500 m.

Diagnosis. Postnasal in contact with first upper labial. Dorsal scales with single apical pits, in 17-17-15 rows (17-17-17 in one Belet Amin specimen); ventrals 158-179 in males, 165-184 in females; subcaudals 30-38 in males, 26-30 in females. Posterior maxillary teeth 11-16. Dorsal white markings may be restricted to a reticulate pattern on the snout and sides of the head, with a white upper edge to each dorsal scale, but usually the whole head and dorsum is heavily stippled with white and the lower

lateral scale rows are almost entirely white. Many specimens also have a white nuchal blotch or collar, which may completely encircle the neck. Skull moderate, without well defined parietal crests.

Etymology. The name *L. taylori* is a patronym in the genitive singular, honouring Colonel R.H.R. Taylor, whose collections made along the boundary between northern (formerly British) Somalia and Ethiopia in 1932/33 were a major contribution to our knowledge of the herpetofauna of this region.

Description. (Paratype variations in parentheses). Supralabials 8, the first in contact with the postnasal, the third, fourth and fifth entering the orbit; infralabials 8, the first 5 (4-5) in contact with the anterior sublinguals; preocular 1; postoculars 2; temporals 1+2. Dorsal scales with single apical pits, in 17-17-15 rows; ventrals 175 (161-175 in males; 169-184 in females); cloacal entire; subcaudals 34 (30-36 in males; 26-30 in females). Maxillary teeth 7+11 to 8+16.

Colouration. Dorsum dark brown, snout and sides of head with a reticulate pattern in white; an irregular white nuchal collar 5 to 9 scales wide dorsally, narrowing to 3 ventrals wide below; dorsal scales white-tipped, the outer two rows more than 50% white and ends of ventrals largely white, forming a pale ventrolateral band which extends to the tail tip. White collars present in two paratypes, large white nuchal blotches present in three, small white nuchal crossbars present in two, no white nuchal markings in three. In most paratypes the head is stippled or mottled with white to a varying extent, the dorsals are often stippled with white and the ventrolateral scales are heavily infuscated with white. The ventrum is uniform brown apart from some white stipple on the chin and white lateral edges to the ventrals.

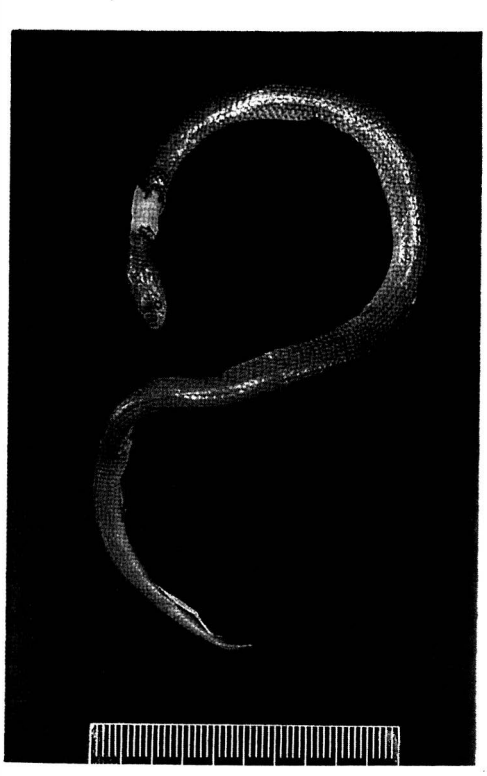

Fig. 2. *Lycophidion taylori*: dorsolateral view of the holotype, scale in mm (BM 1949.2.1.76 from Borama District, Somalia). Photo: Natural History Museum, London.

Size. Holotype 210+27 mm; largest male (BM 1949.2.1.79) 280+34 = 314 mm; largest female (BM 1949.2.1.83) 450+46 mm, tail tip missing.

Additional material examined. SOMALIA. Afgoi (Scor., 1939) MSNG 46360; Balad (Scor., 1939) MSNG 46301 (2 males with V 169-170, SC 37); Belet Amin (Scor., 1939) MSNG 46350 (27 specimens, one male has V 158 and supralabials 7 (3,4) on one side); Harrar MSNG —. KENYA, 2 km southwest of Kakuma CAS 131002 (male with V 171, SC 31 and a broad white collar 9 scales wide encircling the neck). CHAD. Abéché MNHN 9893 (female with 192 ventrals, 27 subcaudals and a broad white collar). SENEGAL. 15 km N of Kaffrine, Sine-Saloum USNM 161990 (female with 179 ventrals, 24 subcaudals, but no white collar).

Lanza (1972) records two specimens from the Awash National Park, one with the distinctive white collar, but does not give scale counts: they are assumed to be *L. taylori*.

LYCOPHIDION DEPRESSIROSTRE Laurent

Lycophidium jacksoni Boulenger (part), 1893: 340.

Lycophidium acutirostre (not Günther) Sternfeld, 1912: 268.

Lycophidion capense (not A. Smith) Loveridge, 1929: 20 (part); Scortecci, 1930: 16 (part) and 1931: 204 (part); Parker, 1949: 54 (part); Pitman, 1974: 82 (part).

Lycophidion capense capense (not A. Smith) Loveridge 1933: 233 (part) and 1956: 43; Bogert, 1942: 2.

Lycophidion capense >< *acutirostre* Loveridge, 1936: 242.

Lycophidion capense uzungwensis (not Loveridge) Bogert, 1940: 31.

Lycophidion depressirostre Laurent, 1968: 472 (Torit, Sudan); Spawls, 1978: 4; Hoevers & Johnson, 1982: 185.

Lycophidion capense subsp. Laurent, 1968: 476 (part).

Diagnosis. Postnasal in contact with first upper labial (rarely spearated in Tanzanian material). Dorsal scales with single apical pits, in 17-17-15 rows; ventral and subcaudal counts, see Table 1. Posterior maxillary teeth 19-24. Brown, each dorsal scale with pale speckling distally; an ill-defined speckled pale band round the snout and often some pale speckling on top of the head; ventrum dark except for some pale stippling on chin and pale lateral edges to the ventrals. Skull elongate, with strongly developed curved parietal crests.

Size. Largest male (MCZ 53355 - Torit, Sudan) 315+49 = 364 mm; largest female (MCZ 53357 - Torit, Sudan) 440+42 = 482 mm.

Localities. SUDAN. 30 km N of Juba ZFMK 26028; Torit (Lov., 1956; Laur., 1968) FMNH 58414, 62338-9; MCZ 53347-8, 53350, 53352, 53354-7; ZMB 876. SOMALIA. No precise locality (Scor., 1930) MF 23785; Afgoi MF1106-8; Eggi MF 2297; Giohar MF 5377; Haud (Park., 1949; Laur., 1968) BM 1949.2.1.80-82; Mareri (Hoevers & Johnson, 1982) CAS 153329-30, MF 27062-3; Oddur MF 23753-5; Wagga, Goohi Mts (Park., 1949) BM 1905.11.7.44. ETHIOPIA. Aware Melka (Park., 1949; Laur. 1968 - as *L. capense*

subsp.) BM 1916.6.24.4-5; Bourkia MNHN 1905-191; Harar (Park., 1949) BM 1909.12.4.4. UGANDA. Kampala (Lov., 1933; Laur., 1968) MCZ 30115. KENYA. No precise locality ZMB 22455; Changamwe (Lov., 1936); Giriama NMK 89; Jadini-Diani Beach BM 1960.1.2.16-18; Kaimosi (Lov., 1929) USNM 49388; between Kaimosi and Kapsabet NMK 1547; Kibwezi (Lov., 1936) MCZ 40478; Kilibassi (Bogert, 1942) AMNH 61661; 7 km west of Laisamis CAS 129746; Lamu (Blgr, 1893) BM 87.11.3.15; Malindi (Lov., 1936) MCZ 40481; NMK 1340; Mombasa NMK 90; Mount Kulal LACM 66396; Mount Mbololo (Lov., 1936) MCZ 40480; Moyale BM 1958.1.1.92; Mtoto Andei (Lov., 1929) USNM 48590; Samburu NMK 102; Sankuri (Bogert, 1940) AMNH 50792; Shaffa Dika (Bogert, 1942) AMNH 61644; Sigor MCZ 96857; Sokoki Forest (Lov., 1936); Tana ZMB 15680; Voi BM 98.1.18.13; MCZ 96889-90; NMK 564; Wajir Bor CAS 140310.

LYCOPHIDION CAPENSE JACKSONI Boulenger

Lycophidium jacksoni Boulenger (part), 1893, Cat. Snakes Brit. Mus.,1: 340, pl. XXI, fig. 3 (Kilimanjaro).

Lycophidium abyssinicum Boulenger, 1893. Cat. Snakes Brit. Mus. 1:342, pl. XXII, fig. 1 (Southern Ethiopia). 1895: 536 and 1896a: 553; Sternfeld, 1908: 240.

Lycophidium horstockii (not Schlegel) Günther, 1894: 88.

Lycophidium capense (not A. Smith) Boulenger, 1896b: 216 and 1909: 303; Angel, 1922: 357; Loveridge, 1929: 20 (part); Scortecci, 1930: 16 (part); Parker, 1949: 54 (part).

Lycophidion capense capense (not A. Smith) Loveridge, 1933: 233 (part), 1936a: 23 (part), 1936b: 241 (part), 1942: 268 (part) and 1956: 43 (part).

Lycophidion capense jacksoni Laurent, 1956: 109 and 1968: 474; Spawls, 1978: 4.

Diagnosis. Postnasal in contact with first upper labial. Dorsal scales with single apical pits, in 17-17-15 rows; ventral and subcaudal counts, see Table 1. Posterior maxillary teeth 13-19, usually 15-17. Dark brown, each dorsal scale with a pale apical spot or border, an ill-defined pale band round the snout, but top of head usually immaculate; juveniles pale below, but ventrum darkens from the tail anteriorly, so that adults are dark below except for the throat and free edges of the ventrals. Skull elongate, with well defined angular parietal crests.

Size. Largest male (ANSP 4705 - west of Juba River, Ethiopia) 350+58 = 408 mm; largest females (NMK 315 - Nairobi, Kenya) 530+50 = 580 mm and (NMK 1706 - Nyambeni Hills, Kenya) 541+25 = 566 mm.

Localities. SUDAN. Disa BM 1909.10.15.47; 1967.1880; Gilo (Lov., 1956; Laur., 1968) MCZ 53342; Imurok (Lov., 1956; Laur., 1968) MCZ 53343; Juba (Laur., 1968) FMNH 58500; Katire (Laur., 1968) FMNH 62308; Latome (Lov., 1956; Laur., 1968) MCZ 53344; Li Rangu FMNH 58317; Nimule (Lov., 1956; Laur., 1968) MCZ 53345; Roseires BM 1909.10.15.48; Talodi BM 1930.11.12.8; Terangole (Lov., 1956; Laur., 1968) MCZ 53346; Torit (Lov., 1956; Laur., 1968) MCZ 53349, 53351; Yegiyegi (Lov., 1956) MCZ 53358; Yei (Laur., 1968) FMNH 58322. SOMALIA. Ouarka MNHN 1902-311. ETHIOPIA. No precise locality MNHN 4343 (2); MSNM 1771; "Southern Abyssinia" (Blgr, 1893) BM 73.4.25.15; Adi Ugri MF 167, 2498-9; Anseba "River" MSNG 30244; between Awash and Addis Ababa (Scor., 1930); Danol MSNM 1859 (2); Daroli NMW 19339; Dibessa River Bridge AAM H.389; Endessa MNHN 1905-189; "Eritrea" MF 676; Gambela AAM H.541, 882; Ghinda (Blgr, 1896a) MSNG 29031; Gondar MSNM 1983(2); Harar (Lov., 1936a) FMNH 4026; Hieka MNHN 1905-190; 15 km southeast of Kebre Mengist (R.O.S. Clarke coll.); Lake Asawa BM 1973. 3252; Lake Haramaia (Sternfield. 1908) ZMB 27466; Sheikh Hussein (Blgr, 1895) ANSP 4706; Sidamo Province BM 1975. 2142; west of Juba River (Blgr, 1896b) ANSP 4705; "between Ethiopia and Kenya" (Laur., 1968) USNM 66928. UGANDA. Bisu NMZB 172; Budda Coast (Laur., 1968) AMNH 5259, 24284; Bukalasa NMZB 170; Bugala Island MSNG 30273; Bugoma Forest LACM 39046; Bussu MSNG 30289; 37611A; Butiaba (Laur., 1968) BM 1951.1.3.30, 1960.1.2.20; Bwanba Forest LACM 121604-5; "Eastern Province" BM 1933.9.8.20; Entebbe BM 1901.6.24.45-6; 1960.1.6.62; 1963.952-4; Fort Portal BM 1901.6.24.48, and 40 km north USNM 206992; Gulu BM 1960.1.2.19 (2); Hoima BM 1960.1.6.63; Jinja (Lov., 1933; Laur., 1968) BM 1954.1.11.93-4; MCZ 30116; Kianja BM 1951.1.4.89; NMK 92, 101; NMZB 130; Kampala BM 96.5.28.15-17; Kasiriya NMZB 171; Katebo BM 1960.1.2.4; 1960.1.6.57; Katunguru BM 1951.1.4.91; Lower Semliki BM 1954.1.11.95-6; Lwampanga BM 1960.1.2.5; Masese NMK 528; Mjanji BM 1954.1.4.90; Mount Elgon NMK 655; Nakifulube NMZB 173; Nyenga (Laur., 1968) AMNH 63770-2; Sango Bay Forest LACM 39224; Sebei, Mt Elgon (Lov., 1936b; Laur., 1968) MCZ 40467; Semliki BM. 1954.1.12.32; Sesse Archipelago (Blgr, 1909) MSNG 27756(2), 40762(2); Serere BM 1960.1.6.58; Soroti NMK 100. KENYA. Baringo BM 1901.1.6.4.47; Chemelil CAS 141534, 148000-1, 148036, 150925, 152789, 154411; Chuka, Mt. Kenya NMK 1663, 1665; Kabartonjo CAS 111762; Kabluk CAS 111776-8; Kakamega Forest BH 8464, 8466, 8469; CAS 122741; Kariti (Günther, 1894) BM 93.11.21.47; Kiambu NMK 99; Kijabi (Laur., 1968) FMNH 2430; Kisumu BM 1978.991-3; Kitui District NMK 83; Kilimanjaro (Blgr, 1893) BM 87.11.3.82; Lake Sirgoit (Laur., 1968) SMW R. 3176; Lariagoia Game Refuge LACM 63148; Lemek Valley (Angel, 1922) MNHN 1922-34; Lumbwa MCZ 160073-4 and 7 km northwest MCZ 159772-3; Malindi (?) NMK 882-3; 12 km southwest of Maralal LACM 60078; Mombasa (?) MNHN 1901-450; Mount Kenya to Muranga USNM 41133; Mumias CAS 141788, 147942, 147944; Muranga (formerly Fort Hall) BM 1906.8.25.2; Mweiga LACM 50630; Mzima Springs FMNH 79146; Nairobi (Angel, 1922; Lov., 1936a; Laur., 1968) MF 6947; MNHN 1922-35, 1940-182 to 185; NMK 88, 94-7, 315, 532, 569, 1901; NMW 19335; USNM 40966-7; ZMUC R. 60507; 27 km southeast of Nakuru CAS 85729; Ndabibi NMK 1906; Nyambeni Hills NMK 1698, 1702-3, 1706-7.1715, 1718, 1764-5, 1767-8, 1780-1; Parklands (Laur., 1968) MCZ 18190; UMMZ 61206; Ramuruti NMK 98; 5 km north of Sergoit LACM 63384; Sigor MCZ 96858; Thika NMK 2085; Wambuga (Laur., 1968) USNM 40885.

Remarks. There are three specimens of *L. c. jacksoni* from the Kenya coast (Malindi and Mombasa). If the locality data is correct and these specimens have not been accidentally translocated by man, then this form is at least parapatric with *L. c. loveridgei*. This suggests that the latter form may be a full species. On the other hand, the high ventral counts from

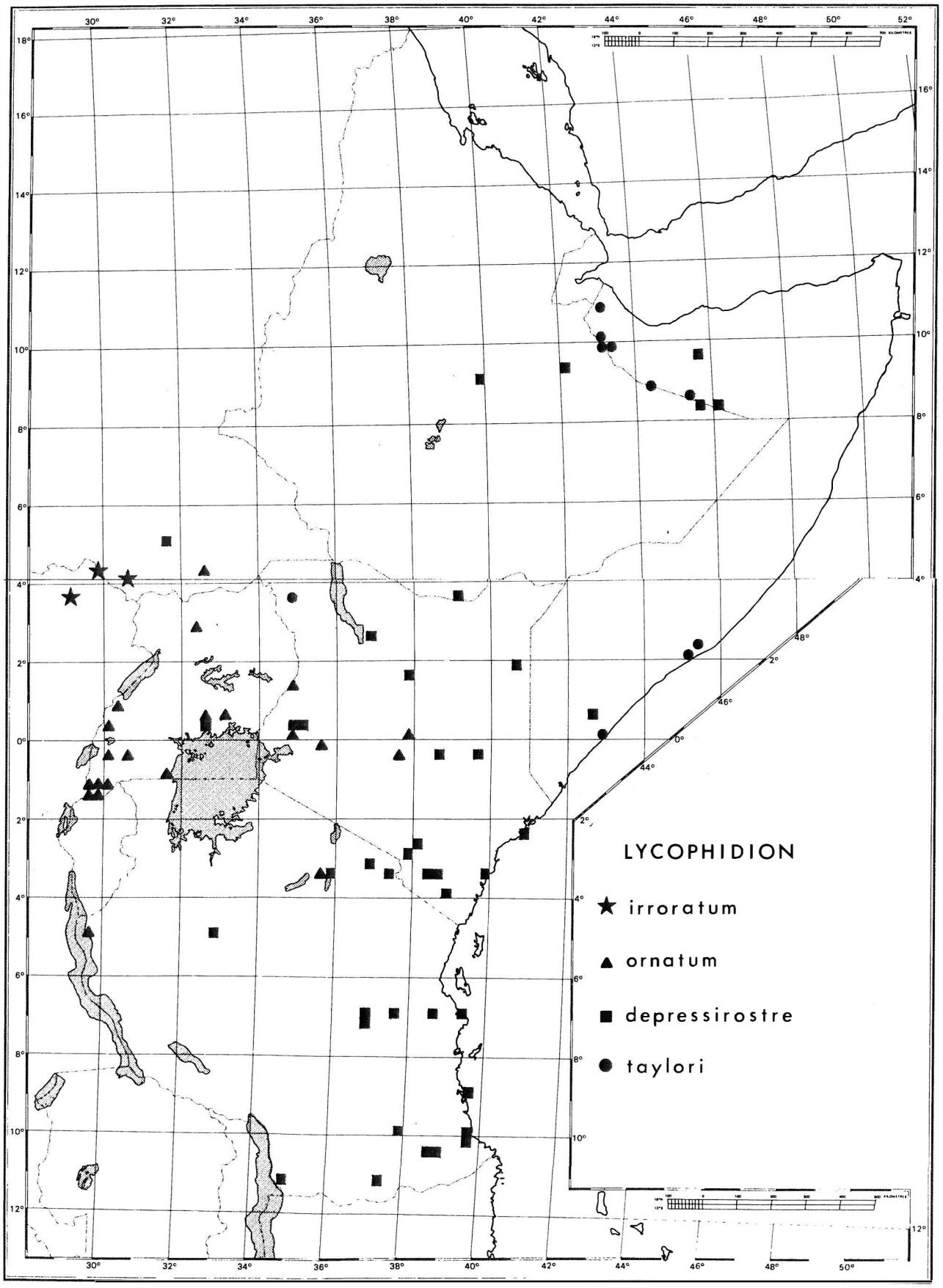

Fig. 3. Distribution of various *Lycophidion* species in northeastern Africa.

