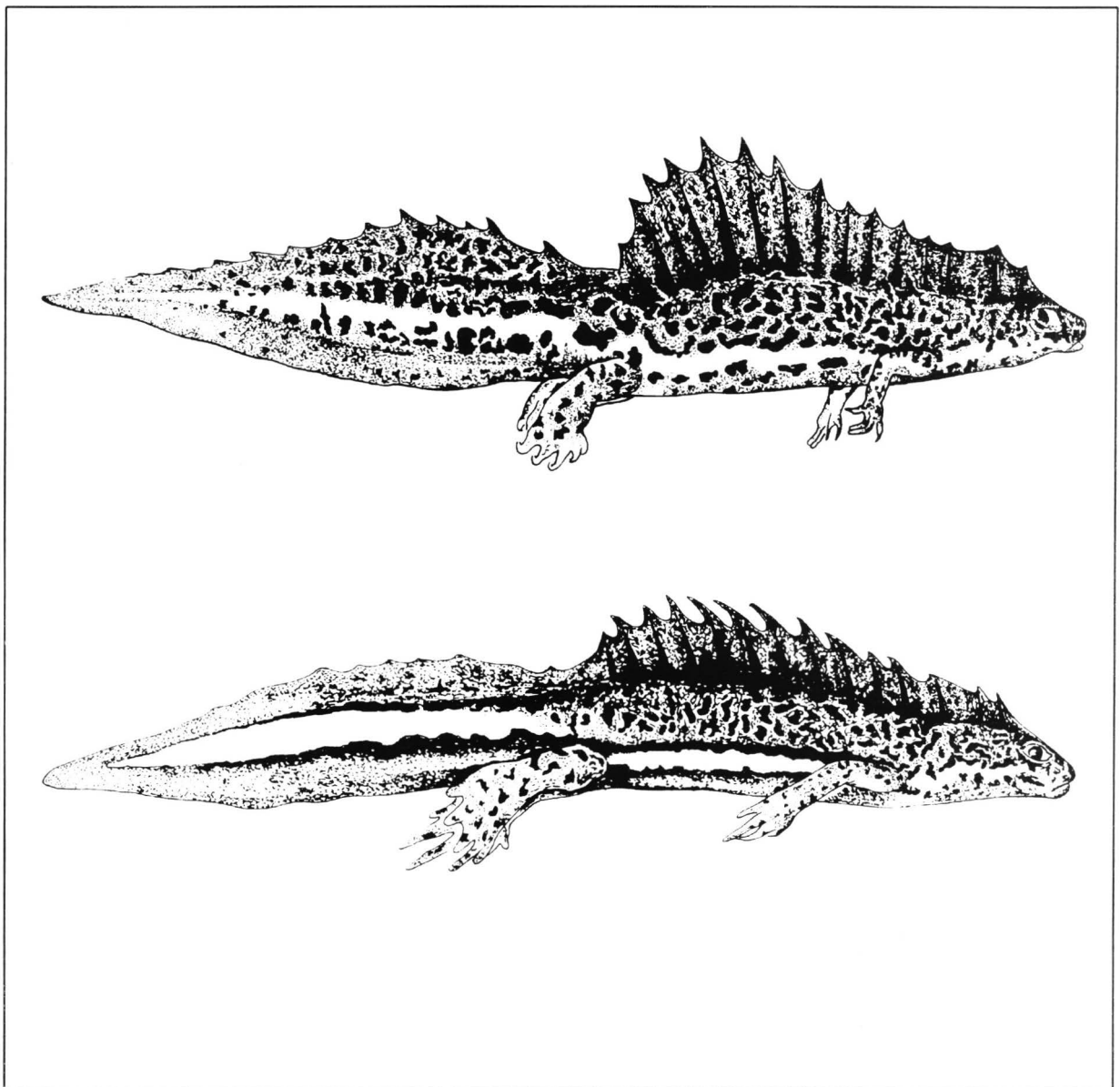


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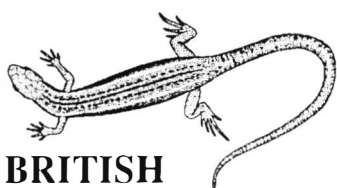
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FRONT COVER: *Triturus vittatus cilicensis* (top) and *T. v. vittatus* (bottom). K. Olgun.

THE BRITISH HERPETOLOGICAL SOCIETY: THE FIRST 50 YEARS, 1947-1997

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Twenty-one members attended the founding meeting of the British Herpetological Society on 1 July 1947. At the inaugural meeting the founding President, Dr Malcolm Smith, stressed the importance of studying the behaviour and ecology of reptiles and amphibians, appreciating that here was an opportunity for the professional and aspirant herpetologist alike. Membership grew to over 200 by 1950, and to over 1000 by 1990. The Conservation Committee was established in 1969, with the aim of protecting Britain's three rare and endangered species. There followed, in 1976, the Captive Breeding Committee, which would advise members on the care and breeding of species in captivity. Starting in 1970, the biannual *Newsletter* became the *Bulletin* in 1980, and this has been published quarterly since 1985. Filling a gap for the rapid communication of news and views to members, the monthly *Natterjack* came into being in 1995. Education has always been recognized by the society as important, and in 1983 the Education Officer established the Education Committee, which was responsible for co-ordinating activities of the Junior Section of the Society. During the 1980s the scientific standing of the society grew steadily and in 1985 the journal was renamed *The Herpetological Journal* to reflect the increasingly international nature of the papers published. Seven years later the journal became quarterly, and the submission rate of papers has continued to increase year-by-year to the present day. The increasing scientific activity within the society's ranks led to the formation of the Research Committee during the run-up to the First World Congress of Herpetology, held in Britain in 1989 and co-hosted by the Society. From a society which catered primarily for an interest in animals in captivity, the British Herpetological Society has broadened its remit over the past 25 years to one concerned with conservation, captive breeding, education and research.

INTRODUCTION

Although the pursuit of natural history is well-en-gained within the cultural history of Britain, the professional biologist is a relatively recent development. Until the present century, discoveries about the natural world were largely reported by enlightened amateurs, often regarded as pillars of local society. Typical among the early naturalists were physicians, classicists, clerics, barristers and soldiers, and it is salutary that it is just such a group that gave rise to the embryonic British Herpetological Society. Dr Malcolm Smith, a physician by training, returned to Britain in 1925 after serving in the Royal Court of Siam. His retirement allowed him time to produce a series of publications, primarily focused on the herpetofauna of south-east Asia. The end of the Second World War allowed the people of Britain to rediscover personal hobbies and interests, and as Malcolm Smith was turning his attention to preparing a definitive work on the natural history of reptiles and amphibians in Britain (Smith, 1951), the time seemed ripe for a formal association of like-minded people to be formed.

The founding meeting of the British Herpetological Society was held on 11 July 1947 in the rooms of the Linnean Society of London, and was attended by twenty-one members. Some fifty people had agreed to join, and Captain J. D. Romer had been acting as Secre-

tary. The account that follows of the first 25 years is based mostly on descriptions of the Society's early days by a former President in respectively the *British Journal of Herpetology* and *BHS Bulletin* (Frazer, 1977; 1983a), and by me in *BHS Bulletin* (Lambert, 1980).