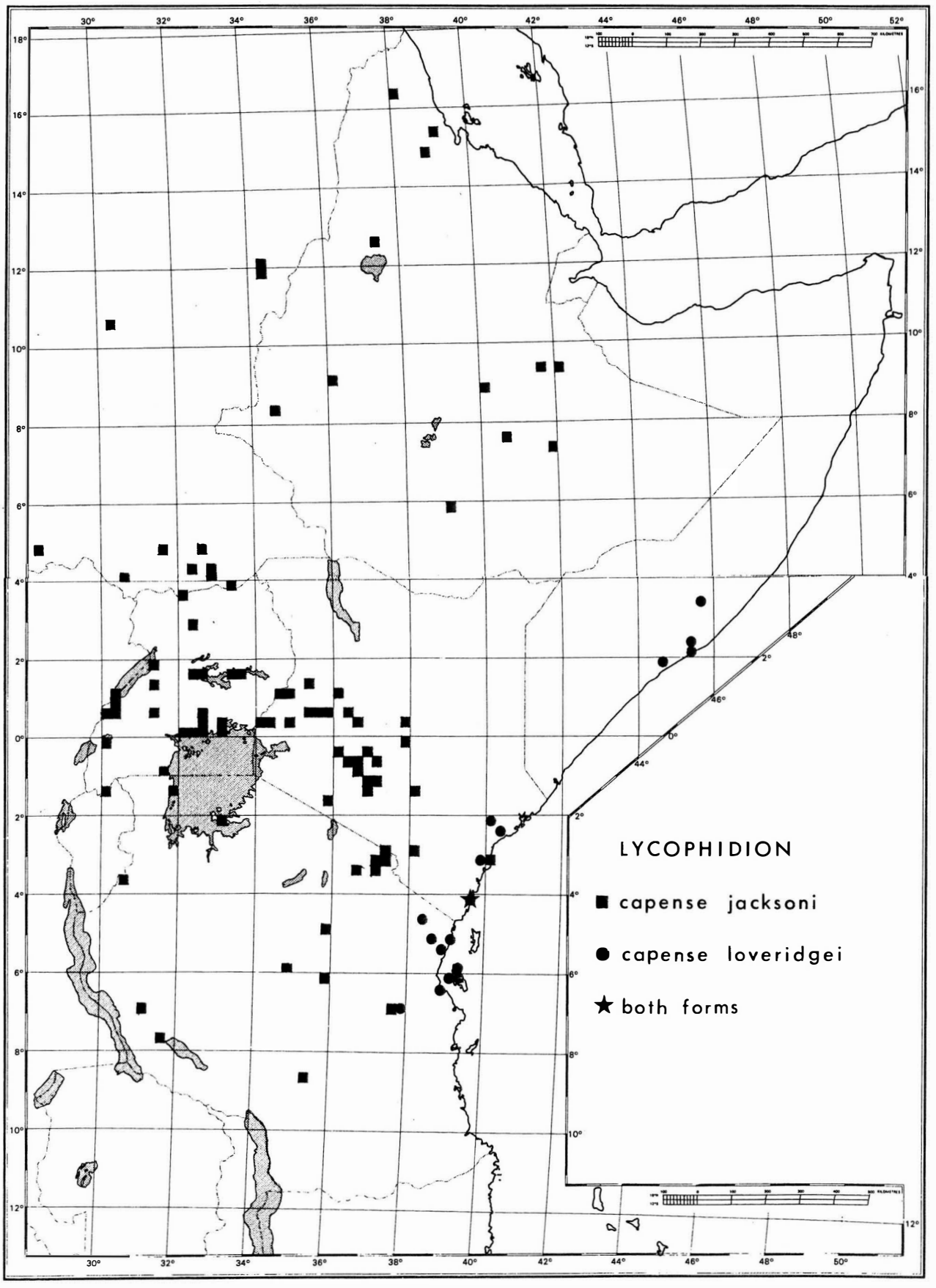

Fig. 4. Distribution of *Lycophidion capense* in northeastern Africa.

"north" populations of *L. c. jacksoni* (Table 1) suggest possible intergradation with *L. c. loveridgei*: however, the latter taxon is still readily distinguished by its high subcaudal counts.

LYCOPHIDION CAPENSE LOVERIDGEI Laurent

? *Lycophidium semicinctum* (not Duméril & Bibron) Scortecci, 1930: 16.

Lycophidion capense capense (not A. Smith) Loveridge, 1936*b*: 241 (part) and 1942: 268 (part).

Lycophidion capense loveridgei Laurent, 1968, Bull. Mus. comp. Zool.Harv. 136: 476 (Amani, Usambara Mts, Tanzania); Spawls, 1978: 4.

Diagnosis. Postnasal in contact with first upper labial. Dorsal scales with single apical pits in 17-17-15 rows; ventrals 195-209 in males, 195-221 in females; subcaudals 47-58 in males, 40-55 in females. Posterior maxillary teeth 14-18. Dark brown, each dorsal scale with a pale apical spot and sometimes white stipple also; head shields with pale stippling or vermiculation; ventrum white in juveniles, darkening from the tail, but with a pale throat and white stippling on ventrals. No skull has been examined.

Size. Largest male (MF 1105 - Genale, Somalia) 410+83 = 493 mm; largest female (MCZ 40475 - Ngatana, Kenya) 415+62 = 477 mm.

Habitat. Spawls (1978) records this form from both forest and savanna in the coastal strip.

Localities. SOMALIA. Balad (Scor., 1930); Eggi MF 2288; Genale MF 1105; Mogadiscio MF 901. KENYA. Jilore Forest (Spawls, 1974); Kilifi (Spawls, 1974); Likoni, on mainland opposite Kilindini (Lov., 1942; Laur., 1968) MCZ 48266; Mkonumbi (Lov., 1936b; Laur., 1968) MCZ 40474; Mombasa (Spawls, 1974); Ngatana (Lov., 1936b; Laur., 1968) MCZ 40475.

KEY TO THE GENUS *LYCOPHIDION* IN NORTHEASTERN AFRICA

1a. Apical pits on dorsal scales paired.....*irroratum*

1b. Apical pits on dorsal scales single 2

2a. Dorsal scales in 17 rows up to the vent; first labial separated from postnasal.....*ornatum*

2b. Dorsal scale rows reduced to 15 before the vent; first labial in contact with postnasal.....3

3a. Dorsal scales dark with pale stippling, or with a white mark on the upper distal edge of each scale; ventrum dark throughout life except for white stipple on chin and throat, pale edges and sometimes ends to the ventrals; ventrals usually less than 175 in males and 180 in females.....4

3b. Dorsal scales dark with an apical white spot; ventrum white in juveniles, dark in adults except for a light patch.on the throat and pale free edges to the ventrals; ventrals.usually more than 175 in males and 180 in females.....5

4a. Dorsal scales with white stippling covering the entire scale or restricted to a white mark on the upper distal edge of each scale, white stippling usually heavier on lower flanks and ends of ventrals; often a white blotch or collar on neck.....*taylori*

4b. Dorsal scales with white stippling restricted to the apex, not much heavier on lower laterals; no white blotch or collar on neck.....*depressirostre*

5a. Subcaudals 34-48 in males, 27-37 in females; distribution in highlands.....*capense jacksoni*

5b. Subcaudals 51-57 in males, 42-45 in females; distribution in coastal lowlands.....*capense loveridgei*

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HERPETOLOGICAL JOURNAL, Vol. 3, pp. 19-25 (1993)

INDIVIDUAL GROWTH AND ALLOMETRY OF YOUNG GREEN TURTLES (*CHELONIA MYDAS* L.)

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ABSTRACT

Twelve young green turtles (*Chelonia mydas* L.) varied considerably in growth rate when fed satiation rations (mean specific growth rate ranged from 0.01045-0.01462), but individual animals had constant specific growth rates. The following mean morphometric relationships were found: $\log y = -3.42 + 2.94 \log x$ (where y = live weight (g) and x = carapace length mm)); $\log y = 0.069 + 0.93 \log x$ (where y = carapace width (mm) and x = carapace length (mm)); $\log y = -0.115 + 1.01 \log x$ (where y = plastron length (mm) and x = carapace length (mm)); $\log y = -0.417 + 2.04 \log x$ (where y = plastron area (mm^2) and x = plastron length (mm)). Growth was isometric throughout the period of study. There was no significant relationship between the allometric coefficients of the individual turtles and their specific growth rates or between carapace length/width ratios and specific growth rates. No turtle shape, or pattern of shape/weight change is associated with high or low rates of specific growth. The plastral scute patterns of green turtles are stable over time and are individually identifiable. Carapace scutes grow asymmetrically, with little posterior or medial growth, most scutal growth taking place anteriorly and laterally. Photocopying of the plastron and scute patterns as a growth/identity technique was shown to be effective and inexpensive.

INTRODUCTION

This paper reports part of an investigation of individuality of growth and nutrition in young green turtles *Chelonia mydas* L. Much study of the physiology and biochemistry of animals, including reptiles, has been concerned with the estimation of average responses, using statistical techniques to eliminate obscuring variability. This approach has been enormously valuable, but there are circumstances in which study of individual variability may answer questions which are not easily answered by the usual techniques of pooling results and calculating means. A proponent of the study of individuality of response in marine biology has been J.C. Aldrich of Trinity College, Dublin (e.g. Aldrich, 1975, 1986; Aldrich & Regnault 1990).

Experience with previous nutritional studies on young green turtles (Davenport & Oxford, 1984; Davenport *et al.*, 1989) led to the suspicion that there was substantial variation in inherent growth rate amongst turtles, even though there seemed to be no dominance hierarchy of the sort that affects growth in crocodiles (e.g. Davenport *et al.*, 1990), and the animals were well fed. However, although satiation rations were sometimes used in these earlier studies, they were not supplied continuously to the animals, so it remained possible that larger turtles took a disproportionate amount of available food on some occasions, thereby suppressing the growth of smaller animals and exaggerating variability. It was decided that a group of young turtles should be studied intensively and individually during a period of several months when they would always be fed to satiation. The objectives were (1) to determine the degree of variability in growth rate and allometric relationships; (2) to find out whether there were any morphometric differences between 'good' and 'poor' growers; (3) to establish whether there were correlations between growth rate, appetite, metabolic rate and assimilation of nutrients. This communication addresses objectives (1) and (2); the third objective will be discussed in a later paper.

MATERIALS AND METHODS

COLLECTION, MAINTENANCE AND FEEDING

Twelve hatchling green turtles (of unknown but certainly mixed parentage and unknown sex) were sent from the Lara Reserve, Cyprus to the U.K. on 21st October 1989. At this stage they were 40-60 days posthatching. On arrival in the U.K. they were identified by placing hoops of coloured bell wire (four colours available) around the roots of the foreflippers. They were held in a large plastic aquarium (Fastank; 6m x 1m x 1m) filled with sea water (33‰) at a temperature of 25±1°C. The sea water was gradually replaced by a trickle supply; the contents of the tank were circulated through a biological filter at a flow rate of about 5 l min^{-1}. Throughout the experimental period the animals were fed daily on trout pellets. Great care was taken to ensure that the trout pellets were always offered in satiation amounts (i.e. that the animals were always given more food than they could eat), and that no feeding hierarchy could develop to interfere with feeding. The latter objective was achieved by offering trout pellets on large trays suspended a few centimetres below the water surface in the holding tank. The pellets were spread out over a large area so that each animal could feed in undisturbed fashion. Antagonistic behaviour between the turtles during feeding sessions was rare and did not seem to be related to body size; small turtles were as likely to bite bigger animals as the latter were to be the aggressors.

WEIGHING AND MEASURING

Weighing and measuring required handling of the turtles. This was thought to be stressful to a certain extent, so weighing (the least time-consuming procedure) was carried out most frequently (at intervals of roughly seven days). Animals were weighed on top-loading balances (to the nearest 0.1 g).

At intervals of 3-4 weeks the animals were measured in the following manner. Firstly, the plastron surface appearance of each turtle was recorded by photocopying the animal, ventral surface down, on a photocopier (the eyes were shielded during this process). Photocopies are not exactly the same size as the original, but the difference (about 1-2%) is consistent for a given machine; pieces of graph paper were also photocopied to allow precise measurement of plastron length and plastron area. Plastron areas were estimated (to the nearest 5 mm^2) by use of a planimeter (accuracy ca. 1%).

Next, the animals were photographed from above by a Pentax 35 mm camera fitted with a macro lens and mounted on a tripod. The field of view included a scale. Measurements of carapace length were made by inspecting negatives under a binocular microscope fitted with an eyepiece graticule; outlines of carapace scute patterns were traced under a *camera lucida* attached to the microscope. Linear dimensions were recorded in mm (to the nearest 0.1 mm). Ideally shell height would have been measured too. However, young green turtles change their shell heights to some extent when breathing (the shell is flexible) and a stress-free technique applicable to the full size range studied could not be devised.

RESULTS

Growth Rates

Fig. 1 shows the patterns of growth in the 12 turtles over a period of 176 days. Clearly, at this early state of their development, turtles fed a satiation ration exhibit an accelerating (exponential - see Fig. 2) weight increase, with no hint of tailing off. It is also clear that there is considerable variation in growth rate. To investigate this variation further, specific growth rates (g) were calculated as follows:

$$g = \frac{\ln (Wt/Wo)}{t}$$

where g = specific growth rate, t = elapsed time between weight measurements, Wo = initial weight, Wt = weight after time t.

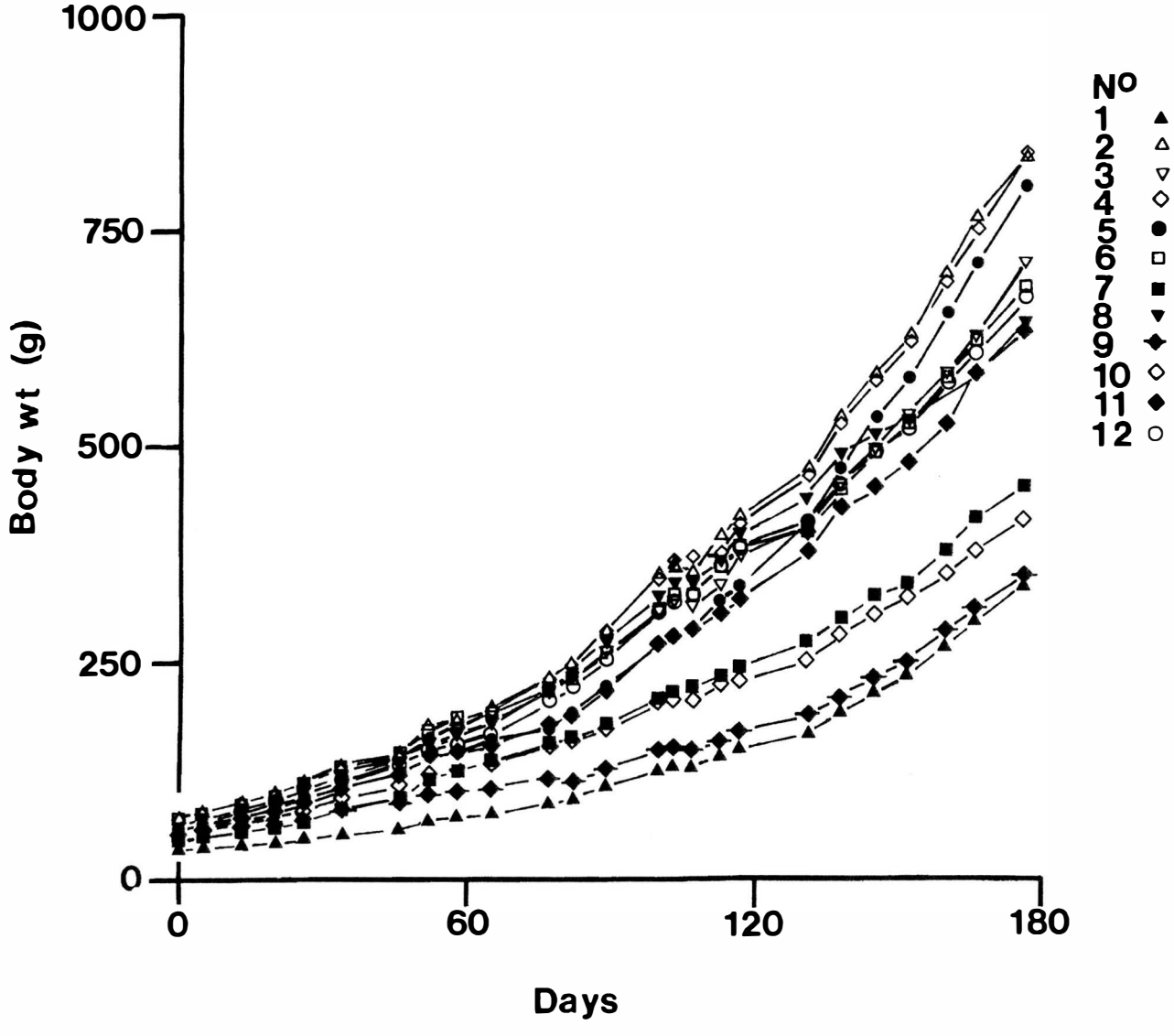

Fig. 1.Growth of 12 specimens of *Chelonia mydas* during the period of study. Symbols identify individual animals.

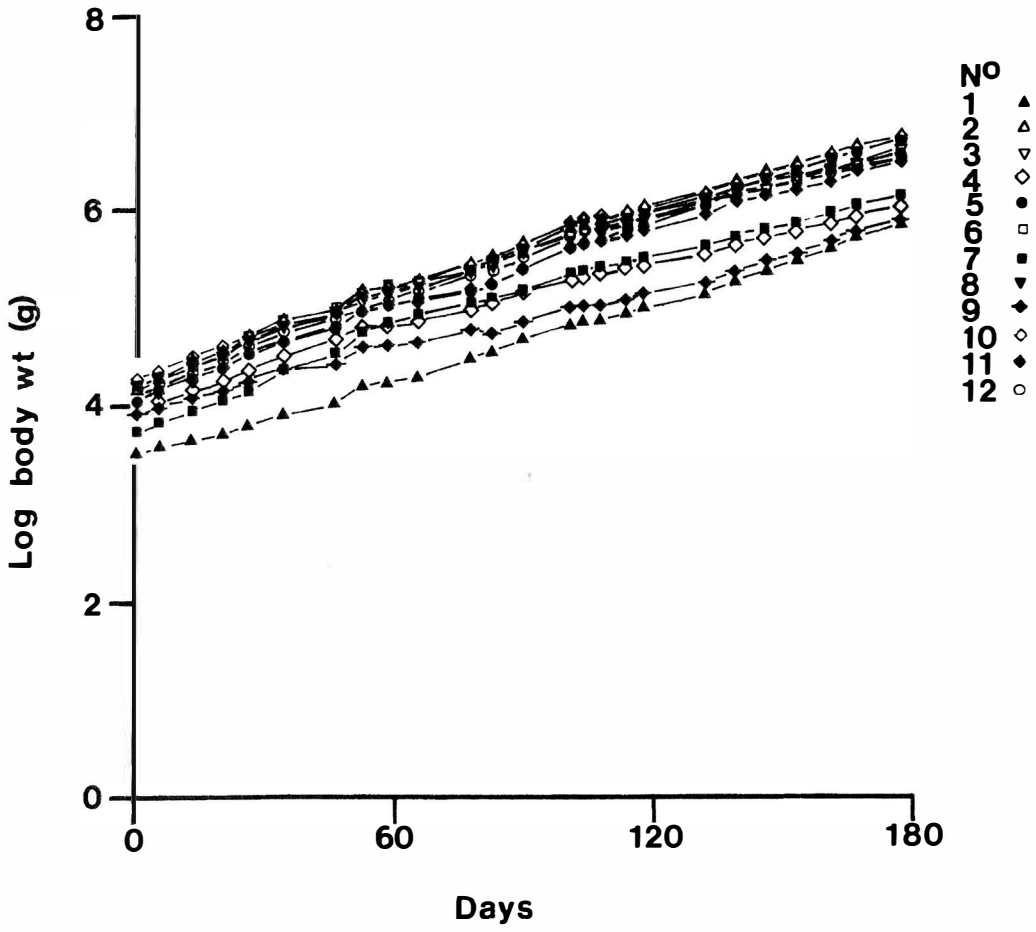

Fig. 2.Growth of 12 specimens of *Chelonia mydas*. Body weights have been logarithmically transformed (ln). Symbols as in Fig. 1.

Values of specific growth were calculated in two ways. Firstly they were calculated for each inter-weighing interval, and then an overall mean value obtained. Secondly, the weights were replotted as ln body weights (Fig. 2) and linear regression carried out upon the data. From Table 1 it may be seen that there is reasonable correspondence between these two approaches.

Although green turtles vary considerably amongst themselves in their growth rates, individual animals have remarkably constant specific growth rates when fed satiation rations (Fig. 2; Table 1); this results in a strong correlation between the rank order of their body weights at the beginning of the experiment and the rank order at the end (Spearman rank correlation coefficient: $r_s = 0.895$; $P<0.002$).

Allometric Relationships

The allometric equation $y=ax^b$ is used in comparisons of proportions of animals (see Gould, 1966; Reiss, 1989 for discussion). This equation can be conveniently rewritten as $\log y = \log a + b \log x$, so that log-transformed data may be plotted graphically to yield straight line relationships. If the proportions of an animal do not change as it grows (isometric growth or geometric similarity) then, if y and x are linear dimensions $b = 1$. If y is an area and x a length $b = 2$. If y is a weight (or volume) and x a length $b = 3$. In each case the b values were compared with the null hypothesis (isometric growth) using a t-test:

$$t = \frac{ß - b}{s/\Sigma(x-\bar{x})^2}$$

where ß = expected slope if growth is isometric; b = actual slope; s = standard deviation of b; $\bar{x}$ = mean of values of x. t values are compared with critical t values for n-2 degrees of freedom.

In recent years there has been some criticism of simple model I regression analysis of this type (see Rayner (1985) for discussion), but if the correlation coefficients for the data are very high (as is the case in this study) there are negligible differences between the b values derived from model 1, model 2 or reduced major axis models. Values of the exponent b in the model 2 regression equations can be found by using the values of r, the correlation coefficient, and b in the model 1 equation (from rb).

The mean carapace length: live weight relationship from the green turtles investigated here was as follows:

$$y = 0.00038\, x^{2.94},\ (r^2 = 0.996;\ n = 9)$$

where y = live weight (g) and x = carapace length (mm).

A t-test against the null hypothesis showed that the b value (2.94; S.D.=0.068) did not differ significantly from 3, so the mean relationship indicates that young green turtles grow isometrically. Table 2 shows the carapace length : live

Turtle No.	Wg (g) (day 0)	Wt (g) (day 217)	Mean specific growth rate (*A*)	Mean specific growth rate (*B*)
1	33.5(12)	338.9(12)	0.01358 (10)	0.01313 (9)
2	65.4(2)	839.3(2)	0.01470 (2)	0.01405 (3)
3	58.9(5)	711.9(4)	0.01444 (3)	0.01382 (5)
4	51.4(9)	415.7(10)	0.01152 (11)	0.01150 (11)
5	56.7(6)	803.8(3)	0.01552 (1)	0.01462 (1)
6	64.7(3)	681.9(5)	0.01407 (7)	0.01302 (10)
7	42.0(11)	454.8(9)	0.01383 (8)	0.01329 (8)
8	64.3(4)	645.2(7)	0.01365 (9)	0.01357 (7)
9	49.9(10)	350.9(11)	0.01100 (12)	0.01045 (12)
10	70.5(1)	840.2(1)	0.01444 (4)	0.01391 (4)
11	52.3(8)	633.2(8)	0.01440 (6)	0.01372 (6)
12	56.6(7)	669.9(6)	0.01441 (5)	0.01413 (2)

TABLE 1. Mean specific growth rates of individual young green turtles *Chelonia mydas*). Calculated either as mean value estimated from growth rates calculated for each interweighing interval (*A*), or from linear regression analysis of all weights recorded during the period of observation (*B*). Figures in parentheses represent rank orders of weight and growth rate, with 1 being highest and 12 lowest.

weight relationships for the twelve individual animals. In no case was there any statistically significant deviation from isometric growth, although 11 out of the 12 animals showed *b* values slightly below 3, suggesting that a longer study might eventually reveal slight negative allometric change in body weight, with weight increasing a little more slowly than carapace length.The mean carapace length: mean maximum carapace width relationship was as follows:

$$y = 1.72\, x^{0.930},\ (r^2 = 0.997;\ n = 9)$$

where y = carapace width (mm) and x = carapace length (mm).

The *b* value (0.93; S.D.=0.019) does not differ significantly from 1 (t=1.466; P>0.1) so from regression analysis it is evident that there is no statistically significant deviation from isometry. However, 11 out of 12 turtles showed an increased carapace length: carapace width ratio during the course of the study. The mean initial (1.16) and final (1.23) ratios differ significantly (P<0.001; t-test preceded by F-test for comparability of variance). Taken together, these findings indicate that a more prolonged study (or possibly a study involving more turtles) would reveal a positive allometric relationship, with carapace length increasing faster than carapace width (this is compatible with the slight tendency to decreased weight with increasing carapace length indicated above).

The relationship between carapace length and plastron length was as follows:

$$y = 0.767\, x^{1.01},\ (r^2 = 0.992;\ n = 8)$$

where y = plastron length (mm) and x = carapace length (mm).

In this case the *b* value (1.01; S.D.=0.034) is very close to 1 (t=0.125, P>0.05), so the relationship between plastron length and carapace length is isometric. There was no statistically significant difference between the mean carapace length : plastron length ratios measured at the start and finish of the course of the study (1.22 on Day 0; 1.21 on Day 217). Plastron area was related to plastron length by the following equation and again confirms isometry as the *b* value (2.04; S.D.=0.035) is not significantly different from 2:

$$y = 0.383\, x^{2.04},\ (r^2 = 0.998;\ n = 9)$$

where y = plastron area (mm^2) and x = plastron length (mm).

Regression analysis was performed to determine whether there was any relationship between the allometric coefficients of the individual turtles and their specific growth rates, and between carapace length/width ratios and specific growth rates. No significant relationships were revealed (r^2 values were very

Turtle No.	Equation	r^2	t	significance
1	$\log y = -3.42 + 2.92 \log x$	0.994	0.367	NS
2	$\log y = -3.42 + 2.94 \log x$	0.992	0.239	NS
3	$\log y = -3.32 + 2.88 \log x$	0.995	0.610	NS
4	$\log y = -3.25 + 2.84 \log x$	0.995	0.682	NS
5	$\log y = -3.34 + 2.91 \log x$	0.995	0.480	NS
6	$\log y = -3.54 + 2.99 \log x$	0.995	0.037	NS
7	$\log y = -3.77 + 3.10 \log x$	0.995	0.377	NS
8	$\log y = -3.29 + 2.88 \log x$	0.995	0.607	NS
9	$\log y = -3.55 + 2.96 \log x$	0.990	0.103	NS
10	$\log y = -3.12 + 2.82 \log x$	0.993	0.854	NS
11	$\log y = -3.17 + 2.81 \log x$	0.993	0.833	NS
12	$\log y = -3.32 + 2.89 \log x$	0.995	0.555	NS

TABLE 2. Carapace length (x, mm) and live weight (y, g) relationships in young green turtles (*Chelonia mydas*). Critical t at P<0.05) is 2.365 (7 d.f.)

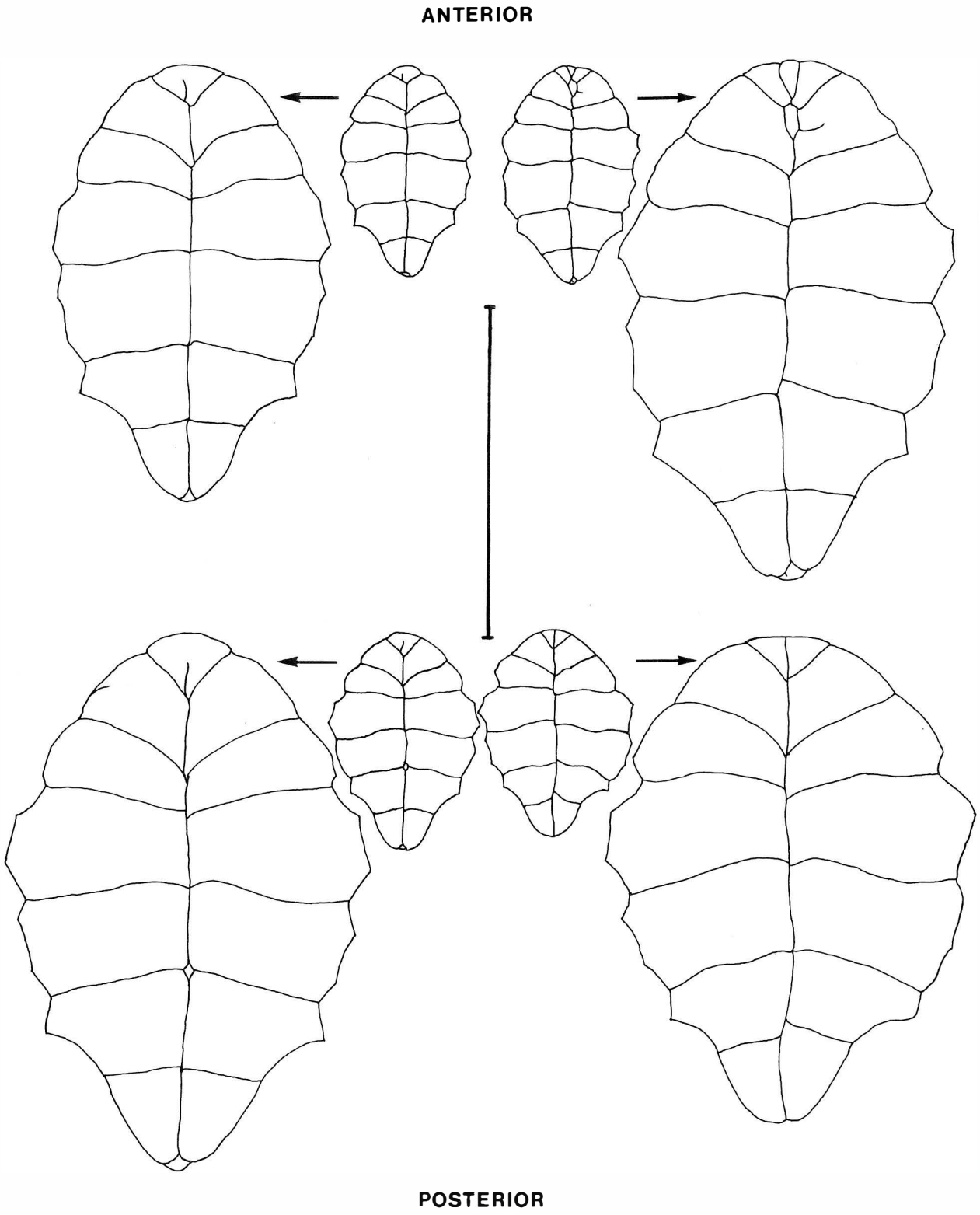

Fig. 3.Comparison of plastral scute patterns recorded from animals on 21-11-89 and 18-6-90. Vertical line has a length of 100 mm.

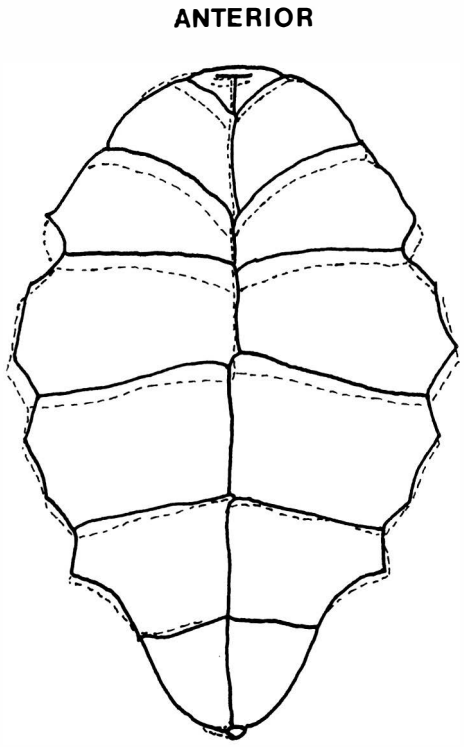

Fig. 4. Comparison of plastral scute patterns of turtle no. 3 recorded on 21-11-89 (solid line) and 18-6-90 (dotted line). The pattern recorded on 21-11-89 has been enlarged to match the plastral length recorded on 18-6-90.

low (<0.1) in all cases); it is clear that no turtle shape, or pattern of shape/weight change is associated with high or low rates of specific growth.

Scute Patterns

Fig. 3 shows plastral scute patterns for some of the young turtles. These show that scute patterns are stable over time and are individually identifiable, at least amongst fairly small numbers of turtles. Although the plastron photocopies allowed easy recognition of individuals amongst an experimental group, slight differences in scute proportions did take place during growth over periods of several months (Fig. 4). Scute patterns are therefore unlikely to be useful for long term identification of individual turtles until they have reached maturity.

Zangerl (1969) considered scute growth in relation to the embryonic scutes present at hatching, noting that the scutes of the diamondback terrapin *Malaclemys* grew symmetrically around the embryonic scutes, while the scutes of the box turtle *Terrapene* grew wholly anteriorly and laterally to the embryonic structure. Inspection of photographs of the carapaces of all of the juveniles studied here showed that the scutes of *Chelonia mydas* also grow asymmetrically, with little posterior or medial growth, most scutal growth taking place anteriorly and laterally.

DISCUSSION

Growth in green turtles is extremely variable amongst individuals, even when large quantities of high quality food are available; the specific growth rate (which includes a logarithmic component) of the fastest growing animal in this study (no. 5) was 41 % higher than that of the slowest (no. 9). On the other hand, individual specific growth rates are stable, indicating that each turtle has a different maximum growth rate programmed by its characteristic physiology/biochemistry. The wide range in growth rate is to some extent surprising: it has long been postulated that the life history strategy of sea turtles involves rapid growth to a size where likelihood of predation is substantially reduced. Given this strategy, it would seem probable that there would be substantial selection pressure in favour of uniformly high growth rates. Yet of the 12 animals studied, two (nos. 1 and 9) grew so slowly that they weighed less than 400 g even when nine months old, and were much less than half the weight of the largest animals. It is difficult to accept that these animals would ever survive to maturity in the wild where their growth would be even slower (as they would have to expend energy in foraging for food of lower quality than the trout pellets supplied in this study). Quality of offspring is a concept that clearly merits further study in sea turtles, particularly as the results of this investigation indicate that quality in terms of specific growth rate may be estimated reliably within a few weeks on a satiation diet.

The finding that young green turtles grow isometrically (individually as well as on average) during the first few months of life is not too surprising. As Alexander (1971) points out, animals with external shells (e.g. crabs, snails) tend to grow isometrically, whereas animals with internal skeletons (e.g. fish, lizards, mammals) usually grow in negative allometric fashion. Turtles effectively have both internal and external skeletal elements. The chelonians investigated by Meek (1982) all showed b values for the length:weight relationship which were very close to 3, again indicating isometry for this group which is so constrained by its shelled nature. However, the isometry of growth in these animals means that they are tending to lose "the struggle to increase surface [area] in proportion to volume" (Haldane, 1928), and presumably have to accept/counteract reductions in the efficiency of transport processes as they grow. Despite these findings, in all chelonian species, including *Chelonia mydas*, it is quite easy to distinguish a well-grown juvenile animal from a hatchling, even from photographs which do not include a scale. The reason for this discrepancy between the indications of simple allometric measurements and the reality of an animal's appearance, is that proportions of structures such as the eyes, nostrils, claws, neck and pectoral musculature (plus fine details of skin and scute surfaces) do change during growth, but are less easy and more stressful to quantify in live animals than weight, length, breadth and area of shell.

As a by-product of the study, the use of photocopying of the plastron and scute patterns as a growth recording technique was shown to be simple and considerably less expensive than photography; it is also less stressful in sea turtles which will not stay still on their backs unless exhausted. Because modern photocopiers allow the ready scaling up and scaling down of images, the photocopier has considerable potential as a tool for allometric studies on animals with rigid shells.