The founding members of the Society included a very strong body of naturalists and scientists: such names as Dr Malcolm Smith, Dr L. Harrison Matthews, FRS, Dr Maxwell Savage and Dr (later Prof.) Angus d'A. Bellairs are, even today, well-known beyond herpetological circles. There were also H.W. Parker (from the Natural History Museum), Louis Lantz, Prof. Jack Haldane, Major Maxwell Knight, OBE (an early broadcaster and writer on wildlife, producer of a television interview series on wildlife, and considered to be the original M in the James Bond stories!), Oliver Hook (a very fine amateur naturalist) and Jack Lester (Curator of Reptiles at the London Zoo).

YEARS TO THE JUBILEE, 1947-1972

The founding Secretary, John Romer, accepted a posting in Hong Kong in 1947, and Mr Alfred Leutscher took over as Honorary Secretary, circulating a *Bulletin* on 1 August 1947 to announce the successful inauguration of the Society. It was decided that the Society's publications should take the form of (1) a

Bulletin to be issued to members, as and when necessary, to convey information as to the Society's activities, meetings, progress, etc; and (2) a *Journal* of proceedings, free to members, to be published annually, and containing work submitted by members.

During discussions at the inaugural meeting, Dr Smith stressed the great importance of study into the habits and ecology of reptiles and amphibians as much had yet to be learnt in this field: here was an opportunity for professional and aspirant herpetologists alike. It was considered that the journal should be left in the hands of the Committee with Angus Bellairs as editor.

The bulletin was subsequently referred to as the *Notice*, and No. 2 was circulated in September 1947. The work and objects of the Society read: (1) to encourage the study of herpetology, in particular of this country and Europe; and (2) to publish a journal containing papers and reviews on all aspects of herpetology.

The Society's first General Meeting was held on 26 September 1947 at University College, London, and, although attended by no more than seventeen members, was very successful and stimulating. Malcolm Smith, as President, spoke on aspects of British herpetology which still required attention. These included research on distribution of species in the wild, and on changes in colour and growth, which could best be studied in captivity under conditions as near as possible natural, on movements in the wild (and the necessary methods of marking individuals), and on sexual cycles, which should be studied both in the wild and in the laboratory. Interesting live and preserved specimens were exhibited, including metamorphosed hybrids between *Rana esculenta* and *R. ridibunda* (Helen Spurway) and a fully grown neotenus *Triturus vulgaris* from Enfield, Middlesex (Malcolm Smith). Wartime controls were still active, and it was very difficult at this time to import livestock. The Society therefore negotiated a licence with the Board of Trade to import living reptiles and amphibians, in order to assist members' research and studies.

It was agreed that the journal should be called *The British Journal of Herpetology*, as an alternative to such names as *Coronella* or *Anguis*, and this was announced in *Notice* No. 4 (January 1948).

The First Annual General Meeting of the Society (October 1948) was held in the Linnean Society's rooms, Burlington House, London, and four additional Committee members were elected. Helen Spurway's resignation was regretfully accepted when, upon the retirement of her husband (the distinguished professor of natural history, J. B. S. (Jack) Haldane), she joined him in India.

Herpetological knowledge in the late 1940s was scanty: both field and laboratory techniques were still in a primitive state. Malcolm Smith's definitive book on amphibians and reptiles in Britain in Collins' New Naturalist series was not published until 1951, and it was appropriate that the first number of the Society's journal (June 1948) should comprise a paper on the dis-

tribution of species in the British Isles (Taylor, 1948), which was probably the first detailed distribution survey compiled anywhere.

Much of the information concerning observations in the field, and preliminary results from experimental studies, were passed on by word of mouth. Society meetings were held quarterly, at the London Zoo on Saturday afternoons, usually with one or more speakers on a set theme. These were followed by a visit to the Reptile House, especially to see Jack Lester's private vivarium there, where he kept a number of species not normally considered easy to maintain in captivity. Among those attending these meetings were David Attenborough, and Gerald Durrell, who went on to establish the Jersey Wildlife Preservation Trust in the Channel Isles.

The next AGM was in April 1949, and at this time it was made clear that the study of reptiles and amphibians "could take the form of scientific research, field study, or for that matter observations on animals in the vivarium". It was stressed that the intention was to help beginners. Around this time field outings were a regular activity, and included visits to see *Rana esculenta* at Ham gravel pits, Surrey, and to observe *R. ridibunda* on Romney Marsh, Kent.

By January 1950, there were over two hundred members, and it was announced in *Notice* No. 14 (July 1950) that two branches would probably be formed within the Society: a London Branch and a Northern Branch. However, through lack of support and internal differences, the Northern Branch had disbanded by 1951. The inaugural meeting of the London Branch was fixed for 12 October 1950.

The eight yearly meetings of the London Branch, held in the rooms of the Linnean Society of London, eventually superseded those of the Society which were held less frequently at London Zoo. Members displayed animals they were breeding in captivity, and commented on any difficulties or particular successes they had had with them. Geoff Haslewood, who was later to chair the Conservation Committee and sadly died in 1993, recalled Malcolm Smith on one such occasion calmly handling adders using the arm of his spectacles as a makeshift snake stick!

Fieldwork in herpetology at this time was mainly observational. Maxwell Savage had carried out the first detailed survey of *Rana temporaria* in the 1930s, his data subsequently being published in what is now the *Journal of Zoology* (Savage, 1934; 1935; 1937; 1939), and one in the *British Journal of Herpetology* some years later (Savage, 1950).

Malcolm Smith resigned as President (at the age of 80) in March 1955. Already aged 72 when he became President, he had been the founding spirit and driving force of the Society, and a strong guiding hand in its early development. He died on 22 July 1958, and a succeeding issue of the journal became a memorial number to him, including an obituary by Tenison (1959), followed by an appreciation by Bellairs (1959). An

appreciation was also made by His Royal Highness Prince Chula of Thailand (1960), one of Dr Smith's former patients! These accounts portrayed the man and his part to perfection.

In accordance with elections held at the AGM 1955, Malcolm Smith was succeeded as President by Deryk Frazer, and Monica Green became Assistant Secretary to Jim Menzies. During 1956, the Secretary took up an overseas appointment, and Monica Green took over his duties. Her appointment as Secretary was confirmed at the AGM in 1957. Remarkably, forty years on, Mrs Green still carries out the duties of secretary and treasurer with vigour and dedication. Indeed, this is a post she has held almost continuously since that time. Six Honorary Life Members were elected over this period: Dr Gerald Leighton (1952), A. E. Leutscher (1952), Dr Malcolm Smith (1953), J.D. Romer (1957), Monica Green (1960) and B.M. Smith (1962). Even 37 years ago, the Society was fully aware of the great debt owed to Monica Green in her capacity as Secretary.