ACKNOWLEDGEMENTS

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INDIVIDUALITY OF GROWTH, APPETITE, METABOLIC RATE AND ASSIMILATION OF NUTRIENTS IN YOUNG GREEN TURTLES (*CHELONIA MYDAS* L.)

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ABSTRACT

Mean appetite and oxygen uptake were highly variable amongst the 12 young green (*Chelonia mydas* L.) turtles studied. Neither appetite nor oxygen uptake had a statistically significant influence on specific growth rate. Amongst the efficiencies of assimilation of nutrients, there were quite wide individual variations in the rates of assimilation of energy, lipid and dry mass, but protein was assimilated with a uniformly high efficiency. Assimilation efficiencies of lipid and dry mass were significantly and positively correlated with specific growth rate. There were also strong positive correlations between the efficiencies of assimilation of different nutrients. There were weak negative correlations between appetite and the assimilation rates for energy and dry mass. These suggest that turtles compensate for a low efficiency of assimilation of these nutrients by an increased rate of food intake. Lipid assimilation in the turtles was lower than for the other nutrients. It was found that fatty acids are not all absorbed to the same extent. Saturated fatty acids and monounsaturated fatty acids were relatively poorly absorbed by comparison with polyunsaturated fatty acids.

INTRODUCTION

This paper reports the second part of an investigation of individuality of growth and nutrition in young green turtles (*Chelonia mydas* L.) fed on satiation rations. The first part (see Davenport & Scott, 1993) established that the specific growth rate of individual hatchling/juvenile turtles was stable, but that there was great variability of growth rate amongst individuals. However, allometric measurements demonstrated that no turtle shape, or pattern of shape/weight change was associated with high or low rates of specific growth. The part of the study reported here was designed to establish whether there were correlations between specific growth rate and various physiological/biochemical variables, viz: appetite, metabolic rate and assimilation of energy, lipid, protein and dry mass. As in the earlier paper, the experimental approach adopted stems from the investigations of individuality of response in marine biology by J.C. Aldrich (Aldrich, 1975, 1986; Aldrich & Regnault 1990) and previous nutritional studies on young green turtles (Davenport & Oxford, 1984; Davenport *et al.*, 1989).

MATERIALS AND METHODS

COLLECTION, MAINTENANCE AND FEEDING

Twelve hatchling green turtles (of unknown but certainly mixed parentage and unknown sex) were sent from the Lara Reserve, Cyprus to the U.K. on 21st October 1989. At this stage they were 40-60 days posthatching. On arrival in the U.K. they were identified by placing hoops of coloured bell wire (four colours available) around the bases of the foreflippers. They were held in a large plastic aquarium (Fastank; 6 x 1 x 1 m) filled with sea water (33‰)at a temperature of 25±1°C. The sea water was gradually replaced by a trickle supply; the contents of the tank were circulated through a biological filter at a flow rate of about 5 l min^{-1}. Throughout the experimental period the animals were fed daily on trout pellets. Great care was taken to ensure that the trout pellets were always offered in satiation amounts (i.e that the animals were always given more food than they could eat), and that no feeding hierarchy could develop to interfere with feeding. The latter objective was achieved by offering trout pellets on large trays suspended a few cm below the water surface in the holding tank. The pellets were spread out over a large area so that each animal could feed in undisturbed fashion. Antagonistic behaviour between the turtles during feeding sessions was rare and did not seem to be related to body size; small turtles were as likely to bite bigger animals as the latter were to be the aggressors.

WEIGHING AND MEASURING

These measurements have been described in detail in Davenport & Scott (1993). Weighing and measuring were carried out over a period of 176 days. Further weights were collected up to 217 days after the start of the experiment.

MEASUREMENT OF APPETITE

For each animal, the size of appetite was measured on six separate occasions (after 26, 82, 89, 107, 117 and 152 days). Appetite was measured for each animal in the following fashion. The animal was weighed, placed in the holding tank for two hours with the day's meal of trout pellets and allowed to feed to satiation. It was removed from the tank and reweighed. Meal size was taken to be the difference between the two weights. In all cases appetite was expressed in weight-specific form (i.e. as % body weight).

MEASUREMENT OF OXYGEN CONSUMPTION

Oxygen uptake was measured in animals at rest in humid air at 25°C as described by Davenport *et al.* (1982). Three separate recordings were made from each animal between days 138 and 142 of the study. Each animal was weighed after oxygen uptake had been recorded.

ASSIMILATION OF NUTIRENTS

For each turtle, three estimates of the efficiency of assimilation of nutrients were made during the following periods of the study:- 14-22 days, 59-71 days, 111-128 days. To do this,

turtles were fed on trout pellets mixed with an indigestible marker, chromic oxide. Large quantities of trout pellets were ground up with the green coloured marker (2% w/w), thoroughly blended with a little water, extruded from a large syringe and dried. Turtles were fed continuously on the labelled pellets until they had produced green faeces for 4 days. A faecal collection was then carried out by placing each turtle on a chicken mesh floor in a separate plastic vessel filled with filtered sea water. The turtles were inspected at hourly intervals so that fresh, intact faecal pellets could be collected. Food and faecal samples were freeze-dried for subsequent analysis.

Chromic oxide content of samples was analysed by wet oxidation to dichromate and subsequent spectrophotometric determination by the diphenylcarbazide reaction (McGinnis & Casting, 1964). Energy content was established by wet oxidation, while lipid content was measured gravimetrically after extraction by the method of Folch *et al.* (1957). Protein content was determined by the micro-Kjeldahl technique. Dry organic matter content was established by ashing freeze-dried food and faecal samples of known weight at 680°C for six hours and reweighing.

Absorption of Fatty Acids

Since lipid assimilation had not been studied previously in green turtles, further analysis was performed to investigate absorption of fatty acids from the trout pellet diet. The fatty acid composition of the diet and of faeces from three turtles (collected for gravimetric analysis of lipid as described above) was determined as follows. The lipid of each sample was extracted by the method of Folch *et al.* (1957). The extract was incubated in methanol:dichloromethane solvent under nitrogen at 100°C for 1 h. The resultant material was mixed with a pentane:distilled water mixture and shaken. The upper (pentane) phase was collected, evaporated to dryness and dissolved in hexane. Samples (1 ml) of the solution of fatty acids in hexane were passed through a Carla Erba gas chromatograph and the fatty acid profiles displayed on a Hewlett Packard 3390A integrator. Identification of fatty acids was carried out by comparison with commercial standards. Quantification of data was achieved by measuring the area beneath each fatty acid peak and expressing that area as a percentage of the total area beneath the fatty acid trace.

Turtle No.	Wt (g) (day 0)	Wt (g) (day 217)	Mean specific growth rate (day 0-176)
1	33.5(12)	338.9(12)	0.01358 (10)
2	65.4(2)	839.3(2)	0.01470 (2)
3	58.9)5)	711.9(4)	0.01444 (3)
4	51.4(9)	415.7(10)	0.01152 (11)
5	56.7(6)	803.8(3)	0.01552 (1)
6	64.7(3	681.9(5)	0.01407 (7)
7	42.0(11)	454.8(9))	0.01383 (8)
8	64.3(4)	645.2(7)	0.01365 (9)
9	49.9(10)	350.9(11)	0.01100 (12)
10	70.5(1)	840.2(1)	0.01444 (4)
11	52.3(8)	633.2(8)	0.01440 (6)
12	56.6(7)	669.9(6)	0.01441 (5)

Figures in parentheses represent rank orders of weight and growth rate, with 1 being highest and 12 lowest.

TABLE 1. Weight changes and mean specific growth rates of individual young green turtles (*Chelonia mydas*). From Davenport & Scott (1993).

RESULTS

Growth Rates

Specific growth rates were calculated as follows:

$$g = \frac{\ln (W_t/W_o)}{t}$$

where g = specific growth rate, t = elapsed time between weight measurements, W_o = initial weight, W_t = weight after time t.

Values of specific growth were calculated for each interweighing interval, and then an overall mean value was obtained (see Table I).

Appetite, Oxygen Uptake and Assimilation of Nutrients

Data for all of these variables are displayed in Table 2. Assimilation efficiencies were calculated after Maynard and Loosli (1969) as:

$$E = 100 \times 1 - \frac{(c^d/n^d)}{(c^f/n^f)}$$

where E = assimilation efficiency (%), c^d = chromic oxide content of diet, n^d = nutrient content of diet, c^f= chromic oxide content of faeces, n^f = nutrient content of faeces.

Mean appetite was highly variable amongst the turtles (range 2.05-3.98 % body wt d^{-1}) as was mean oxygen uptake (range 0.127-0.249 ml g^{-1} h^{-1}). However, neither appetite nor oxygen uptake had a statistically significant relation to specific growth rate (see Table 3). Amongst the efficiencies of assimilation of nutrients, there were quite wide inter-individual variations in the rates of assimilation of energy, lipid and dry mass, but protein was assimilated at a uniformly high level of efficiency (Table 2), significantly greater ($P<0.05$) than for all other nutrients. It was therefore not surprising to find that there was no significant correlation between the efficiency of protein assimilation and specific growth rate. Assimilation efficiencies of two nutrients (lipid and dry mass) were significantly and positively correlated with specific growth rate (i.e. the higher the assimilation rate, the higher the specific growth rate). Amongst the nutrient data there was a general trend towards strong positive correlations between the efficiencies of assimilation (i.e. a high rate of assimilation of one nutrient was associated with high rates of assimilation of other nutrients). Again the narrow range of protein assimilation efficiencies recorded tended to be an exception to this rule, but even so the correlations between protein assimilation efficiency and assimilation efficiency for dry mass, lipid and energy were all close to significance at the 5% level.

Two other regression analyses are of interest; those between appetite and the assimilation rates for energy and dry mass. In both cases there are negative correlations

Turtle No.	Specific growth rate	Mean assimilation rate of nutrients (%*)				Mean Appetite (%* bw d^{-1})	Mean Oxygen Uptake (ml O_2 $g^{-1}h^{-1}$)
		energy	protein	lipid	dry mass		
1	0.01358	66.87	86.43	58.30	66.65	3.395	0.148
2	0.01470	74.64	91.12	68.72	74.50	2.050	0.204
3	0.01444	64.64	88.25	61.09	66.36	2.193	0.200
4	0.01152	68.48	90.31	56.63	63.50	2.438	0.179
5	0.01552	76.51	89.39	71.53	71.70	2.332	0.187
6	0.01407	72.43	88.58	67.67	72.07	2.222	0.192
7	0.01383	67.69	89.21	60.07	60.68	3.912	0.127
8	0.01365	64.11	87.84	47.22	64.65	2.435	0.162
9	0.01100	60.04	87.12	49.72	54.26	2.857	0.206
10	0.01444	70.77	92.26	68.44	70.77	2.937	0.249
11	0.01440	71.27	91.07	60.92	71.12	2.670	0.175
12	0.01441	57.23	88.57	59.23	59.66	3.978	0.183
mean	0.01380	68.02	89.28	60.90	66.43	2.750	0.184
SD	0.00130	5.88	1.89	7.62	6.13	0.700	
Coeff. of variation	9.4%	8.6%	2.1%	12.5%	9.2%	25.5%	16.8%

* mean and standard deviations were calculated after arcsin transformation

TABLE 2. Specific growth rate, assimilation of nutrients, appetite and metabolic rate (measured as oxygen uptake rate) in individual young green turtles (*Chelonia mydas*)

(significant at the 10% level, but not at the 5% level) which suggest that turtles compensate for a low efficiency of assimilation of these nutrients by increasing their rate of food intake.

Individuality of Nutrition

The picture that emerges from the regression analyses is that growth rate is predominantly controlled by the efficiency of assimilation of nutrients, rather than by size of appetite or level of metabolic rate. This is highlighted when we consider individual turtles that exhibited particularly low or high specific growth rates. From the data for the slowest-growing animal (9), growth rate was ranked 12th, energy assimilation efficiency 11th, protein assimilation 11th, lipid assimilation 11th and dry mass assimilation 12th. In contrast, its metabolic rate and appetite were above average (5th and 2nd respectively).

For the fastest growing turtle (5) assimilation rate rankings were as follows; energy 1st, protein 5th, lipid 1st and dry mass 3rd. Its appetite was below average (9th) and metabolic rate about average (6th).

Comparison of animals 7 and 2 (the second slowest and fastest growers respectively) provides further support for the view that slow growing animals have low assimilation efficiencies for nutrients other than protein, yet have a relatively large appetite. Fast growers have high assimilation rates and relatively low appetites.

Absorption of Fatty Acids

Fatty acid compositions for food and faeces are displayed in Table 4. From these data it is obvious that different fatty acids are not all absorbed to the same extent. The results vary somewhat between the three turtles, but it is evident that saturated fatty acids (SFAs; 14:0, 16:0, 18:0) and monounsaturated fatty acids (MUFAs; 16:1, 18:1, 20:1, 22:1) were relatively poorly absorbed by comparison with the polyunsaturated fatty acids (PUFAs; 18:2, 18:4, 20:5, 22:5, 22:6), all of which appeared to be completely assimilated.

DISCUSSION

The levels of appetite, oxygen uptake and assimilation efficiencies for energy, protein and dry mass recorded in this study are consistent with those reported in earlier studies upon captive green turtles (Wood & Wood, 1981; Davenport *et al*, 1982; Hadjichristophorou & Grove, 1983; Davenport & Oxford, 1984; Davenport *et al*., 1989). Lipid assimilation efficiencies have not previously been recorded for sea turtles, so it is interesting to note that the values presented in this study are lower than for the other nutrients. This difference probably results from the variable capacity for absorption of individual fatty acids. The fatty acid assimilation data presented here are limited, but it appears that the turtles are relatively efficient at assimilating PUFAs, but less efficient in assimilating SFAs and MUFAs. This differential capacity for fatty acid assimilation presumably limits total lipid assimilation from trout pellets (mean = 60.9%). Comparisons with other species are consequently very difficult. For example, although Sargent *et al.* (1979) reported that herring (*Clupea harengus*) could assimilate 99.4% of dietary lipid, the fish were being fed a zooplankton diet very rich in wax esters. A diet rich in PUFAs could be devised for green turtles to see if higher levels of lipid assimilation could be achieved.

Variables				
y	x	equation	r^2 (%)	P
Appetite	S.G.	$y' = 10.2 - 52\,x$	0.0	>0.05
O_2 uptake	S.G.	$y = 0.162 + 1.65\,x$	0.0	>0.05
Energy	S.G.	$y' = 37.6 + 1304\,x$	15.5	>0.05
Protein	S.G.	$y' = 65.1 + 422\,x$	1.4	>0.05
Lipid	S.G.	$y' = 18.5 + 2380\,x$	43.8	<0.05
Dry mass	S.G.	$y' = 27.6 + 1953\,x$	42.8	<0.05
Lipid	Dry mass	$y' = 1.0 + 0.922\,x$	53.1	<0.01
Lipid	Energy	$y' = -1.70 + 0.954\,x$	53.4	<0.01
Lipid	Protein	$y' = -52.8 + 1.47\,x$	25.0	<0.10>0.05
Protein	Energy	$y' = 56.2 + 0.265\,x$	23.1	<0.10>0.05
Dry mass	Protein	$y' = -29.2 + 1.18\,x$	23.2	<0.10>0.05
Dry mass	Energy	$y' = 4.90 + 0.894\,x$	71.3	<0.001
Appetite	Dry mass	$y' = 19.0 - 0.173\,x$	25.0	<0.10>0.05
Appetite	Lipid	$y' = 12.7 - 0.061\,x$	0.0	>0.05
Appetite	Protein	$y' = 19.15 - 0.140\,x$	0.0	>0.05
Appetite	Energy	$y' = 19.0 - 0.101\,x$	21.6	<0.10>0.05
Appetite	O_2 uptake	$y' = 12.3 - 15.1\,x$	9.1	>0.05

Notes: 'Energy', 'Protein', 'Lipid', 'Dry Mass' refer to the assimilation efficiencies (%) of these nutrients, in this table arcsin transformed to degrees; 'S.G.' = specific growth rate; 'Appetite' = mean appetite (% body wt d^{-1} again arcsin transformed to degrees); 'O_2 uptake' = mean O_2 uptake (ml $O_2 g^{-1} h^{-1}$).

TABLE 3. Results of linear regression analysis of the data shown in Table 2 (after arcsin transformation to degrees in the case of percentages).

The most important findings of the study concern the relationships between growth rate, appetite, metabolic rate and assimilation of nutrients. For such young animals, in which little energy will be diverted into the development of gonadal material, energy flow equations (see Crisp, 1984) can be simplified thus:

$$A = G + R + U + F \quad [1]$$

where A = appetite (food consumption), G = growth, R = respiration, U = excretory output, F = faecal loss of material.

$$\text{Absorption, } Ab = A - F = G + R + U \quad [2]$$

Absorption of organic material is obviously a function of assimilation of nutrients across the gut wall.

Equations [1] and [2] can be rearranged as:

$$G = A - R - U - F \quad [3]$$

$$G = Ab - R - U \quad [4]$$

A priori, it would be expected that high growth rates would be associated with high appetite (high A), low metabolic rate (low R) and high rates of assimilation of nutrients (high Ab, low F). The results derived from the investigation presented here contradict several of these predictions. No systematic relationships between appetite, respiration rates and growth rates were evident. To some extent this may be an artifact of a captive existence in which little energy was required to capture food; in the field, an animal would have to expend more energy in satisfying a large appetite.

Protein assimilation rates were uniformly high despite great variations in growth rate. This is surprising since poor growth (albeit in animals suffering from 'runt syndrome') was recently attributed to impaired protein assimilation in salt-water crocodiles (Davenport *et al.*, 1990). However, the present study clearly demonstrated that fast growing turtles had high rates of assimilation of energy, lipid and dry mass whereas assimilation rates were low in the slow growers. In the case of assimilation of energy and dry mass, there were

Fatty acid	Food composition (% total fatty acids)	Faecal composition (% total fatty acids)		
		Turtle 2	Turtle 3	Turtle 7
14:0	7.6	6.1	12.5	5.2
16:0	20.3	32.9	69.8	24.5
18:0	3.6	4.1	12.2	6.2
16:1ω7	6.5	7.0	5.6	3.5
18:1ω9	13.7	7.9	0.0	6.6
18:1ω7	5.1	5.9	0.0	11.4
20:1ω9	8.4	14.9	0.0	17.0
22:1ω11	10.0	21.1	0.0	25.5
18:2ω6	3.5	0.0	0.0	0.0
18:4ω3	2.8	0.0	0.0	0.0
20:5ω3	10.5	0.0	0.0	0.0
22:5ω3	0.8	0.0	0.0	0.0
22:6ω3	7.1	0.0	0.0	0.0

TABLE 4. Absorption of fatty acids from a diet of trout pellets

strong indications that low rates of assimilation were associated with compensatory large appetites (and vice versa). This makes sense; there is evidence from mammalian studies that the circulating levels of carbohydrates and fatty acids control appetite (low levels being stimulatory).