From 1957, the Society maintained a steady pattern over the next 12 years of eight yearly meetings, including AGMs, at which there were talks, but mostly during which animals were displayed in the rooms of the Linnean Society of London. The Society was run on an intimate level, and had a very informal basis: in many ways it was more like a club, with a restricted range of interests and limited impact, than a Society *per se*. This was to change dramatically in later years.

The 1950s were a period of great academic freedom and the halcyon days of traditional British natural history. Before a visit to the Channel Islands, Deryk Frazer remembers asking Malcolm Smith's advice about published work on species there, and was firmly instructed to write something himself. This was subsequently published in the journal (Frazer, 1949). As is the case today, some members had a wealth of herpetological knowledge, but rarely put pen to paper to share it with others. Jack Lester once passed on some novel observations while in conversation with Malcolm Smith, who in turn submitted a manuscript to the journal under Lester's name! Angus Bellairs, returning from North Africa, once arrived unexpectedly at Deryk Frazer's London flat with a collection of amphisbaenids. These were examined on the bathroom floor, and Bellairs subsequently published research on their anatomy. At this time Edward Elkan was also breeding and maintaining *Xenopus* at Shrodells Hospital, and this subsequently led him, as many members will know, to a vast variety of research on diseases of both amphibians and reptiles.

By the late 1950s, the older members of the Society were beginning to pass away, and many of their names nearly 50 years later will not now be familiar to younger members. Jack Lester died in 1956, unexpectedly early after his second Zoo Quest with David Attenborough to South America. At the suggestion of Maxwell Knight and James Fisher (primarily an ornithologist), the Society hired the Royal Festival Hall for a programme in his memory, where the speakers were

Maxwell Knight and James Fisher themselves, David Attenborough and Peter Scott. Some of the proceeds (the remainder going to Jack's widow) were used to put up the bronze plate which can be seen to this day at the entrance of London Zoo's Reptile House.

Up until this time, ethical and conservation issues had received relatively little attention within the Society. However, at the 1951 AGM, Monica Green drew attention to the fact that many tortoises, *Testudo graeca*, were being imported during the winter months, and she represented the Society on a joint working party with the Fauna Preservation Society (now Fauna & Flora International), the Universities Federation for Animal Welfare (UFAW) and the Royal Society for the Prevention of Cruelty to Animals (RSPCA).

Public awareness of environmental issues was increasing during the 1960s, and towards the end of that decade it had become clear that British amphibians and reptiles were under increasing threat from a great range of factors, particularly habitat changes, but also other environmental factors. There was grave concern over these, and a desire to take action. In 1969, Keith Corbett proposed that the Society should form a Conservation Committee, aimed at protecting Britain's rare and endangered species. This was chaired by J. W. (Josh) Steward (who died in January 1997 with an Obituary in the *Guardian*) until 1971, when Michael Lambert took over. Surveys of the declining status of the sand lizard (*Lacerta agilis*), smooth snake, (*Coronella austriaca*) and natterjack (*Bufo calamita*) were followed by conservation measures in conjunction with landowners, and involving liaison with county nature conservation trusts and representatives of the Nature Conservancy Council and other official bodies. Active habitat management was undertaken with the help of the British Trust for Conservation Volunteers with generous aid from the Carnegie Trust Fund and World Wide Fund for Nature. Meanwhile, the threat of collection for the pet trade was reduced by the listing of these species in Schedule 1 of the Conservation of Wild Creatures and Wild Plants Act, 1975.

In January 1970, Monica Green re-established the Bulletin as *BHS Newsletter*, which she continued to produce until January 1976 (No.13), after which it became the *British Herpetological Society Bulletin*.

FROM THE JUBILEE TO THE HALF CENTURY, 1973 to 1997

The second 25 years of the Society has seen substantial change, with enlargement, diversification, and an increased range of activities giving rise to sub-committees and additional Council posts. The Committee was renamed Council to avoid confusion with such sub-committees as the Conservation Committee, and Captive Breeding Committee (formed in 1976). With Monica Green's resignation in 1976, Michael Lambert and Mr P. A. W. Bennett were confirmed as Joint Secretaries at the 1977 AGM. With detached duty overseas

TABLE 1. List of officers on the Committee and Council of the British Herpetological Society, 1947-97, based on extant posts in 1997

| President | Chairman | Secretary/ Treasurer | Journal Editor | Librarian | Bulletin Editor | Chair, Conservation Committee |
|--|----------------------------------|--|--------------------------------------|---------------------------------|--|-------------------------------------|
| M. Smith (1947-55) | M.R.K.Lambert (1977-91) | J.D. Romer (1947) | A. Bellairs (1947-55; 1957-67) | B.M. Smith (1954-61) | M. Green (1973-77) | J.W. Steward (1969-71) |
| J.F.D. Frazer (1955-81) | T.J.C. Beebee (1991-96) | A.E. Leutscher (1947-54) | M. Savage (1955-57) | H. Munro (1961-69) | J. Pickett/ S. Townson (1977-85; 1987-94) | M.R.K. Lambert (1971-77) |
| Earl of Cranbrook (1981-91) | | J.I. Menzies (1954-57) | H. Fox (1967-77) | R.J. Swindells (1969-74) | J. Pickett/ M. Matthewson (1985-87) | K.F. Corbett (1977-78) |
| J.L.Cloudsley -Thompson (1991-96) | | M. Green (1957-77; 1984-present) | M. Peaker (1977-81) | D.L. Tamarind (1974-76) | N. Clark/ S. Townson (1994-95) | T.J.C. Beebee (1978-83) |
| R.A. Avery (1996- present) | | P.A.W.Bennett (1977-80) | R.A.Avery (1981-85) | J. Pickett (1976-85) | J. Spence/ S. Townson (1995-97) | G.A.D. Haslewood (1983-88) |
| | | D.G.D. Lucas (1978-82) | T.J.C. Beebee (1985-91) | P.H. Eversfield (1985-91) | | W.J. Whitaker (1988-92) |
| | | J. Ridout- Sharpe (1982-83) | R.A. Griffiths (1991-present) | D.R. Bird (1991-present) | | J. Clemons (1992-97) |
| Chair, Captive Breeding Committee | Chair, Education Committee | NW England Representative | Scottish Representative | Chair, Research Committee | Trade/Legal Officer | Development Officer |
| S. Townson (1976-87; 1991-92) | V.F. Taylor (1979-91) | R. Paul (1985-94) | D.R. Blatchford (1986-94) | T.R. Halliday (1988-95) | P.C. Curry (1988- present) | B. Banks (1992-94) |
| M. Linley (1987-91) | C. Fitzsimmons (1991-95) | P. Wisniewski (1994-present) | A.W. Darby (1988-97) | C. Cummins (1995-present) | | M. Swan (1994-present) |
| T.A. Thatcher (1992-95) | D. Freeman (1995-present) | | W. Wales (1997-present) | | | |
| J. Spence (1995- present) | | | | | | |

in 1977, Michael Lambert was replaced as Chairman of the Conservation Committee by Keith Corbett until December that year, when Trevor Beebee replaced him, his post being confirmed at the 1978 AGM. Malcolm Peaker also took over from Harold Fox as Journal Editor in 1977, and Michael Lambert shortly after became Chairman of Council. The list of Council officers from 1947, and in posts still extant in 1997, is shown in Table 1.

SOCIETY PUBLICATIONS

The Journal. As indicated earlier, the first editor of *British Journal of Herpetology* was Prof. Angus

Bellairs. The journal was very dependent on contributions from members, and many of the issues comprising volume 1 included no more than notes on a range of observations from the field or laboratory. Some contributors had never written anything for publication before, and yet made useful observations. Indeed, many of the articles were not unlike the unrefereed articles seen now in *BHS Bulletin*.

There was some excitement when the Royal Society provided a grant towards the costs of publishing a paper on toad migration by Moore (1954) which became something of a minor classic in its day. In volume 2 perhaps the most significant articles were obituaries on

both Jack Lester, who died at the early age of 47, and Malcolm Smith.

A revised survey by Taylor (1963) of the distribution of British herpetofauna appeared in vol. 3. Dr H. R. Bustard had become a regular contributor with notes on Australian reptiles. By vol. 3 (9), December 1965, Dr Harold Fox had taken over the Editorship.

Volume 4 (No. 4) caused a small stir in publishing, in French, a paper by Hubert Saint Girons on erythrocyte morphology. John Cloudsley-Thompson, later to become the Society's President, also became a regular contributor. The final issue of this volume contained a policy of amphibian and reptile conservation in Britain, compiled by the Conservation Committee, which included basic principles to be followed, and was the first public expression of the Committee's intention.

A change in page size in mid-volume was met with some consternation by many of the libraries from around the world, which by now were receiving the journal as regular subscribers. An historical outline of the Society over the first 30 years was published by J.F.D. Frazer, then President of the Society, in no. 8, June 1977, by which time the Editorship had passed on to Malcolm Peaker. Through crisp editing, he included a large number of articles in two of the journal's numbers, and thereby overcame the backlog of papers that had started to accumulate. Volume 5 (No. 12) included

a main paper on habitat management and sand lizard conservation in Britain (Corbett & Tamarin, 1979).

The period covered by volume 6, from 1979 to 1985, was one of consolidation and modest growth, but increasing reputation, reflected by the number of papers submitted from home and abroad (Fig. 1). The size of the journal increased to A4. Dr Roger Avery took over the editorship from Malcolm Peaker for four years from 1981, to be followed by Trevor Beebee.

At this point, discussions on the journal in Council included the possibility of a merger with the American-based *Journal of Herpetology*. However, it was eventually decided to continue the British journal, but to seek a new name, and this and other major changes took place in December 1985. "British" was dropped from the title without undue soul-searching and the title *Herpetological Journal* was adopted to reflect the increasingly international outlook of papers published. British herpetology continued to be well represented, however, and the period of volume 1 of the new journal - from December 1985 to June 1991 - was a time when many substantial contributions to knowledge were made. The early 1980s were a boom time for amphibian research in Britain, with vigorous groups at the Open University, University of Wales Institute of Science and Technology (UWIST) - led by the late Paul Gittins - and Leicester, and this activity was reflected in the

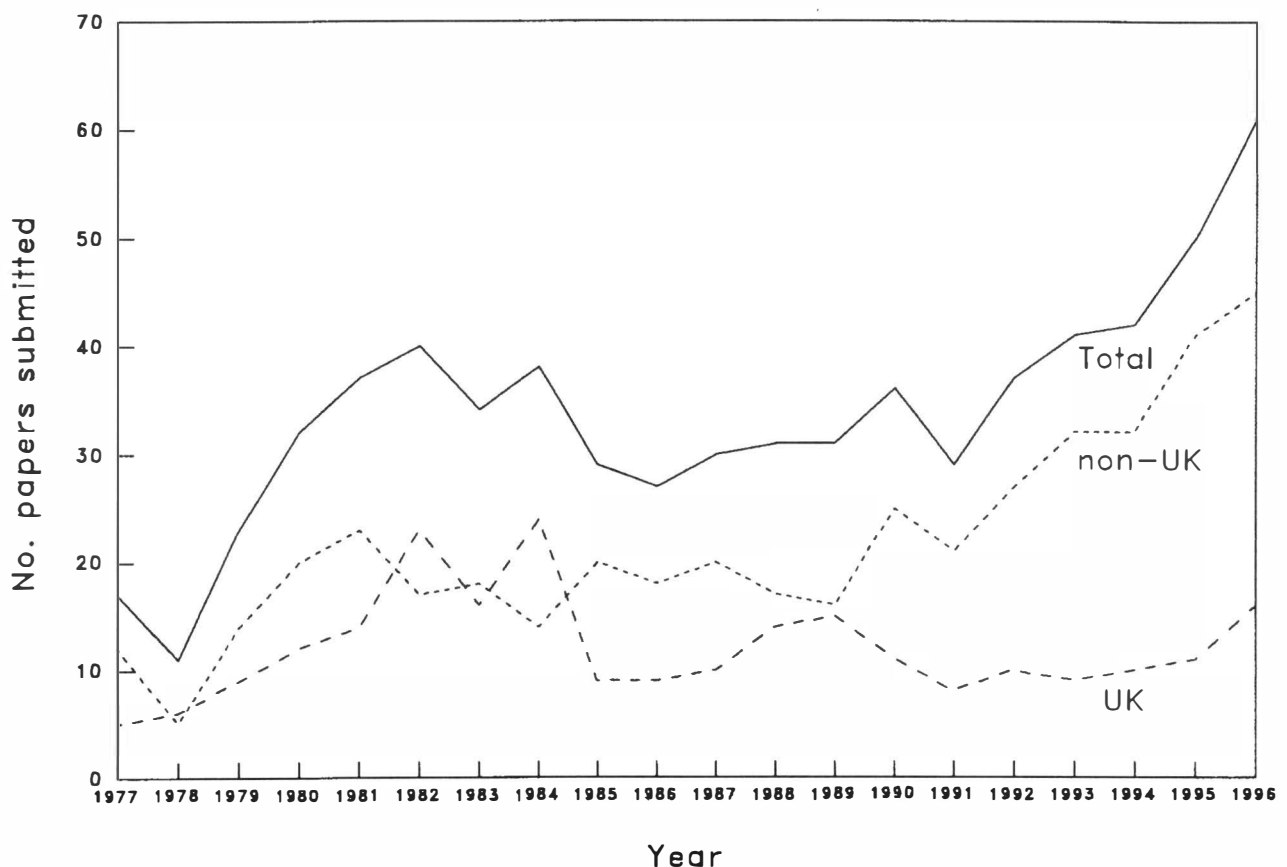


FIG. 1. Manuscript submissions to the *British Journal of Herpetology* (1977-85) and the *Herpetological Journal* (1985-96), showing the total number of papers plus those originating from within and outside the United Kingdom.

pages of the journal. This was also the period of the publication of an influential series of papers on *Natrix maura* in Spain by Adrian Hailey and Peter Davies. Otherwise it is interesting that almost all the significant contributions to British herpetology in the journal at this time related to amphibians. There were only six papers about British reptiles in the entire volume. Sadly, the last issue of this volume in 1991 contained the obituary of Angus Bellairs, one of the major figures in British herpetology for more than 35 years.