It is also interesting that high rates of assimilation of one nutrient are positively correlated with the ability to assimilate other nutrients at high rates. There is no obvious biochemical reason why this should be so, since the assimilation of different nutrients will depend upon different enzyme systems and carrier molecules, and different nutrients may be assimilated in different parts of the gut. However, since all exchange systems are influenced by the surface area over which exchange can take place; if turtles vary in gut length and surface area, this probably contributes to the observed variations in assimilation rate.

This study, and the earlier study of Davenport & Scott (1993), demonstrate considerable individual variability of growth, metabolic rate and nutritional physiology in young green turtles. The experimental animals were all incubated together and were from the same geographical population (though of mixed parentage). The sex of the turtles was unknown, but is in any case determined by incubation temperature. It is therefore probable that the observed variability reflects underlying genetic differences rather than environmental influences.

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OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOUR OF THE SMITH FROG, *HYLA FABER*

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ABSTRACT

The reproductive behaviour of the Smith Frog, *Hyla faber*, was studied in an artificial permanent pond in southeastern Brazil. Males built nests at the edges of this pond where eggs were laid. Reproductive activity continued from late October, 1988 through early March, 1989. Twenty five males and 20 females were marked at the pond. There was no sexual dimorphism in size and females did not choose the larger males. Mean male residency was 15.5 nights; only two females were observed for more than one night. Three different vocalizations were emitted during female attraction and courtship. Courtship behaviour was complex and nearly invariable. Male reproductive success varied between 1-7 matings and was not correlated with male size, but was positively correlated with length of residency. Only one female was observed mating more than once. Except for minor details, the reproductive behaviour of the Smith Frog is very similar to that observed for *Hyla rosenbergi*, an ecologically and phylogenetically related species.

INTRODUCTION

The basis of what is known about Neotropical anurans is based on natural history observations. Several aspects of anuran natural history have been studied in recent years, especially social behaviour (reviews in Salthe & Mecham, 1974; Wells, 1977; Cardoso, 1984; Duellman &Trueb,1986). However, with a few exceptions, most of these data are fragmented. The few detailed studies are highly cited references and some of them were the stimulus for further studies and theoretical discussions. Recent instances are the studies of Kluge (1981) on *Hyla rosenbergi*, M. Ryan, M. Tuttle, S. Rand and colleagues on *Physalaemus pustulosus* (review in Ryan, 1985), K. Wells on dendrobatids (references in Wells, 1980), and K. Wells, J. Schwartz, and colleagues on *Hyla ebraccta*, *H. microcephala*, and *H. phlebodes* (review in Wells, 1988).

The Smith Frog, *Hyla faber*, a member of the *boans* group of the genus *Hyla*, occurs from northern Argentina to eastern Brazil, and reproduces in permanent ponds near streams in the Atlantic Forest. Six species morphologically related to *H. boans* are known to build nests for egg deposition: *H. biobeba*, *H. boans*, *H. faber*, *H. pardalis*, *H. rosenbergi*, and *H. wavrini* (Goeldi, 1895; Lutz, 1960*b*; Duellman, 1970; Jim, 1980; Kluge, 1981; Martins & Moreira, 1992).

Except for Kluge's (1981) study on *Hyla rosenbergi*, data on the natural history of the other species of the *boans* group are scarce. Fragmented observations on *H. faber* are found in Goeldi (1895), Lutz (1960*a*, 1973), and Cei (1980). Recently, Martins & Haddad (1988) described four different vocalizations and some aspects of the reproductive behaviour of the Smith Frog in a forest in southeastern Brazil. However several aspects of the natural history of the Smith Frog are still poorly known or are unknown.

Here I describe reproductive behaviour in a population of the Smith Frog reproducing in a permanent, artificial pond in an open area near Campinas, São Paulo State, southeastern Brazil. Data on aggression and territoriality, nests and premetamorphic stages, and predation will be published elsewhere.

STUDY SITE

This study was conducted in an artificial permanent pond at Fazenda Santa Monica (FSM) (22°54'S; 46°53'W; ca. 800 m elev.), 8.5 km from Joaquim Egidio, Municipality of Campinas, São Paulo State, Brazil. The pond, formed by the damming of a small stream, has its source at a secondary forest (100 m from the pond) and cuts a pasture area. At the time of the study, the hillsides of this valley were covered with grasses and small shrubs. The pond has muddy water and a nearly rectangular shape (9.5 m x 20.0 m) and its deepest point is up to 1.0 m deep in the rainy season. The lower end of the pond has muddy banks (flooded during heavy rains) with small sedges and grasses and the upper part is nearly completely covered by cattail (*Typha* sp., Typhaceae), with no mud on the banks. In the rainy season, with the flooding of the pond, a small stream flows from the pond through a swamp covered by cattails. According to local inhabitants, the region of FSM was originally covered by upland forests cut mainly at the beginning of this century for coffee culture. Of this original vegetation, only a few very disturbed "islands" remained.

Besides the Smith Frog, seven additional anurans reproduced at the pond during the study. Two other reproductive aggregates of the Smith Frog were observed in a swamp and a small pond 150 m and 200 m from the study area, respectively. I never found an individual marked at the study area at these places.

Fig. 1 shows the weekly rainfall and minimum and maximum temperatures from July 1988 to June 1989 for Barão Geraldo, 22 km from FSM. In the rainy season of 1988/1989 the rains at southeastern Brazil were reduced by the Anti-El Niño (Molion, 1989). At Campinas region, the rains that normally begin to fall in September began to fall with high intensity only in late October. At FSM, besides this delay, there was a long drought between mid-November and early December (shorter at Barão Geraldo. Fig. 1).

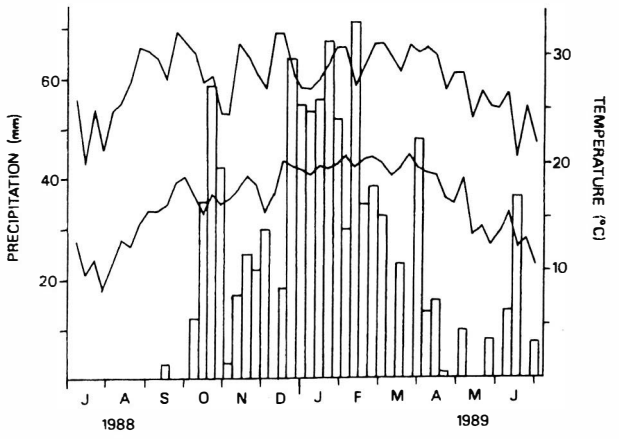

Fig. 1. Mean weekly precipitation (in millimetres, vertical bars) and maximum and minimum temperatures (in °C, lines) from July 1988 to June 1989 at Barão Geraldo, 22 km northwest of the study site.

METHODS

I made observations on the reproductive behaviour of Smith Frogs from early November 1988 through mid-March, 1989. I made visits to the study area every two or three days, totalling 57 observation nights. Observations began in the evening (1630 h-1830 h) and ended when Smith Frog activity diminished or ended (2100 h-0130 h). I marked each adult Smith Frog by toe-clipping and with waistbands (Kluge, 1981). Waistbands were made of white flexible plastic tape 8 mm wide, and had diameters of 14 mm-18 mm depending on frog size. A number corresponding to a toe-clipping code was written on the waistband with indelible ink. Adequate sized waistbands and their numbers persisted to the end of the study. No individual was seen trying to remove the waistband and, apparently, waistbands did not impede normal behaviour. For each marked individual I recorded: (1) day and time of marking, (2) sex, (3) snout-vent length (SVL) to the nearest 0.1 mm, and (4) additional observations (e.g., presence of eggs in females, behaviour, natural marks).

At each observation night I walked slowly along the pond bank recording every new nest and for each nest I recorded presence/absence of clutches. For each adult I recorded every activity I could see ("all occurrence sampling", Martin & Bateson, 1986). Nocturnal observations were made with a headlamp, some of them with a red filter installed in the headlamp. Statistical tests follow Sokal & Rohlf (1981).

RESULTS

Smith Frog males at FSM had a mean SVL of 84.0 mm (78.0-91.4 mm, SD = 3.5 mm, n = 25) and females 83.8 mm (77.5-91.4 mm, SD = 4.2 mm, n = 20). There was no significant difference between SVLs of males and females (t = 0.163, P> 0.1). Mean SVLs of males and females from ten amplectant pairs were also not significantly different (t = 0.687, P > 0.1).

Smith frog reproduction at FSM lasted nearly four months. Fig. 2 shows the nights when 45 marked males and females were seen at the pond. The first individuals (three calling males) were observed at my first visit to the pond (4th November, 1988); however, the analysis of some nests present on this night indicated that reproduction began on 30 or 31 October. The last calling male was observed on 10 March, 1989 and the last female on 6 March. Mean length of residency at the

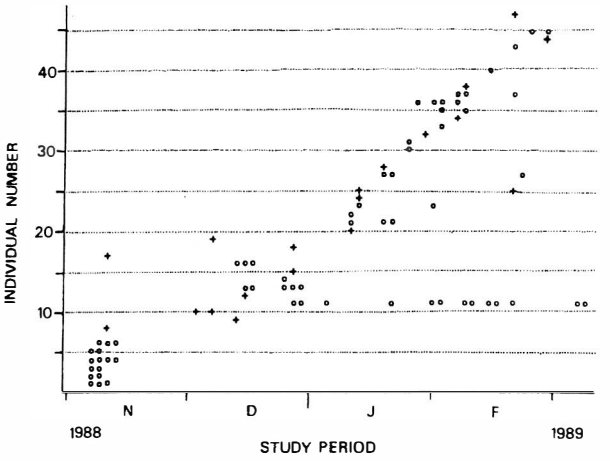

Fig. 2. Nights on which each marked male (circles) and female (crosses) Smith Frog was observed at the study site.

pond (the time from the first to the last observation of an individual, Kluge, 1981) for 25 marked males was 15.4 days (1-74 days, SD = 15.4 days). Nearly two thirds of the males were observed for less than five days, and only two were observed for more than 20 days (Fig. 2). Only two females were observed more than once at the pond: female no. 10 was observed on three occasions with intervals of two days, and female no. 25 on two occasions with an interval of 37 days (Fig. 2).

The number of males and females, marked and unmarked, observed each night at the pond is shown in Fig. 3. The number of females observed each night is probably underestimated because, unlike males that were located by their calls and eyeshines, females were located only by their eyeshines. Recruitment was nearly constant during reproductive period for males and females, except during the drought from mid-November to early December when no male called at the pond (Fig. 2).

The first vocalizations were always emitted from the pond margins or from the cattails. After beginning to call, males moved toward the pond margins and there they looked for their own nests, reoccupied abandoned nests, or, rarely, called without a nest. Females appeared at the cattails mostly after 2000 h

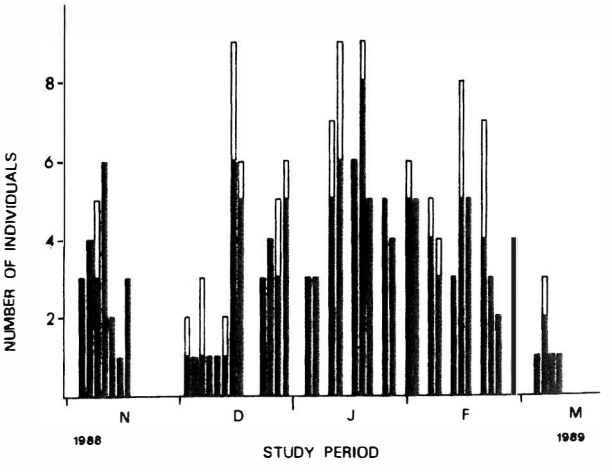

Fig. 3. Total number of marked and unmarked male (solid bars) and female (white bars) Smith Frogs observed on each observation night. Note that no individual was observed during the drought from mid November through early December (see Fig. 1).

and moved toward calling males wherever these males were. Females jumped over calling males without nests on several occasions. After perceiving the females, these males invariably reoccupied or built a nest, from where they resumed calling.

Three different types of vocalizations were emitted during reproductive behaviour: advertisement, courtship, and "initial" calls. The advertisement call is described in Martins & Haddad (1988). The courtship call is an advertisement call with very high note repetition rate (88-196 vs. 180-210 calls per minute) and was emitted when a female approached a calling male. This increase in note repetition rate was easily elicited by disturbing the vegetation around the nest of a calling male, simulating a female approaching. The initial call sounds similar to the advertisement call, but have clearly longer notes (not measured); although heard almost every observation night, I could not asociate a function to this call.

Fig. 4 shows a schematic profile of the courtship behaviour I observed in the Smith Frog at FSM, based on eight observations of parts of the courtship of several pairs (a detailed description of the courtship is found in Martins & Haddad, 1988). Every

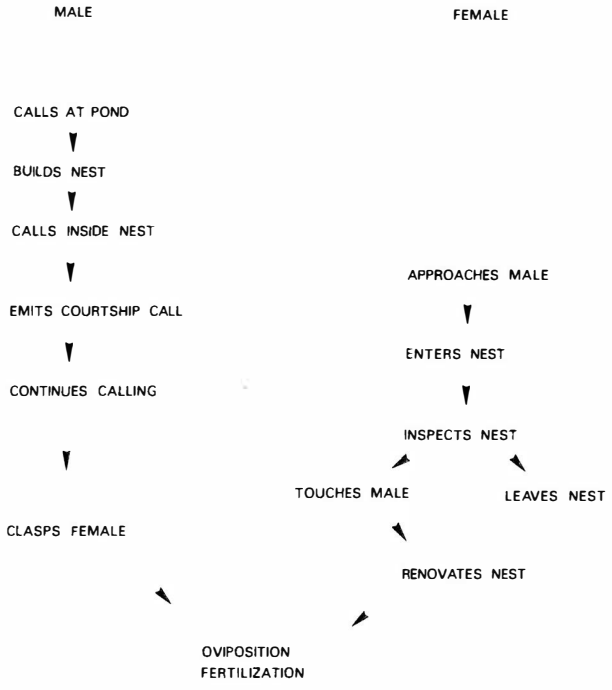

Fig. 4. Schematic summary of the courtship observed for the Smith Frog at the study site.

time I observed an amplectant pair I found an egg clutch in their nest at my next visit to the pond.

Excluding those males marked at my first visits to the pond (reproduction began some days earlier, and consequently data on mating for these frogs are probably incomplete, see above), mean male reproductive success (number of amplexes, Kluge, 1981) at FSM was 1.9 amplexes (0-7, SD = 2.3, n = 18 males). These reproductive successes are certainly underestimated because, as my visits to the pond occurred every two or three days, not all clutches could be associated to the males who fertilized them. Male reproductive success was not significantly correlated to male SVLs (r = -0.37, P > 0.05, 16 df), but was positively correlated to length of residency at the pond (r = 0.80, P < 0.01, 16 df, Fig. 5). Only one female was observed in amplexus twice, with an interval of 37 days.

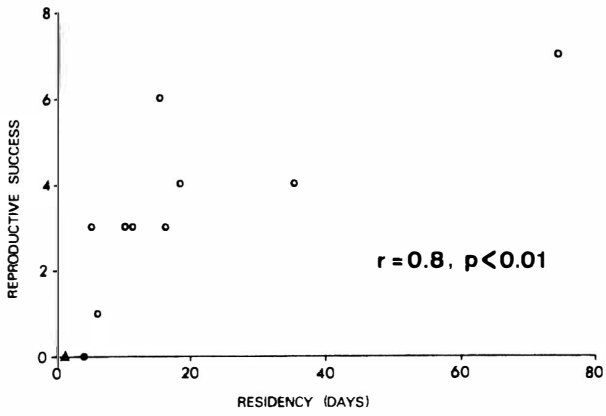

Fig. 5. Reproductive success (number of amplexes) in relation to time of residency in the Smith Frog. The triangle represents seven observations.

DISCUSSION

Martins & Haddad (1988) also found no sexual dimorphism in size in the Smith Frog. Smith Frog females do not seem to choose larger males as in other *Hyla* (e.g., Gatz, 1981; Lee & Crump, 1981). Alternatively, nest characteristics, probably perceived through inspection before amplexus, seem to be the main factor in male choice in the Smith Frog.

The number of adults that reproduced at FSM during this study was certainly higher than that of individuals marked because my observations were not made daily. Furthermore, I found 75 egg clutches during the study and this, associated with a low recapture of females, indicates that more females reproduced at the pond than those marked. Even so, total density during reproduction was higher in *H. faber* at FSM (25 males and 20 females along 9.5m of margins) than that observed by Kluge (1981) for *H. rosenbergi* at Panama (69 males and 55 females in 1977 and 26 males and 23 females in 1978, along 180 m of creek margins), probably reflecting distinct availability of sites for nest building in these two sites.

Kluge (1981) also observed a gradual adult recruitment in *H. rosenbergi*. Gradual adult recruitment at reproductive sites may be a consequence of individual differences in sexual maturation (Kluge, 1981). Mean male residency in the Smith Frog (15.4 days) was also similar to those found by Kluge (1981) for *H. rosenbergi:* 16.5 days in 1977 and 23.3 days in 1978. Assuming that Smith Frog males did not migrate during reproduction (I found no male marked at FSM in nearby reproductive aggregates), time of residency may indicate survivorship (see Kluge, 1981). Indeed, *H. faber* was heavily preyed upon during this study (five effective, or attempts of, predation by snakes and an owl were observed during the study).

Contrary to this study, Kluge (1981) observed that all *H. rosenbergi* calling males had nests and those newly arrived generally spent their first night without calling. In *H. faber*, for newly arrived males, calling in their first night means the possibility of mating in that same night. Kluge (1981) suggests that newly arrived *H. rosenbergi* males did not call while looking for a nest or building a new one because their

calls could attract predators. In fact *H. rosenbergi* seemed to be preyed upon mainly by accoustically oriented predators (see Kluge, 1981:88-90) while at FSM *H. faber* was preyed upon mainly by chemically oriented predators (nocturnal snakes, pers. obs.).

The vocal repertoire of the Smith Frog is very similar to that of *H. rosenbergi*, probably reflecting their close phylogenetic relationship besides their ecological and behavioural similarities.

Courtship behaviour observed in this study was very similar to that observed by Martins & Haddad (1988), except that males did not abandon their nests to guide females to them. Courtship behaviour in the Smith Frog was very similar to that observed for *H. rosenbergi* by Kluge (1981), except that this author observed females renovating nests before amplexus in the latter species.

As in *H. rosenbergi* (Kluge, 1981), male Smith Frogs were observed mating up to seven times in a single reproductive season. If the short mean length of residency observed in male Smith Frogs is considered an estimate of survivorship (see above), it would be profitable to a male to mate as frequently as possible to assure its contribution to the gene pool of future generations. In fact, males do tend to mate several times in short periods (e.g., I observed a marked male mating six times in only 15 days; furthermore, this may be an underestimation because I was not present every night at FSM). Kluge (1981) also found male reproductive success correlated to length of residency in *H. rosenbergi*. Mean reproductive success in the Smith Frog (1.9) was not significantly different from that observed by Kluge (1981) for *H. rosenbergi* (1.2), although Kluge (1981) observed *H. rosenbergi* nearly every night. A higher male reproductive success in the Smith Frog than in *H. rosenbergi* could reflect, at least in part the presence of parental care in the latter species: *H. rosenbergi* males defend clutches for one or two days after fertilizing them and do not call or attract females during this period, whereas in *H. faber* neither this form of parental care nor the pause in reproductive activity were observed.

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FUNCTIONS OF THE FOAM IN FOAM-NESTING LEPTODACTYLIDS: THE NEST AS A POST-HATCHING REFUGE IN *PHYSALAEMUS PUSTULOSUS*

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ABSTRACT

At 28°C, isolated *Physalaemus pustulosus* eggs hatch after approximately 40 hours incubation. However, few tadpoles emerge from foam nests at this time. From nests incubated so that the foam remains moist, emergence occurs progressively over the next day. If the foam is allowed to dry on top, complete emergence takes even longer. Manipulation of the incubation environment shows that emergence is not stimulated by dark or light, nor does it occur at a particular time of day. Since hatching occurs at Gosner stage 21 and the last tadpoles to emerge from foam have reached Gosner stage 23-24, it is suggested that late emergence allows hatchlings to continue development to a more advanced stage in a protected environment: the foam acts as a post-hatching refuge. However, it is also shown that tadpoles emerging early are able to grow to Gosner stage 25 by the time the last tadpoles leave the nest: remaining in the nest therefore bears a cost. In addition, part of the delay in emergence may simply result from the time small tadpoles take to wriggle free from a large mass of cohesive foam.

INTRODUCTION

While it is well-known that many members of the anuran family *Leptodactylidae* deposit their eggs in foam nests, either in burrows or floating on the surface of water, it is less clear what the functions of these foam nests are. Possible functions have been suggested by several authors (reviewed by Downie, 1988) but experimental evidence has often been entirely lacking or anecdotal at best: see, for example, Hödl's (1990) interesting but very briefly documented suggestion that foam nests prevent egg predation by conspecific tadpoles. Downie (1988, 1990) investigated a number of possible functions for the floating foam nests of the common neotropical leptodactylid *Physalaemus pustulosus* and found best evidence for foam as a protection against egg predation, mainly by tadpoles of other species. This work considered the foam nest as a container for eggs. However, Kenny (1969) noted that *P. pustulosus* tadpoles (named *Eupemphix pustulosus* in his paper) may remain some days in the foam after hatching and it is therefore possible that the nest has some useful properties for these later stages of development. The purposes of this paper are to document the timing of nest departure by *P. pustulosus* tadpoles, to investigate possible environmental cues for nest departure, and to consider the possible reasons why *P. pustulosus* tadpoles remain in the the nest after hatching.

MATERIALS AND METHODS

COLLECTION OF NESTS

The *Physalaemus pustulosus* foam nests used in this study were found in drainage ditches near the University of the West Indies campus at St Augustine, on the Caroni plain in Trinidad during July and August 1991. Freshly-made nests were collected early in the morning following wet days or nights. Eighteen complete nests collected on four separate days contributed to this study.

NEST, EGG AND TADPOLE INCUBATION

Foam nests were incubated floating on the surface of dechlorinated tapwater. Since incubations were relatively short, and foam is at the water surface, no aeration was necessary. Whole nests were incubated in 2 l rectangular polythene tubs containing 1.5 l water, either with the lid on or off. I cut other nests into pieces so that different treatments could be given to eggs from the same batch, and incubated each piece at the surface of 150 ml water in a 250 ml glass beaker with a plastic petri dish lid. To compare the time of emergence from foam with the time of hatching, I removed 10 eggs from each nest and incubated them singly at the surface of water in 250 ml glass beakers. To allow eggs to float, one or two foam bubbles were kept attached to each egg. Most nests were incubated in a laboratory with artificial light on during the day, but subject to natural lighting at night (in July and August, it is dark by 19.00 h and light again by 06.00 h). This treatment is hereafter termed 'ambient'. Some nests were incubated in this laboratory in constant darkness and some under constant artificial lighting. The laboratory air temperature remained fairly constant at 28-29°C, with the temperature of the water in beakers and tubs about 1°C less. To vary the time of day at which hatching could be expected, I incubated some eggs and nest pieces in an air-conditioned laboratory at an air temperature of 25-26°C and water temperature of 24-25°C, (hereafter termed 'cool' temperature); others were incubated outside in the shade, where the temperature during the middle of the day rose a little over 30°C. After hatching, some tadpoles were grown in 2 l polythene tubs in 1.5 l aerated dechlorinated tap-water with a mud bottom to simulate field conditions. Tadpoles were fed with crumbled tropical fish food flakes.

DETERMINATION OF TADPOLE DEVELOPMENT

To assess the stage of development after different times and treatments, tadpoles were fixed in Bouin's fluid and staged using Gosner's (1960) table. Body lengths (anterior tip to junction of tail and body) were also measured, using an eyepiece graticule in a Wild M5 stereo-microscope, magnification x12.

INFLUENCE OF TIME OF DAY, LIGHT AND TEMPERATURE ON HATCHING AND EMERGENCE FROM FOAM

Five nests, collected on two separate mornings, were used in this experiment. Each was sub-divided into 10 approximately equal pieces (1.5 x 1.5 x 1.0 cm) and each piece floated on water in a beaker. For each nest, I incubated two pieces in

each of five ways: outside, cool temperature, and ambient temperature in the dark, in constant light or with ambient illumination. For each nest and for each treatment, 10 eggs were isolated and incubated as single eggs floating on the surface of water. Numbers hatching (as single eggs) and entering water (from floating foam) were counted at intervals. To assess whether the onset of darkness or daylight acted as a stimulus for hatching or entering water, I recorded numbers at 18.00 h (an hour before dark), 20.00 h - 21.00 h (just after dark) and at 06.00 h (dawn).

Influence of Nest Size and State of Hydration on Emergence From Foam

To assess whether complete nests showed the same hatching and emergence pattern as cut-up pieces, I incubated 10 whole nests in 2 l tubs under normal lighting and temperature conditions. Six of these were incubated with the lid on (where the foam surface remains moist) and four with the lid off (foam surface becomes dry as the upper part of the nest dehydrates) to assess whether dehydration is a factor in tadpole emergence. Ten single eggs were withdrawn from each nest and incubated in beakers to determine the time of hatching.

Assessment of Loss of Growth When Tadpoles Remain in Foam

In this experiment, I incubated four complete nests in 2 l tubs with the lid off (this maximises the time spent in foam - see Results) in ambient conditions of temperature and lighting. Once more than five tadpoles had emerged into the water, a few were fixed for staging and the others transferred to tubs for feeding. Once all tadpoles had emerged from a particular nest, a sample of the last emergers was fixed, and also those early emergers which had been allowed to grow.

RESULTS

Influence of Time of Day, Light and Temperature on Hatching and Emergence From Foam

The times of hatching and emergence from foam for tadpoles from five different sub-divided nests collected on two separate mornings and incubated under different conditions are given in Fig. 1. For ease of comparison the data are plotted as if all eggs were fertilised at midnight during the night before collection. In practice, it is likely that the time of fertilization differed for the different nests: hatching was consistently earlier in nest 1 than in 2 and 3, and a little later in 4 and 5. The data are presented for individual nests, rather than giving mean values, because of this variability and because the demands of other field work made it impossible to count hatchlings at precisely the same times of day for the two different batches of nests.

Batches of single floating eggs hatched, under all conditions, over a relatively short period. At 'ambient' temperature and lighting, no hatchlings were seen at 33 h, but all had hatched by 42 h. For nests 4 and 5, all hatched between 38 and 42 h. An ANOVA was carried out, using the time to hatching of each floating egg as the dependent variable, to assess the differences between incubation in ambient conditions, constant light and constant dark. This gave $F_{2,147} = 5.77$ with $0.01 > P > 0.001$. There was a significant difference between eggs incubated in constant light (mean time to hatching ±SD, 40.1 ± 2.5 h) and those in constant darkness (41.5 ± 2.0) but neither of these treatments was different from the ambient group (40.9 ± 1.8). However, I should point out that hatching time was only measured as those hatched after 2-4 hourly intervals, rather than the precise hatching time. It is possible that this method has masked variability in the data, thereby producing a spurious statistical difference. It would be worthwhile to repeat this experiment to collect finer resolution data.

Incubation outside depended on temperature: nests 1 and 2 were incubated outside on a hot day, and hatching occurred a little earlier than normal; nests 3, 4 and 5 were incubated on a cooler cloudy day and hatching occurred at the same times as in the laboratory. Cooler incubation conditions, not surprisingly, delayed hatching. Of the 'cool' group, nests 1 and 2 were kept at 23.5-24°C. till 54 h, then transferred to ambient conditions: hatching occurred between 45 and 58 h. Nests 3, 4 and 5 were kept at the cool temperature only till 38 h: as a result, hatching was completed earlier, by 54.5 h.

Emergence from foam consistently occurred over a much longer time-span than hatching from single eggs. Commonly, one or two tadpoles emerged from foam at the same time as single eggs hatched, but most tadpoles emerged much later. At ambient temperature, the interval between the observation of 100% hatching of single eggs and 100% emergence from foam was 17±1.9 hours (n=8, mean ±SD.). Constant darkness and constant light had no consistent effect on the pattern of emergence. Although most emergence at 'ambient' temperature occurred during the hours of darkness, there was no evidence that darkness acted as a stimulus for emergence. Counts made at 20.00 h or 21.00 h, soon after sunset, showed no surge in emergence compared to the time before sunset. Neither did dawn (06.00 h) mark any change in the rate of emergence. In support of this conclusion of a lack of a dark-light effect, incubation of nests 3, 4 and 5 at 23.5-24.0°C till 38 h achieved an approximate 12 h delay in emergence, with the majority of tadpoles emerging during daylight hours.

Emergence From Complete Foam Nests and an Effect of Dehydration

Since it was possible that the subdivision of complete nests could affect the emergence pattern, two sets of complete nests were incubated, one covered, the other open, and the numbers of tadpoles emerging counted at intervals. The 'covered' treatment simulates nests in wet conditions when the foam remains moist at the surface. The 'open' treatment simulates dry conditions when the foam becomes dry and crusty at the surface: both commonly occur in the field. Sets of single eggs were removed from some of these to assess hatching time. The results are shown in Fig. 2. It is clear that tadpoles remained in the complete nests for some time after the hatching of single eggs, just as occurred in sub-divided nests. However, the data suggest that tadpoles remained somewhat longer in complete nests than in sub-divided ones, and longer in dehydrated nests (incubated in the open) than in moist ones (incubated in closed containers). Since only some nests were followed to completion, comparisons need to be made at earlier stages. At 58 h incubation, subdivided nests at 'ambient' temperature and lighting showed a mean emergence of 87.7%, whereas complete nests by the same time showed 45.6% with lids on and only 5.6% with lids off. A Students t test performed on arcsin-transformed percentages for complete nests showed that the difference between lid-on and

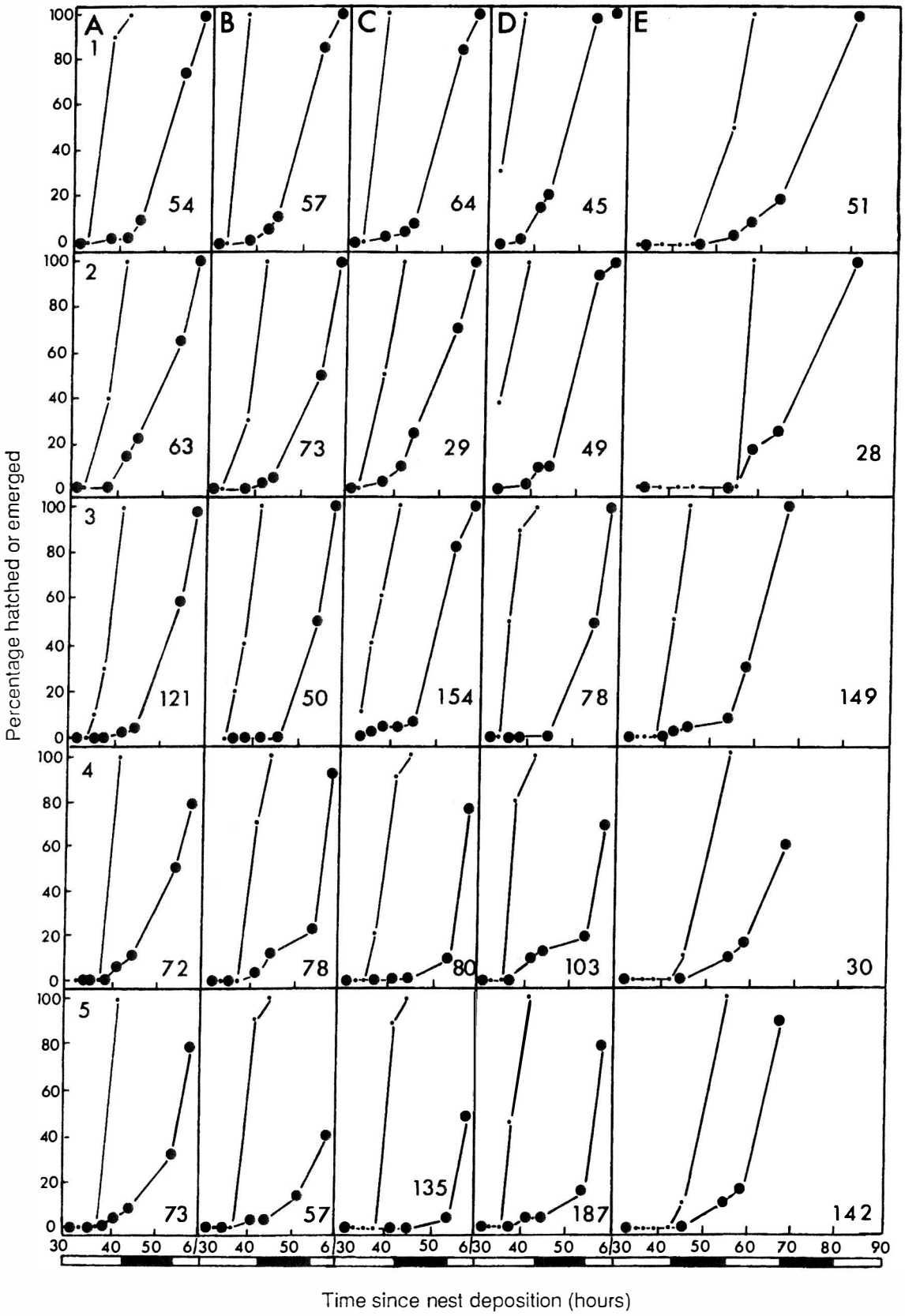

FIG. 1 Hatching and emergence from subdivided nests incubated in different conditions. Numbers hatched or emerged are given as percentages of the total number. Time is measured since a standardised time of nest deposition (see text). Conditions are A - normal temperature and lighting; B - normal temperature, constant darkness; C - normal temperature, constant light; D - incubated outside; E incubated in cooled laboratory part of time (see text). There are samples from five (numbers 1-5) nests for each condition. Small dots show hatching from groups of single eggs. Large dots show emergence from pieces of foam. Figures at the bottom right of each box denote the total number of tadpoles emerging from foam at each treatment. The bar at the bottom of the figure denotes hours of daylight (clear) and darkness (black).

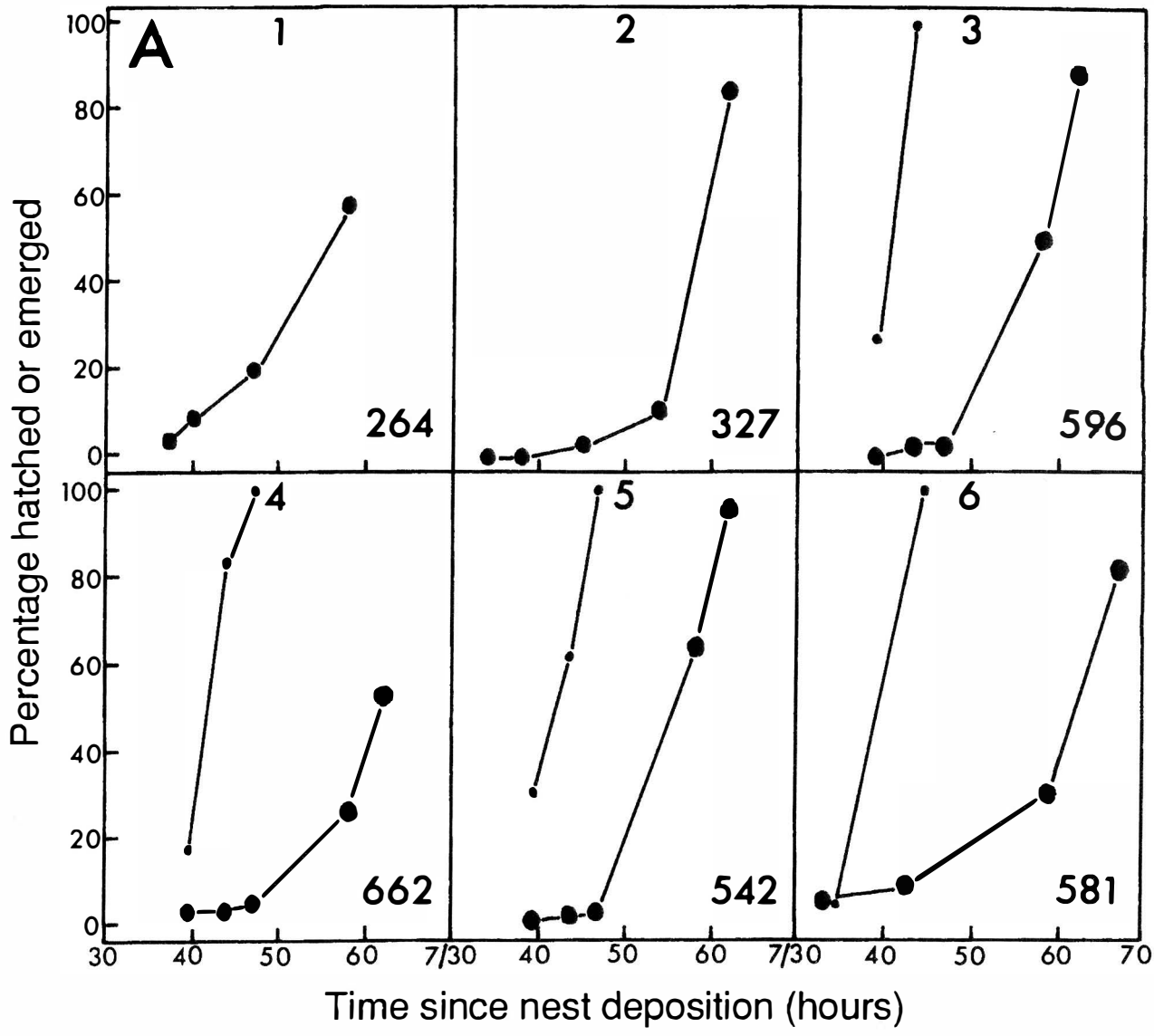

FIG. 2 (Above and opposite) Hatching and emergence from complete nests, incubated with lid on (nests A 1-6) or lid off (nest B 1-8). Numbers hatched or emerged are given as percentages of the total number. Time is measured since a standardised time of nest deposition. Small dots show hatching from groups of single eggs (not carried out for all nests). Large dots show emergence from complete nests. Figures at the bottom right of each box denote the total number of tadpoles emerging from each nest.

lid-off treatments was highly significant ($P < 0.001$). For complete nests, the moist-dehydrated difference was maintained at 67 h: 81% emergence with the lid on and only 36.6% with the lid off ($0.05 > P > 0.02$ in this case).