Richard Griffiths took over the Editorship (a post which he still holds) in 1991. Further sweeping changes were immediately made, including the appointment of an editorial board to streamline manuscript processing. Costs of production were reduced with the acquisition of a "desktop" publishing system, enabling a larger number of papers to be published per issue at no increase in cost. The journal began to appear quarterly in yearly volumes, and its international reputation and standing continued to grow: in the fourth issue of volume 6 (1996), there were seven major papers, six of them relating to non-British species. Submission rates doubled between 1991 and 1996 (Fig. 1), and the *Herpetological Journal* has become one of the big players in the herpetological arena, with an "impact rating" that compares well with that of comparable journals. Indeed, it is currently the only herpetological publication produced outside North America which is cited in the influential *Current Contents* listings.

The BHS Bulletin. Starting in January 1970 under Monica Green's editorship, and running in this form until January 1976 (No. 13), the biannual *BHS Newsletter* included regular reports from the Conservation Committee, announcement of Society Officers and other items of general interest to the membership, especially pertaining to keeping species in captivity. There were also reports on the Library.

The newsletter also provided a vehicle for different views on herpetology in Britain to be expressed. A topical exchange was that between a relatively small number of vivarium-keepers and fanciers at one end of the spectrum and certain conservationists at the other. The co-editors trenchantly commented on many of these views at length. Number 20 included an interesting article by Pickett (1979), which summarized the Acts of Parliament as they affected collection, possession, import, export, and sale of amphibians and reptiles.

June 1980 saw the publication renamed the *British Herpetological Society Bulletin*. The format was essentially the same, with a softbound cover and improved production, and a declared purpose "to publish news, meetings programmes, informal articles and papers on all aspects of herpetology, and members' letters and advertisements". It was intended "to increase the international interest of the bulletin, and welcome news, correspondence, and articles from foreign herpetologists". An article by Michael Lambert out-

lined the development of the Society from the beginning, based on information provided by BHS publications and organization announcements that he had to hand. Indeed, the bulletin thence included a wide range of articles on all aspects of herpetology, many from contributors based outside Britain. It has become an extremely popular publication among Society members, providing lively, entertaining and often quirky reading.

By 1985, the bulletin was receiving enough contributions to be published quarterly. *BHS Bulletin* No. 17 (September 1986) included colour plates for the first time, as a centre page spread, and showed photographs by Stephen Peltz of the water monitor *Varanus salvator* in Sri Lanka.

Although articles published in the bulletin are not refereed, the nature of many over the last ten or so years is comparable to those in the early *British Journal of Herpetology*. However, with a present adult UK and foreign membership of nearly 900, the scope and range of subjects covered by articles in four bulletin issues a year is very much greater than in the journal during the 1950s and 60s, when there were scarcely more than 200 members.

The Natterjack. With the transformation of *BHS Bulletin*, it was felt that there was a need for keeping members informed of events on a more regular basis. Edited by Trevor Rose as an initiative of the Captive Breeding Committee, the first issue of this new monthly newsheet was circulated to members in February 1995. It aimed to bring updates to events arranged by the Society, topical herp news from around the world, hints, tips, members advertisements and much more. At the outset, an appropriate, catchy and original name for the monthly publication was sought, and the winner of a competition to provide this would win £10. Issue 26 had been distributed by the 50th Annual General Meeting in March 1997, and included items under five main headings: *Warts and All* (articles from newspapers, journals and other sources); *Members' Spot* (short accounts on observations and views of interest); *Talk Back* (committee communications); *Dates for Your 1997 Diary*; and *Lineata* (wanted and for sale). The *Natterjack* has proved to be a popular item among members.

THE LIBRARY

The Library contains a large collection of books, journals and journal articles, which have been acquired through donation, purchase, exchange with other societies, or inherited from deceased members. By 1974 the library had acquired a distinguished home within the library of the Linnean Society of London in Burlington House, Piccadilly. The opening hours of the library were therefore those of the Linnean Society Library, and although the Society had its own librarian (at the time, David Tamarind) the Linnean Society Librarian co-ordinated loans and renewals. With David Tama-

rind's departure from London at the end of 1975, John Pickett became Librarian. In 1976, he requested the return of loans which had been taken out some three or so years earlier and had still not been returned. Regrettably, the library's books at this time were also on open shelves in the basement of the Linnean Society, but this resulted after a year or so in the theft of certain important works. John Pickett reorganized the Library in 1978. By 1989 the Linnean Society of London had moved the BHS Library to its upper galleries to prevent further theft of books, but then required the space for their own ever-increasing collection. In 1993 the Society's collection of books was transferred from the Linnean Society to the home of the new librarian, David Bird, who subsequently set about producing an up-to-date catalogue of its contents. Books can now be borrowed by post or through personal visit by arrangement with the librarian.

COMMITTEES OF THE SOCIETY

Conservation Committee. The Conservation Committee was formed in November 1969 under the chairmanship of J. W. Steward, and members started work on the distribution and habitat conservation of the sand lizard. It was quickly found that three species: *Lacerta agilis*, *Coronella austriaca* and *Bufo calamita* had so decreased in range and numbers that there was danger of them disappearing from Britain altogether if proper conservation measures were not applied. Following a report published in *BHS Newsletter* No. 2 (June 1970), Mr Steward presented an update on the work of the Conservation Committee at a Society meeting in November 1970, and a future conservation policy for Britain was laid down in a joint meeting of the main Council and Conservation Committee before the end of the year. Mr Steward resigned his chairmanship at the AGM in March 1971, and a report by Michael Lambert, who replaced him, on the Committee's activities appeared in *BHS Newsletter* No. 4 (June 1971).

Among the Conservation Committee's main functions and activities from the earliest days were winter tasks involving the clearance of scrub, as part of habitat manipulation, on the lowland heaths of southern England. These have been organized every year since the committee's inception. The bulk of this work has been at sand lizard and smooth snake sites in Surrey and Dorset. The tasks have always been important social as well as practical events.

The Conservation Committee has also carried out translocations of sand lizards, natterjacks, and occasionally smooth snakes, and as a result established several new populations of each species in suitable habitat around the country. The Committee contributed to the discussion on translocations in Britain through a paper in *British Journal of Herpetology*, June 1983 (vol. 6, 314-316).

The scientific basis of herpetofauna conservation has been extensively developed by Conservation Com-

mittee members. There have been numerous publications in the scientific literature, including Corbett & Tamarind's (1979) paper on habitat management for the sand lizard, and several by Banks, Beebee, Denton and Griffiths on the conservation of other species (e.g. Beebee, 1976; Griffiths, 1985; Banks & Laverick, 1986; Denton 1991). A major contribution towards smooth snake conservation took the form of a national survey of sites for this species funded by the Nature Conservancy Council during the mid-1980s, and the results of this survey were later published in *The Herpetological Journal* (Braithwaite *et. al.*, 1989).