Post-Hatching Behaviour, Development and Growth

As shown in Fig. 1, single eggs at 'normal' temperature hatched at around 38 h after foam deposition. Examination of recently hatched tadpoles showed them to be at Gosner stage 21 whereas the best developed embryos still in their vitelline membranes were at stage 20. After hatching, tadpoles tended to remain motionless for some time, attached to the bottom or sides of the container by their adhesive glands.

One possible explanation for the difference in time between hatching from single eggs and emergence from complete nests could be that the single eggs were the first in a clutch to be fertilised. This is unlikely, given that the single eggs were taken randomly from the nests and hatched over a 4 h period, whereas emergence from foam extended over a much longer period. Another explanation could be that somehow, single eggs floating at the water surface develop faster than those in foam. This possibility was investigated by allowing tadpoles hatched from single eggs to continue developing, without food, until all tadpoles had emerged from floating foam nests. Samples of the last emergers and earliest hatchers were then fixed and compared. A similar comparison was made between the earliest and later emergers from complete foam nests, incubated floating on the surface of water in closed tubs. The results of both tests are shown in Table 1.

It is clear from these results that in terms of morphological developmental staging, there was no detectable difference between early hatchers and emergers, and late emergers, though there were small size differences. Students *t*-tests were performed on the size differences for each nest separately since a nest effect was evident. Numbers were too small to test differences between tadpoles hatching from single floating eggs and

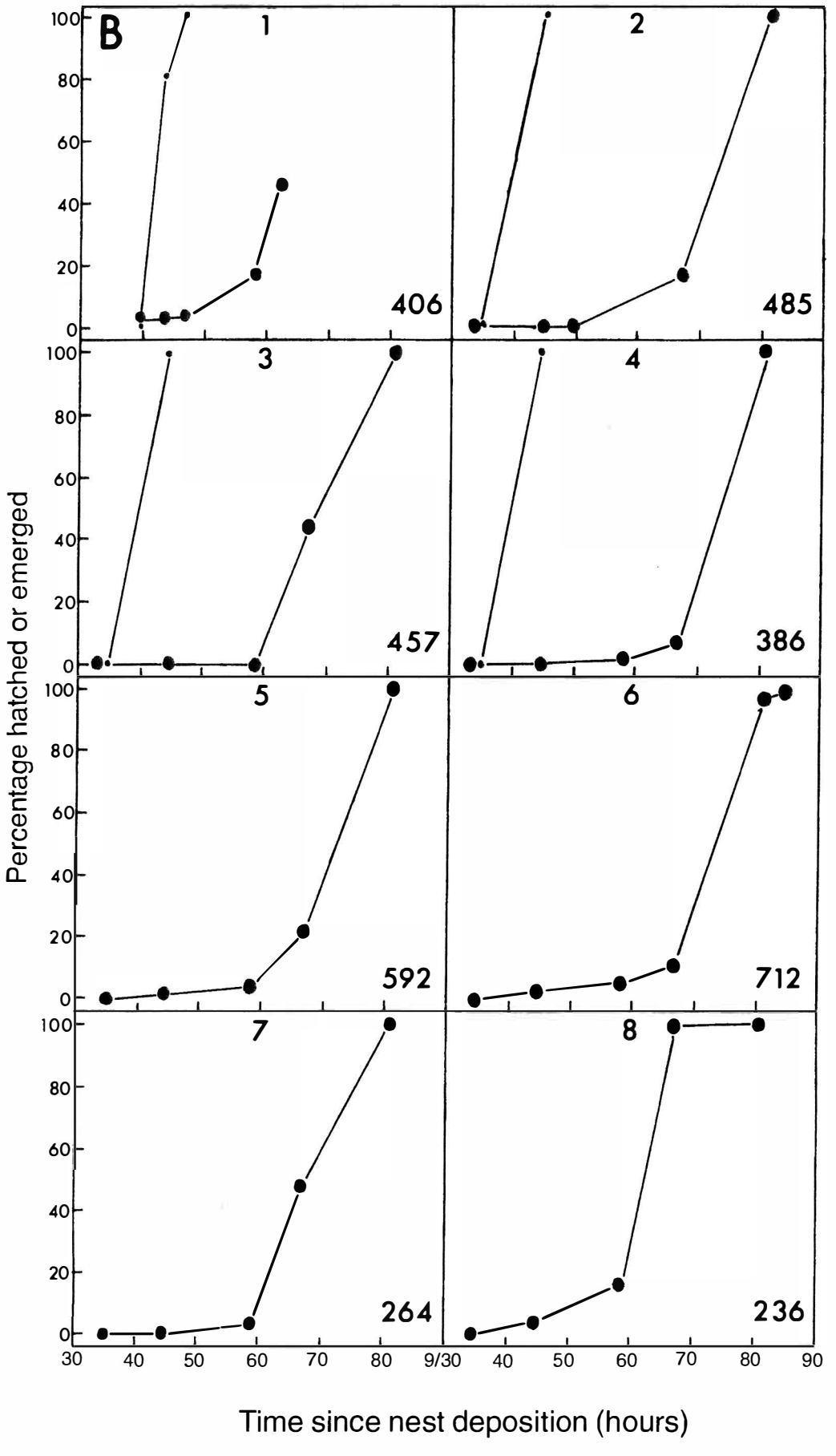

FIG. 2. Continued (previous page and above).

(a) Tadpoles hatched from single floating eggs then kept in water without feeding, compared to latest emergers from floating foam. All measurements soon after time of latest emergence.

		Nest 1	Nest 2
Single eggs:	hatching time (h)	42	42
	number measured	5	10
	Gosner stage	23-24	23-24
	mean body length (mm)	2.82	2.84
	(± SD)	(± 0.07)	(± 0.15)
Floating foam:	emergence time	63.5	63.5
	number measured	2	7
	Gosner stage	23-24	23-24
	mean body length (mm)	2.50	2.75
	(± SD)	(± 0.24)	(± 0.08)

(b) Tadpoles developed in complete foam nests: early emergers compared to latest emergers. All measurements soon after time of last emergence.

		Nest 1	Nest 2	Nest 3	Nest 4
Early emergers:	emergence time (h)	54	54	43.5	43.5
	number measured	14	13	4	9
	Gosner stage	23	23	23	23
	mean body length (mm)	2.53	2.56	2.29	2.17
	(± SD)	(± 0.1)	(± 0.12)	(± 0.29)	(± 0.12)
Late emergers:	emergence time (h)	59.5	59.5	62	62
	number measured	10	15	13	11
	Gosner stage	23	23	23	23
	mean body length (mm)	2.37	2.46	2.13	2.05
	(± SD)	(± 0.08)	(± 0.1)	(± 0.18)	(± 0.08)
	P	<0.001	0.05>*P*>0.02	NS>0.1	0.02>*P*>0.01

TABLE 1. Comparison of morphological stages and body sizes of tadpoles entering water early with those entering late.

		Nest 1	Nest 2	Nest 3	Nest 4
(a) Early emergers:	Number	26	24	7	10
(characters at time	Time (h)	58.8	44.5	58.5	44.5
of emergence)	Gosner stage	22	21-22	22	21-22
	mean body length (mm)	2.17	not clearly	2.08	not clearly
	(± SD)	(± 0.14)	defined		defined
	number measured	3	0	1	0
(b) Early emergers:	Number	23	21	6	8
(characters after	Time (h)	84	84	84	84
growth to time of	Gosner stage	25	24	24-25	25
late emergers)	mean body length (mm)	3.00	2.57	3.17	3.05
	(± SD)	(± 0.1)	(± 0.23)	(± 0.07)	(± 0.17)
	number measured	10	10	4	5
(c) Late emergers:	Number	463	19	136	224
	Time (h)	81	84	81	81
	Gosner stage	23-24	23	24	23-24
	mean body length (mm)	2.59	2.46	2.70	2.66
	(± SD)	(± 0.7)	(± 0.2)	(± 0.08)	(± 0.21)
	number measured	9	16	12	7
	P (*b* v. *c*)	< 0.001	NS>0.2	< 0.001	0.01>*P*>0.001

TABLE 2. Comparison of morphological stages and body sizes of tadpoles entering water early and allowed to grow with those entering late.

those hatching last from floating foam (Table 1a). However, at the same time of fixation, tadpoles emerging early from complete foam nests were significantly longer than those emerging late in three out of the four nests measured (Table 1b). In the remaining nest, there were only four early emergers to measure. Another relevant observation is that in floating foam nests past the stage where hatching has occurred, hatched tadpoles could be seen at the upper surface of the foam, often wriggling around actively. These were not simply hatchlings from eggs which happened to be at the foam surface, since there were normally rather few such eggs, yet many tadpoles were found at the surface. This observation was made only in foam nests where the foam surface was moist. When nests were incubated in open tubs, the foam surface dried out, and tadpoles were not seen at the upper surface.

It is possible that tadpoles that emerge early from nests have some advantage in gaining access to food before those that emerge late. This was tested by isolating groups of early emergers from complete nests, then allowing them to grow in conditions similar to those they would meet in the field in tubs with water over a muddy bottom, with a little food added. These were grown until the time the latest emergers appeared from each nest. Samples of fed and late emerging tadpoles were then fixed for comparison. The results are shown in Table 2. In all cases, tadpoles that emerged early and were given access to food grew and developed so that they were in advance of those that emerged last, though in one case (nest 2), the difference was very small. A Student *t*-test was performed on the body length results for the fed and late emerging tadpoles from each nest separately. The larger size of the fed tadpoles was significant in three out of the four nests measured. In the remaining nest, early fed emergers failed to grow and were no larger than later emergers at the time of fixation.

DISCUSSION

This study began with the hypothesis that emergence from foam might be synchronised as a predator-satiation device. This clearly does not happen in the case of *Physalaemus*. At the ambient temperature used here (28-29°C), eggs hatched into the foam around 38 h after foam deposition: a few emerged from the nest soon afterwards, but it took many hours for all to emerge, the actual time depending on the size of the piece of foam and on whether the foam surface remained moist or became dry. Kenny (1969) reported that hatching into the foam took 72 h and that tadpoles remained there up to seven days. Unfortunately, Kenny did not give data on incubation temperatures: his times are about twice those reported here.

What are the reasons for the delay in tadpole emergence? There are a number of possible explanations, some adaptive, others not. First, the sequence of emergence might simply reflect individual differences in development rate. The evidence is against this explanation. Randomly chosen isolated eggs hatched over a period of as little as 2 h, yet the delay in emergence was 16 h or more. Unfed early emergers were at the same developmental stage as the latest emergers when the latter left the nest. Since Hödl (1990) found that complete nest construction in the related *Physalaemus ephippifer* took only 40 mins, with egg release occurring over only part of that time, there can be little variation in time of fertilization in a complete batch of eggs. My results do show a small difference in body size between unfed early emergers and newly emerged late emergers, but this may simply be due to more complete hydration of the tissue.

Next, the tadpoles might choose a particular time of day to emerge: for example, since many aquatic predators, such as odonate larvae, are primarily visual, there could be an advantage to emerging in the dark. In salmonids, where hatchlings remain many days in gravel nests before emerging, it is well established that emergence is linked to the onset of darkness, with a high proportion emerging in the first dark hour (Brannas, 1987). However, the evidence gives no support to this idea in the case of *P. pustulosus*. Tadpole emergence showed no response to constant dark or light, or to changes in natural light. When low temperature slowed development by approximately 12 h over the normal period to emergence, tadpoles emerged during daylight rather than in the 'normal' darkness.

A different adaptive explanation is to see the foam nest as a protective refuge. Hatching stage larvae may be particularly vulnerable. It may therefore be advantageous to remain some time in the foam after hatching: despite the lack of food, development can continue based on the remaining yolk reserves. Individual tadpoles may then make the choice either to emerge or to remain longer in the nest, retaining the protection but suffering a potential delay in growth. This explanation has no particular evidence against it. Previous work (Downie, 1988; 1990) has shown that foam nests offer effective protection to eggs against predators: they can clearly do the same for hatchlings. Larval development does continue, without additional food, in those that stay in the nest, from Gosner stages 21 to 24. The gradual pattern of emergence fits the idea of tadpoles choosing between protection and potential growth. The ability of early emergers to develop when fed beyond the stage of later emergers shows that there is a real cost in late emergence. Although the delay in emergence and the amount of growth achieved in the first day may both seem small, *P. pustulosus* tadpoles can reach metamorphosis in 2 weeks but live in temporary pools that have a high risk of drying up (Downie, unpublished): in the circumstances, an emergence delay of even one day is significant. What is lacking so far is a demonstration that early emergers (stage 21-22) are more vulnerable to predation than late emergers (stage 24) but this is at least plausible given the maturation of the locomotory and other systems that occurs over this period.

Though this explanation is attractive, a final more trivial possibility must be examined. A *Physalaemus* foam nest is quite large (of the order of 80 cm^3 in volume) and the foam is a highly cohesive material. It may simply be that hatchlings find it difficult to make their way out of the nest and that complete emergence therefore takes time. The following evidence suggests that this is at least part of the explanation for the emergence delay. Total emergence from sub-divided nests is quicker than from complete ones. Drying out of the nest, which makes the foam more cohesive, delays complete emergence. However, this seems unlikely to be the entire explanation. Eggs are distributed throughout the foam, some very close to the bottom and therefore to water, yet very few emerge just at the time of hatching. Finally, the observation that many tadpoles move to the top rather than the bottom of the foam suggests that they have some reason to stay there.

It is not known how common delayed emergence is in amphibians, though it is well known in fish (Brannas, 1987) where hatching is often followed by a long period where the young fish grow using their yolk reserves in the protected environment of a nest (for example, salmonids) or egg case (for example, dogfish). In anurans, delayed emergence only seems a possibility where relatively large eggs are deposited in some sort of protective nest. In the *Leptodactylus* '*fuscus*' species group, tadpoles remain up to several weeks after hatching in nests laid on land in burrows (Downie, 1984). However, where eggs are laid in water singly or in jelly strings as in *Xenopus* and the bufonids, rupture of the outer jelly capsules occurs before hatching from the vitelline membrane (Duellman & Trueb, 1986; personal observation on *Bufo granulosus*): in these species, there is no potential for the delayed emergence seen in *Physalaemus*

The recent study of Magnusson & Hero (1991) demonstrates the importance of anuran egg predation by aquatic invertebrate larvae and by tadpoles. The present study suggests the need to investigate predation pressure on early post-hatching stages too.

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EMBRYONIC AND LARVAL SURVIVAL OF THE COMMON FROG (*RANA TEMPORARIA* L.) IN ACIDIC AND LIMED PONDS

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ABSTRACT

Limestone was added to two acidic ponds in upland, northern England in an attempt to improve the survival of embryos and larvae of the common frog (*Rana temporaria* L.). As expected, the addition of limestone to the ponds resulted in a significant increase in both the pH and the dissolved calcium concentration of the pond water. Fertilization success of common frog eggs was approximately 87% in acidic water and increased to 100% following liming. Embryonic survival in the two acidic ponds increased from 0% and 22% to 69% and 93% respectively following liming. A year after liming, embryonic survival in one pond had decreased significantly from 93% to 79%. It was estimated that at least 2.1% of the eggs deposited in a limed pond gave rise to metamorphs. The environmental implications of liming acidic frog breeding ponds are discussed.

INTRODUCTION

The common frog (*Rana temporaria* L.) is known to breed in oligotrophic waters which are susceptible to anthropogenic acidification (Aston, Beattie & Milner, 1987; Hagström, 1981; Leuven *et al.*, 1986). A number of laboratory studies indicate that acid water, with or without high concentrations of aluminium, can cause sublethal and lethal effects in common frog eggs and larvae (Andrén *et al.*, 1988; Beebee & Griffin, 1977; Cummins, 1986, 1989; Linnenbach, Marthaler & Gebhardt, 1987; Olsson *et al.*, 1987; Tyler-Jones, Beattie & Aston, 1989). There is concern that amphibians might be declining in areas of Britain (Fry, unpubl., cited in Fry & Cooke, 1984) and Sweden (Hagström, 1981) subjected to acidification.

The addition of limestone ($CaCO_3$) to acid waters can increase the pH and reduce the concentration of toxic aluminium species (Underwood, Donald & Stoner, 1987) and consequently increase the abundance and diversity of aquatic organisms (Eriksson *et al.*, 1983; Hasselrot, Andersson & Hultberg, 1984; Raddum *et al.*, 1986; Rosso, 1977). It should be noted, however, that the abundance of certain organisms can decline after the addition of limestone to acid waters, due to a variety of factors such as increased survival of predatory fish (Evans, 1989; Hultberg & Andersson, 1982).

In the present study, limestone was added to two acidic, frog breeding-ponds in northern England in an attempt to improve the survival of common frog embryos and larvae. The main aim of the present study was to assess the survival of common frog embryos and larvae in acidic ponds, before and after liming.

MATERIALS AND METHODS

DESCRIPTION OF SITES

Two acidic ponds (1.4 km apart) in northern England were used in this study, both being on open moorland with a substratum of peat. Pond 1 (altitude, 617 m OD; latitude 54° 46' 56" N. longitude 2° 18' 42" W; National Grid reference NY 800 432) and Pond 2 (altitude, 600 m OD. latitude 54° 47' 40" N, longitude 2° 19' 7" W; National Grid reference NY 796 445) were similar in depth and had surface areas of 70 m^2 and 160 m^2 respectively. Frogs have spawned in pond 1 recently (30 clumps in 1985, 22 clumps in 1988), whereas frogs stopped spawning in pond 2 around 1975.

WATER CHEMISTRY AND TEMPERATURE

Field measurements of pH and conductivity were made using a Radiometer M80 portable pH meter and an EIL MC-1 conductivity meter. Water samples from ponds 1 and 2 were filtered through a 0.45 µ membrane filter and samples for cation analysis were acidified to 1% v/v with Aristar nitric acid.

The concentrations of different aluminium species (acid soluble aluminium; total monomeric aluminium; labile, inorganic, monomeric aluminium and non-labile, organic, monomeric aluminium) were measured in ponds 1 and 2, using a modification of the catechol violet method (Dougan & Wilson, 1974; Seip, Muller & Naas, 1984).

The concentrations of Na and K were measured by flame emission spectrophotometry. Ca, Mg, Fe, B, Cu, Cd, Hg, Mn, Mo, Ni, Pb, S, Si, Ti, and Zn concentrations were measured with a Bausch and Lomb Inductivity Coupled Plasma Atomic Emission Spectrophotometer (Series No. 34000). Cl, SO_4, NO_3, and NH_4 concentrations were measured using an Ion Chromatograph (Dionex).

Maximum/minimum thermometers were placed in both ponds, next to the egg clumps, and were read and reset nine times during the study.

LIMING

Limestone ($CaCO_3$) was used because it is cost-effective and has been shown to be the best material for improving the water quality for fish (Underwood, Donald & Stoner, 1987). On 6 April 1988, powdered limestone was uniformly spread over pond 1 at a dose equivalent to 250 g m^{-2}, while pond 2 was left as an unlimed control. On 22 February 1989, a similar rate of liming was applied to pond 2. Given that both ponds were similar in depth, they each received approximately 333 mg of limestone per litre.

Fertilization Success Following Liming

In the spring of 1988, frogs laid two egg clumps in pond 1 after liming. Samples of approximately 50 eggs were taken from each clump shortly after spawning and reared in the laboratory, in conditions suitable for normal development (i.e. dechlorinated tap-water, pH 7, temperature 15°C), so that fertile eggs could be easily distinguished from infertile ones.

Embryonic and Larval Survival

Field-based experiments were performed to estimate the survival of frog embryos in 1985 (pond 1 only), 1988 (ponds 1 and 2) and 1989 (ponds 1 and 2). In 1988, estimates of embryonic and larval survival at different developmental stages were made. Details of the methods are given below.

On 16 April 1985, samples of approximately 50 eggs (all at the two- or four-cell stage; stages 3 to 4, Gosner, 1960) were taken from 30 egg clumps deposited in pond 1. These samples were placed in numbered vessels which allowed the free circulation of water, and were then returned to pond 1. On 9 May (after 23 days in pond 1), the normal embryos had reached gill circulation (stage 20, Gosner, 1960) and had hatched. The vessels were removed from pond 1 and the numbers of normal embryos hatching successfully and the numbers of dead and abnormal embryos were recorded.

On 6 April 1988, all egg clumps (23) were removed from pond 1 before it was limed. Twenty of these egg clumps (at stages 3 to 4, Gosner, 1960) were each divided into two approximately equal portions. The number of eggs in each half-clump was assessed gravimetrically and a numbered tag was attached to each half-clump. On 7 April, twenty-clumps were replaced in pond 1 (after it had been limed) and the other corresponding twenty half-clumps were placed in pond 2 (unlimed control). No eggs were deposited naturally in pond 2 in the spring of 1988.

To assess embryonic survival at different developmental stages, approximately 20 eggs were taken from each of the 40 half-clumps in ponds 1 and 2 after 7, 14 and 19 days from the start of the experiment (i.e. on 14, 21, and 26 April 1988). These eggs were returned to the laboratory and reared in conditions suitable for normal development (dechlorinated tap-water, pH 7, temperature 15°C) until all the normal embryos had reached stage 20 and had hatched. The numbers of normal embryos hatching successfully and the numbers of dead and abnormal embryos resulting from laboratory culture were recorded.

On 12 July and 8 August 1988, estimates of the numbers of frog larvae in ponds 1 and 2 were made using the successive removal method (Southwood, 1980).

On 10 April 1989, twenty spawn clumps (stages 3 to 4, Gosner, 1960) were taken from pond 1 and divided into approximately equal halves. Each half-clump was then placed in an individually numbered vessel which allowed the free circulation of water over the eggs. One half of each of the twenty clumps was then replaced in pond 1 and the corresponding twenty half-clumps placed in the recently-limed pond 2. On 8 May 1989 (28 days from the start of the experiment) the normal embryos had reached gill circulation (stage 20, Gosner, 1960) and had hatched. The vessels were removed from ponds 1 and 2 and the numbers of normal embryos hatching successfully and the numbers of dead and abnormal embryos were recorded.

Statistical Methods

The numbers of normal embryos hatching successfully and the numbers of dead and abnormal embryos were expressed as percentages. To normalize the distribution of these data, percentages were arcsin transformed (Sokal & Rohlf, 1981). Paired t tests and t tests for independent samples were the statistical tests used.

RESULTS

Water Chemistrty and Temperature

Ponds 1 and 2 were both acidic, oligotrophic ponds before liming (Table 1). The differences between ponds 1 and 2 in pH, conductivity, total monomeric Al, labile inorganic monomeric Al, Ca, K, Mg, Fe, Cl, SO_4 and NO_3 were tested statistically before and after liming (post-lime data for pond 1 in 1988 and 1989 being combined). Before liming, there was significantly more Ca, Mg and total monomeric aluminium in pond 2 than in pond 1 (t=2.64, df=10, P=0.025; t=2.60, df=9, P=0.029; t=2.68, df=5, P=0.044 respectively). Sample sizes were too small to carry out statistical tests on the other water chemistry parameters listed in Table 1. The concentration of Si in pond 2, however, appears to have been much higher than in pond 1.

In pond 1, pH and conductivity were significantly higher after liming (t=6.54, df=3, P=0.0073; t=4.05, df=10, P=0.0023 respectively) as were the concentrations of Ca, K and Mg (t=3.69, df=7, P=0.0078; t=4.17, df=8, P=0.0032; t=4.55, df=9, P=0.0014 respectively).

The pH of pond 1 increased to a maximum value of 8.04 on 14 April 1988 (eight days after liming) and it subsequently fell to a minimum value of 5.90 on 22 February 1989 (322 days after liming). From February to May 1989, the pH of pond 1 increased again to 6.53.

The conductivity of pond 1 increased to a maximum value of 204 $\mu S\ cm^{-1}$ on 14 April 1988 (eight days after liming) and it subsequently fell to a minimum value of 52 $\mu S\ cm^{-1}$ on 30 September 1988 (177 days after liming). From September 1988 to May 1989, the conductivity of pond 1 fluctuated around 76 $\mu S\ cm^{-1}$.

The Ca concentration of pond 1 rose to a maximum value of 32.8 $mg\ l^{-1}$, on 14 April 1988 (eight days after liming) and it subsequently fell to a minimum value of 2.2 $mg\ l^{-1}$ on 10 April 1989 (369 days after liming). From April to July 1989, the Ca concentration of pond 1 increased steadily to 9.0 $mg\ l^{-1}$.

In pond 2, pH and the concentration of Ca increased significantly after liming (t=12.42, df=2, P=0.0064; t=4.40, df=2, P=0.048 respectively).

Both total monomeric and labile, inorganic, monomeric aluminium concentration decreased after liming, but these reductions were not statistically significant (P>0.05), probably due to the small sample sizes.

In 1985, the minimum and maximum temperatures in pond 1 during the embryonic development period (16 April - 9

	POND 1			POND 2	
	pre-lime (1985-88)	post-lime (1988)	post-lime (1989)	pre-lime (1985-89)	post-lime (1989)
pH	4.84 (3)	7.34 (12)	6.23 (4)	3.92 (13)	7.39 (3)
COND.	42 (3)	134 (9)	76 (4)	74 (10)	107 (3)
TAl	0.065 (3)	0.065 (4)	0.022 (3)	0.127 (8)	0.063 (2)
MAl	0.026 (2)	0.006 (4)	0.004 (3)	0.119 (7)	0.035 (2)
Ca	0.627 (4)	28.6 (4)	5.63 (4)	1.096 (9)	39.57 (3)
Na	4.33 (4)	3.5 (4)	5.108 (4)	4.352 (9)	5.293 (3)
K	0.583 (4)	2.690 (3)	1.333 (4)	0.493 (8)	0.943 (3)
Mg	0.451 (4)	1.033 (4)	0.903 (4)	0.681 (9)	1.227 (3)
Fe	1.357 (4)	1.183 (4)	2.695 (4)	0.554 (9)	0.343 (3)
Cl	7.3 (4)	4.918 (4)	10.37 (4)	8.25 (9)	10.293 (3)
SO_4	4.52 (4)	7.103 (3)	2.918 (4)	5.613 (8)	6.84 (3)
NO_3	0.166 (4)	0.105 (3)	0.123 (4)	0.114 (8)	0.306 (3)
NH_4	0.57 (3)			0.74 (3)	
B	0.20 (3)			0.012 (3)	
Cu	0.006 (3)			0.004 (3)	
Cd	0.006 (2)			0.006 (2)	
Hg	0.01 (2)			0.01 (2)	
Mn	0.038 (3)			0.024 (3)	
Mo	0.01 (3)			0.01 (3)	
Ni	0.011 (3)			0.011 (3)	
Pb	0.042 (3)			0.046 (3)	
S	1.67 (3)			1.92 (3)	
Si	0.099 (3)			0.271 (3)	

TABLE 1. Mean values and sample sizes (*n*) are given for pH, conductivity (μS cm^{-1}) and ion concentration (mg l^{-1}), measured in ponds 1 and 2. COND, conductivity; TAl, total monomeric aluminium; MAl, labile inorganic monomeric aluminium. Pond 1, pre-lime, water chemistry measurements were taken in April 1985, 1986 and 1988; post-lime measurements weretaken between April and September 1988 and between February and July 1989. Pond 2, pre-lime, water chemistry measurements were taken in April 1985 and 1986, between April and September 1988 and also in February 1989; post-lime measurements were taken between March and July 1989.

May), were 10 and 15°C respectively. In 1988, the minimum temperatures in ponds 1 and 2 during the embryonic development period (7 - 26 April) were 0 and 1°C respectively, and the maximum temperature in both ponds was 15°C. In 1989, the minimum temperatures in ponds 1 and 2 during the embryonic development period (10 April - 8 May) were 0 and 2°C and the maximum temperatures were 11 and 17°C respectively.

Embryonic Survival

When limestone was added to ponds 1 and 2, the mean percentage survival of embryos increased in the following season, from 22% to 93% and from 0% to 69.3% respectively (Table 2). Embryonic survival in pond 1 decreased from 93% to 79% a year after liming (Table 2).

In 1988, a significantly higher percentage of embryos (at all stages) survived in pond 1 (limed) than survived in pond 2 (unlimed). There was no significant difference between ponds in the percentage of abnormal eggs after seven days, but there was a significantly higher percentage of abnormal eggs in pond 1 after 14 days (Table 2).

In April 1989, a significantly higher percentage of embryos survived in pond 1 (limed in 1988) than survived in pond 2 (limed in 1989) (Table 2). There was no significant difference between ponds in the percentage of abnormal eggs (Table 2).

Larval Survival

On 7 April 1988, 6311 eggs (ie. 20 half-clumps) were placed in pond 1. On three occasions, a total of 1305 eggs were taken from pond 1 to assess embryonic survival at various developmental stages, leaving 5006 eggs in pond 1 on 26 April. On 12 July 1988, there were estimated to be 285 frog larvae (most with hind limbs; stages 36-39, Gosner, 1960) in pond 1 (ie. 5.7% survival from 5006 eggs). On 8 August 1988, there were estimated to be 106 larvae (most with front limbs; stages 42-46, Gosner, 1960) in pond 1 (ie. at least 2.1% survival). Several froglets were also found around the pond, thus survival at this time was probably underestimated due to froglets leaving the pond.

DISCUSSION

As might be expected, there was a significant increase in pH in both ponds following liming. Dissolved limestone neutralizes the acids in the water by a series of chemical reactions outlined by Underwood, Donald & Stoner (1987). The dissolved calcium concentrations in both ponds 1 and 2 increased significantly following liming by approximately 28 and 38 mg l^{-1} respectively. A year later, the mean concentration of dissolved calcium in pond 1 had declined by 23 mg l^{-1} to 5.6 mg l^{-1}. The concentrations of total monomeric and labile, inorganic, monomeric aluminium decreased following liming, although these reductions were not statistically significant, presumably due to the small sample sizes. The aluminium concentration in

	% normal hatch		% dead		%abnormal	
	Pond 1	Pond 2	Pond 1	Pond 2	Pond 1	Pond 2
1985	unlimed	unlimed	unlimed	unlimed	unlimed	unlimed
Stage 20	21.5 (30)	-	76.0 (30)	-	2.5 (30)	-
1988	limed	unlimed	limed	unlimed	limed	unlimed
Stage 14	89.8 (20)	9.2 (19)	7.3 (20)	88.0 (19)	3.0 (20)	2.4 (19)
	t=16.5, n=19, P<0.00001		t=15.8,n=19,P<0.00001		t=1.3, n=19,P=0.2	
Stage 17	92.5 (16)	1.8 (11)	5.9 (16)	97.7 (11)	1.6 (16)	0.5 (11)
	t=22.1, n=11, P<0.00001		t=20.8, n=11, P<0.00001		t=2.8, n=11, P=0.018	
Stage 18	93.2 (13)	-	3.6 (13)	-	3.2 (13)	-
1989	limed (1988)	limed	limed (1988	limed	limed (1988)	limed
Stage 20	79.09 (20)	69.3 (20)	16.4 (20)	27.3 (20)	4.6 (20)	3.4 (20)
	t=2.95,n=20,P<0.0082		t=4.71, n=20, P=0.0002		t=0.66, n=20, P=0.52	

TABLE 2. The fate of eggs in pond 1 (limed once in April 1988) and pond 2 (limed once in April 1989). In 1985 and 1989, newly fertilized eggs were placed in pond 1 and ponds 1 and 2 respectively, and removed when they had developed to stage 20 (gill circulation). In 1988 newly fertilized egg clumps were placed in ponds 1 and 2. Egg samples were taken from the clumps in both ponds after seven days (when the eggs were at the neural fold stage of development [stage 14]), 14 days (tail bud [stage 17]) and 19 days (muscular response [stage 18]) from the start of the experiment. The mean percentage of normal eggs hatching successfully, dead and abnormal eggs are given with the number of clumps sampled (n). Paired t test values, on arcsin transformed percentages, show the significance of the differences between ponds 1 and 2. In 1988 no values were available for pond 2 after 19 days as all the eggs had decomposed. Several of the egg clumps disappeared from pond 1 but the reason for this is unknown.

acidic waters normally decreases following liming (Hasselrot & Hultberg, 1983; Hasselrot, Andersson & Hultberg, 1984; Raddum *et al.*, 1986; Underwood, Donald & Stoner, 1987), due to the precipitation of aluminium compounds following the increase in pH (Underwood, Donald & Stoner, 1987; Wright, 1982).

The mean number of eggs (±1SE) in the clumps produced by upland *R. temporaria* was 631±38.2 (maximum 1134, minimum 403), less than half the number normally produced by lowland frogs in this area (Beattie, 1987). This has implications for the potential recruitment from upland ponds.

When *R. temporaria* eggs were laid in pond 1 after liming, infertility was estimated to be <1%. An earlier study on common frogs in this area (Beattie, Aston & Milner, 1991) showed that fertilization success in pond 1 prior to liming was 87%. Thus fertilization success increased following liming, but in general, fertilization success in the common frog is not greatly reduced in acidic conditions.

Prior to the addition of limestone, the survival of *R. temporaria* embryos in ponds 1 and 2 was 21% and 0% respectively. Mortality in these ponds probably resulted from the combined effects of low pH and high aluminium concentration (forming toxic inorganic, monomeric aluminium) (Andrén *et al.*, 1988; Clark & Hall, 1985; Clark & LaZerte, 1985; Freda & McDonald, 1990; Olsson *et al.*, 1987; Tyler-Jones, Beattie & Aston, 1989). Survival was probably lower in pond 2 because it was more acidic and had a higher aluminium concentration than pond 1. Most mortality occurred in the early stages of development (prior to the formation of the neural fold; stage 14, Gosner, 1960). In 1985, only 21% of the common frog embryos survived to hatching in pond 1. This survival value was lower than would have been predicted from laboratory studies (Tyler-Jones, Beattie & Aston, 1989), given the pH and aluminium concentration of the water in pond 1. It has been shown that pond water can be more toxic than artificial soft water under certain conditions, particularly when the pond water has a high concentration of dissolved organic carbon (Freda, Cavdek & McDonald, 1990). Other variables such as temperature may also be important.

The survival of frog embryos increased in both ponds after liming. Increased survival presumably resulted from a rise in pH. The increase in calcium concentration may have had an ameliorative effect by reducing sodium efflux at low pH (Cummins, 1988; Freda & Dunson, 1984).

A year after liming, embryonic survival in pond 1 had decreased significantly by 14%. Whether this was related to the reduction in the dissolved calcium concentration in the pond is unclear. Pond 1 had a mean pH of 6.23 and a mean total monomeric aluminium concentration of 0.022 mg l^{-1}, during the development period, which should pose no significant threat to embryonic survival. This suggests that other factors may have been responsible for this decline.

More abnormal frog embryos occurred in pond 1 after liming than in pond 2 when unlimed. This is probably because abnormal embryos are able to survive in the limed water whereas they are killed and decompose at an early stage of development in acidic water.

Larval development appeared normal and froglets successfully emerged from limed pond 1. There were estimated to be 106 larvae in pond 1, at the time of emergence (ie. 2.1% survival). This is similar to some lowland, neutral ponds where the survival of common frog larvae at emergence is approximately 1% (Savage, 1961).

Uplands ponds in this area have probably always been acidic due to the surrounding peat. In addition, they have a poor buffering capacity which makes them susceptible to anthropogenic acidification. The frogs in this area are comparatively acid-tolerant ecotypes (Tyler-Jones, Beattie & Aston, 1989). Such intraspecific variation in acid-tolerance has also been recorded in other frogs (Andrén, Mårdén & Nilson, 1989; Pierce & Harvey, 1987). Nevertheless, several ponds are too acidic to support frogs and survival is reduced in others (Aston, Beattie & Milner, 1987; Beattie, Aston & Milner, 1991).

The frogs that live in this upland area appear to be specialized ecotypes (Beattie, 1987) worthy of protection. It is important, however, that other acidophilic species in these ponds are not lost. A compromise would be to lime selected highly acidic ponds, which would restore them for use for both frogs and invertebrates (Rosso, 1977). A balance would have to be struck between saving threatened populations and the danger of diluting the acid tolerant gene pool. Liming acidic waters can be undertaken economically (Blake, 1981) and would provide a reservoir of upland frog-ecotypes in this area.

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