The Conservation Committee has a long-standing input to the politics of herpetofauna conservation. Notable events included a crisis on the Merseyside dunes during the early/mid 1970s concerning the development of housing estates at Ainsdale and Birkdale, culminating in a proposed extension of the local Butlins holiday camp in 1975. Publicity generated by the Conservation Committee was instrumental in curtailing these threats, and led to a wide-ranging series of meetings at the Nature Conservancy Council headquarters between 1977-1983. The outcome was a national policy document on the conservation of Britain's three rare species: sand lizard, smooth snake and natterjack toad.

In 1985 the Conservation Committee appointed Tom Langton as honorary Conservation Officer. Later, in 1986, a Conservation Officer post for Keith Corbett was funded jointly by the Nature Conservancy Council and Worldwide Fund for Nature (UK). This was the first salaried position ever run by the British Herpetological Society.

Conservation of the commoner British herpetofauna has been a source of perpetual debate within the Conservation Committee. In recent years, with the Herpetological Conservation Trust looking after the rare species, the subject, especially in respect of great crested newts and grass snakes, has featured higher on the agenda. By and large, the Conservation Committee has not had the manpower or resources to make a substantial contribution in this area. However, during the mid-1990s, a "common species officer" post was established under the joint supervision of Herpetofauna Conservation International, Herpetological Conservation Trust, the Conservation Committee and the statutory conservation agencies.

During the 1980s, the Conservation Committee became involved in the purchase and lease of nature reserves, aided by generous private donations. Reserves are now owned on heathlands in both Surrey (Gong Hill) and Dorset (Green Pool and Trigon), and there are lease/management agreements at other sites including coastal dunes (with natterjacks) at Sellafeld in Cumbria. At about the same time, and mainly due to the efforts of Brian Banks and Dave Bird, a "Land Fund" was established to accumulate money for the purchase or lease of sites. By 1997, there were more than £40,000 in this fund.

The establishment of the Herpetological Conservation Trust in 1989 was, in an important sense, a triumph for the Conservation Committee in that a professional, well-funded organization was successfully established to perpetuate the main objectives of the Committee on a scale which the British Herpetological Society alone could never have afforded. The success of the Trust may have left the Conservation Committee with a less clear view of its own mission and purpose, but over the past five years, the Committee has taken on a more advisory role and established a database containing over 10 000 herpetofauna records for future analysis, and committee members have continued to assist the Trust with management and surveying programmes. Meanwhile, annual field trips to places of herpetological interest for Society members have been well attended. The Committee has been involved with more great crested newt work and there are plans to contribute, as leading partners, to the UK Biodiversity Action Plan for this species.

In contrast, the old arguments between the Conservation Committee and other sectors of the main Society have subsided over the years. Heated debates and acrimonious discussions on conservation versus captive breeding at AGMs and Council meetings are largely a thing of the past, partly due to the publication of an agreed policy on the subject of animals in captivity, trade and legislation in *BHS Bulletin* No. 53 (Autumn 1995) which took over two years to formulate. There has also been a growing realization that habitat protection is a much more important issue for species conservation than any threat from collection and keeping in captivity, which in any case are now illegal in respect of the rare and endangered species in Britain with the passing of the UK's 1981 Wildlife and Countryside Act.

Captive Breeding Committee. As co-editors of the *BHS Newsletter*, John Pickett and Simon Townson included an article on the contribution of captive breeding to conservation (Pickett, 1976). This in effect represented the basis for the formation of the Captive Breeding Committee, which was realized by the end of the year, with Simon Townson as Chairman. The Committee's function, as given in *BHS Newsletter* No. 15 with a list of founding members, was "to give scientific and practical advice on captive breeding and husbandry of reptiles and amphibians, to provide a liaison service between members, and to give advice relating to the breeding of animals for conservation purposes". By the following year, preliminary aims and policies of the Captive Breeding Committee were laid down. It was indicated in the Introduction that in recent years, there had been great achievements in the breeding of reptiles and amphibians in captivity, and for many species this had been proven to be quite simple. Each year brought new and more regular successes in the field, so that one could begin to look forward to breeding as the norm

rather than the exception. Previously, breeding these animals in captivity was a rare occurrence, and hence there seemed to be little widespread knowledge of many of the techniques and parameters involved. An appeal was also made for information on species kept, in order to build-up a species register.

By the following year, a list of species being bred successfully by members of the Society had come to light, and was published in *BHS Bulletin* No. 18 (July 1978). The main function of the Captive Breeding Committee was found to be that of giving advice on a variety of topics, including breeding techniques, housing of animals and general husbandry, sources of information, and legal requirements for obtaining species from overseas. Members had also asked to be put in touch with others with similar interests for fruitful exchanges of information and/or animals. Committee members had also given talks on various aspects of herpetology to a number of outside organizations. Information sheets for various species were produced on basic care and breeding in captivity (by 1997, there were twelve of these). It was also announced that a book was to be published containing a collection of papers on husbandry, breeding and behaviour, and veterinary aspects.

1980 saw the publication of *The Care and Breeding of Captive Reptiles*. Edited on behalf of the Society by Simon Townson and three other members of the Captive Breeding Committee, this was the first book to be published by the Society. The next book was by Nicholas Mrosovsky, *Conserving Sea Turtles* (1983), which was fairly audacious of the Society to publish, for it contained controversial material, and was widely reviewed. This resulted in substantial sales worldwide and established the Society as a publisher of herpetological works.

A Symposium organized by the Captive Breeding Committee was held jointly with the British Veterinary Zoological Society on 1 October 1983. Papers that were presented were subsequently edited by Simon Townson and Keith Lawrence, and published as *Reptiles: Breeding, Behaviour and Veterinary Aspects*.

In addition to organizing two evening meetings each year in July and September, respectively called "Amphibians and reptiles worldwide: their care and breeding", and "Care and breeding of amphibians and reptiles: an open meeting", there were two Symposia held jointly with other herpetological societies in Britain in 1986 (six other societies) and 1988 (four other societies). Proceedings of both symposia, edited by Jon Coote, were subsequently published by the Society in 1987 and 1990, and included additional papers to complement those read at the symposia.

The pattern of captive breeding meetings during the year became less standardized in 1991, and an autumn meeting was held on a weekend afternoon (from 1992 at New Denham Community Centre, where all captive breeding meetings during the years took place until

1996, when they were back at Birkbeck College, London).

A compilation of 51 papers from *BHS Bulletin* 1980-1992, edited by Simon Townson, was published as a collection in 1994, representing the seventh in a series of miscellaneous volumes by the Captive Breeding Committee of the British Herpetological Society.

Education Committee. Education was recognized as an important facet of herpetology, especially in relation to conservation, and Vic Taylor was Education Officer on the Conservation Committee almost from its inception. A leaflet on the British herpetofauna and its conservation, prepared by Vic Taylor, was circulated to all members of the Society as a centre-page insert with *BHS Newsletter* No. 7 (January 1973). An appeal in this Newsletter was also made for members of the Society with experience in lecturing to schools, natural history societies, youth organizations, etc. who would be interested in forming a consolidated network of part-time lecturers. It was envisaged that members of this network would gain from the pooling of experience and resources, without undue hindrance to individual style!

Vic Taylor had begun to consolidate many of his ideas on education and conservation, and expressed these in an article in *BHS Newsletter* No. 15 (December 1976). He commented on the value of supplying excess frog spawn from overflowing ponds to schools for a valuable educational experience to which children might not otherwise be exposed. He had already acted over the previous three years as Course Director for weekend herpetological courses at Theobalds College, Enfield, and plans were in hand for a course in 1977 aimed at teachers, naturalists and herpetologists interested in playing an active role in the conservation of British amphibians and reptiles.

Vic Taylor became an Ordinary member of the Society's Council in 1977, and provided an outline report on his Theobalds Field Study Centre courses in *BHS Newsletter* No. 18 (July 1978). He foresaw a course being held in Dorset with lectures on reptile and amphibian ecology, together with heathland ecology and management, backed up by site visits. With such involvement in herpetological education, it was recognized that an Education Officer should be created as a separate post of the Society's Council itself, and Vic Taylor was duly elected, the Rules of the Society being amended as necessary. As the Society's Education Officer, he also chaired an education committee.

Hitherto, membership of the British Herpetological Society had officially been restricted to adults. It was announced in *BHS Bulletin* No. 2 (December 1980) that a Junior Section had been formed, nicknamed "J Herps", which gave children and those under 18 a chance to take an active interest in the work of the Society for the first time. An advisory service was also run for J Herps which provided expert advice on specific problems. The J Herps also received their own newsletter (*J Herps Newsletter*) three times a year, containing

news, information and competitions, in addition to *BHS Bulletin* as a subsidy from the main Society. By 1982, there were around 100 J Herp members. Vic Taylor continued at the same time the education programme for the Conservation Committee, and in particular yearly displays at summer events in the Queen Elizabeth Country Park.

In 1983, an Education Committee was established which was responsible for the continued running of the Junior Section of the Society, the extension of junior activities to involve school groups and teachers in both the primary and secondary sectors, and providing a panel of speakers for non-specialist groups and general exhibition work on behalf of the Society. Part of the intention of the Education Committee was that it should bring members in to the Society at the junior stage who would graduate to become adult members once they came of age.

The Education Committee maintained steady progress over the next four years. Colin Fitzsimmons became the Exhibitions Officer in 1988, and at the end of the same year a successful New Year's day children's lecture on herpetology was held jointly with the Zoological Society of London at Regent's Park. This led to a number of joint meetings with the Young Friends of London Zoo at Regent's Park over the next few years.

The post of Education Officer was taken on by Colin Fitzsimmons in 1991, and from 1993, as an employee of the British Herpetological Society, was funded by the Esmée Fairbairn Trust. As a result, the Junior Section went from strength to strength. Membership increased to over 250, and eventually reached 459 by the end of December 1995. The name was changed from J Herps to Young Herpetologists' Club (YHC) in 1993, and editorship of the *Young Herpetologists' Newsletter*, published by the Education Committee, was taken on and given a new look by John Baker. Colin Fitzsimmons's post ran until 1996, and the Education Committee was solely represented on Council by the Chairman, Don Freeman.

Research Committee. A number of Society members are based in university departments and research establishments, and by the late 1980s the British Herpetological Society had become the logical forum for herpetological research in Britain. The proposal to form a Research Committee was approved in 1988. The first Chairman of the Research Committee was Professor Tim Halliday (Open University). The Committee's terms of reference were formulated in its first year, and it was hoped to provide a reservoir of scientific advice for the other Society Committees, and to organize meetings and symposia. It was intended that a dossier of researchers in Britain would also be produced.

A meeting of the Zoological Society of London organized by Tim Halliday on 12 June 1990, on the topic of *Behavioural Ecology of Newts and Salamanders*, tested interest within the scientific community, and was

well-attended. Other contributors at this meeting were Dr J. W. Arntzen (University of Amsterdam, the Netherlands) and Dr R. A. Griffiths (then based at North-East Surrey College of Technology).

The Inaugural meeting of the Research Committee, also organized by Tim Halliday, was held on Saturday, 5 December 1992, at Birkbeck College, London. Following an Introduction by the Society's President, Professor John Cloudsley-Thompson, the meeting was opened formally by the Earl of Cranbrook, former President of the Society (1981-1991) and Chairman of English Nature. At the end of the morning session of two papers, Michael Lambert made a presentation on behalf of the Society to Lord Cranbrook in appreciation of his contribution to herpetology in Britain. The day ended with a discussion led by Tim Halliday and Trevor Beebe - *Global Amphibian Declines: Real Phenomena or False Alarm?*

Tim Halliday resigned as Chairman in 1995, and was replaced by Clive Cummins (Institute of Terrestrial Ecology) who has maintained the all-day December Research Committee meetings at Birkbeck College. In April 1995, regular attendees of these meetings also contributed to an international symposium at the Zoological Society of London, *Venomous Snakes: Ecology, Evolution and Snakebite*, proceedings for which would be published as No. 70 of the *Symposia of the Zoological Society of London*.

REGIONAL GROUPS

The Society has always been aware that, for various reasons, its activities have a focus in southern Britain. As the national society, however, efforts have been made from the early days to cater for the interests of members in other parts of the country. This has not always been easy, particularly during the 1980s which saw a proliferation of independent local herpetological clubs, primarily interested in captive care. The role of the BHS regional groups has therefore been to cater for those with broad-based herpetological interests, encompassing captive breeding as well as field survey and conservation activities.

A request in *BHS Bulletin* for the establishment of regional groups in 1984 was seen by Rajan Paul, who talked to 26 Society members in the north-west region, and held a meeting to establish a group in May which attracted fifteen members. The programme for 1985 began with a visit to the Tropical House at Chester Zoo, courtesy of Keith Browne, Curator of Reptiles. Five meetings were held in the first year, setting the pattern for future years, and most successful was the first Reptile Rally, held at the Wildfowl & Wetlands Trust, Martin Mere, in July 1986. Also in 1986, through association with members of the Society's Conservation Committee, the Group became involved with digging natterjack ponds on Ainsdale Sand Dunes reserve. The position of Chairman was eventually taken up by Bob Worthington with Pat Wisniewski as North-west Representative.

The British Herpetological Society has been represented in Scotland for a little over ten years, and the initial intention of the Scottish Group was to organize meetings in Scotland so that members based there could meet and also benefit from the experiences of visiting speakers. Maintaining links with other herpetological groups in Scotland has resulted in a number of successful joint meetings. In 1988 and 1990, joint meetings were held with the Scottish Herpetological Society at Edinburgh Zoo; the first included Roger Thorpe and Wolfgang Wüster (University of Aberdeen) as speakers. In 1992, a joint symposium with the International Herpetological Society was held at the City Art Gallery and Museum, Kelvingrove, Glasgow, with talks by Chris Mattison and Mark O'Shea. The largest meeting to date was held in the Burrell Lecture Theatre, Burrell Collection, Glasgow, in 1994. Attended by over 120 people, it included a presentation by Quentin Bloxam of Jersey Wildlife Preservation Trust. The Group has also been contacted for input to the Scottish Natural Heritage's Species Action Plan, which is helping to save vulnerable native Scottish species.

OTHER COUNCIL POSTS

Other posts on Council, created to fulfil particular functions on behalf of the Society, include the Conservation and Education Officers (already mentioned), and the Development and Trade Officers. As the first Development Officer, Brian Banks was responsible for finding ways of increasing membership and reducing expenditure; Mary Swan, his replacement, has organized yearly Herpetofauna Recorders Meetings, which have aroused much interest outside the Society. The Trade Officer (initially Legal Officer), has been concerned with legal aspects, especially those concerned with amphibians and reptiles in captivity, and was much involved with formulation of the Society's Policy on animals in captivity, trade and legislation.

THE CHANGING FACE OF HERPETOLOGY IN BRITAIN

During the Society's second 25 years, there have been some events that can be described as highlights. Transformation of the Society started in 1969 with the formation of the Conservation Committee, initiated by Keith Corbett. Described then in certain quarters as a "ginger group" within a Society primarily made up of members interested in keeping species in vivaria, the Conservation Committee brought the Society's attention to the endangered status of Britain's three rare species, which had been on the decline for some years.

Herpetology during the 1960s in Britain was at a generally low ebb, with few or no openings in the field professionally. To a degree, the British Herpetological Society could compensate for this lack, and enable academically trained enthusiasts to pursue their interest under its aegis. In strengthened state, the Society could also influence university departments, governmental

and other research organizations to include herpetology, in pure and applied forms, as a notable discipline forming part of, and yet distinct from zoology as a whole.

I believe that this academically based approach to conservation was in part a cause for resentment among certain members of the Society who, as amateurs themselves and not necessarily with biological training, also saw conservationists as a threat to their hobby of keeping species in captivity for aesthetic appreciation and personal enjoyment. Conflict inevitably arose within the Society, especially when externally the Conservation Committee became the butt of criticism from certain conservation and fauna preservationist quarters for association with a Society of members keeping wild-collected species in captivity. Perhaps a positive response to this on the part of the Society, after reflection on the implications and rationalization of keeping species in captivity, was the formation of the Captive Breeding Committee in 1976. The Captive Breeding Committee could usefully function by ensuring that there was a supply of amphibians and reptiles that could be kept successfully at home in vivaria.

To my mind, certain of those involved with fauna protection were extreme in their view, even intolerant and overstating the situation, and to some extent exaggerating the effects of collection on most species in the wild. It was an objection in principle, based partly on welfare rather than conservation issues, which also applied to commercial suppliers with a profit motive, rather than to individuals wanting to keep a few amphibians and reptiles in normal domestic circumstances.

Associated with conservation, and the use of live animals for display and educational purposes, especially in schools, education plainly had a part to play. The Society responded, and the scope of the Education Officer, already a member of the Conservation Committee, was extended. The Society's Junior Section was established in 1979 through the formation of the Education Committee. Conservation, captive breeding and education could thus run parallel, be integrated and complement each other for the benefit of members and not least the animals themselves.

Pickett's (1976) article in *BHS Newsletter* set the scene well, and laid down the case for tolerance and rational thought on the part of vivarium keeper and conservationist alike. Indeed, near the end of the article, he presents a case for the formation of the Society's Captive Breeding Committee. Beebe (1977) also requested views on a set of principles for keeping reptiles and amphibians in captivity, and stressed that the only thing the Conservation Committee was asking of Society members was acknowledgement that there is such a thing as irresponsible pet keeping (rare species fancying). Some years later in an educational context, Taylor (1987) saw that conservation and vivarium keeping could have a symbiotic relationship, and the Society's Policy on animals in captivity, trade and legislation

(*BHS Bulletin* No. 53, Autumn 1995) effectively bought an end to the whole discussion. Allaying suspicions between both interests, the strengthened Society could nurture and develop an interest in herpetology on a broader basis.

During the early 1980s, following the particularly successful European Symposium at Oxford, organized by John Coborn of Cotswold Wild Life Park (on behalf of the Association for the Study of Reptiles and Amphibians - ASRA), the Society broadened its outlook to consider herpetological activities outside Britain. Lambert (1983a) compiled a list of herpetological societies in Europe and the Commonwealth, together with a first series of reports on herpetological activity in British Universities (Lambert, 1983b) that reflected a substantially increased interest in herpetology in Britain. Cranbrook & Lambert (1983) also put together some ideas on the future role of the Society in the Commonwealth, in consideration of the richness and diversity of herpetofauna of tropical member states, which was followed by a series of articles on herpetology in different Commonwealth countries, mostly by Michael Lambert, in subsequent numbers of the *BHS Bulletin*.

Another highlight of the Society was the First Malcolm Smith Dinner, held on 16 December 1983 in the Peers' Dining Room of the House of Lords, Westminster, hosted by the Earl of Cranbrook, and during which he gave his Presidential Address. A major aim of the Society at this time was to gain the support of all those in the UK who counted themselves as professional herpetologists. Lord Cranbrook expressed a hope that all active scientists might wish to join the Society in order to give it support and make it genuinely representative of herpetology in this country. He exhorted existing members to encourage their colleagues to join. As an august social occasion, the Dinner was much enjoyed by participants, and a notice recording it appeared under 'Court & Social' of *The Times* the following day. Beside simply being a social event, it was hoped that the First Malcolm Smith Dinner would help to establish herpetology as a notable discipline in Britain, a status already enjoyed by such subjects as entomology and ornithology.

A possible outcome of the desire for the Society to reflect herpetology in Britain professionally was in its agreeing to co-host the First World Congress of Herpetology, which was held in September 1989 at the University of Kent at Canterbury. The Secretary-General of the Congress, Professor Kraig Adler (Cornell University, Ithaca, New York) - a long-standing BHS member - opted, with his casting vote, for Canterbury (there was a tie with Florence) as the Congress venue. The Congress Patron was His Royal Highness the Duke of Edinburgh, who accepted the invitation forwarded to him on behalf of the Congress Executive Committee by Lord Cranbrook. Ian Swingland was Conference Director. Professional herpetologists among Society members all became members of the National Executive involved with the Congress's organization.

Upon taking up the Chairmanship of English Nature in 1990, Lord Cranbrook resigned as President, having served the Society in this capacity since 1981. He had been involved with the Wildlife & Countryside Act 1981, which ratified the 1979 Berne Convention, during its bumpy course through Parliament. Britain's rare and threatened herpetofauna featured strongly in this bill. In transferring from Viscount Medway, Lord Cranbrook continued the Society membership of his father, the 4th Earl. Lord Cranbrook's period of office as President coincided with a time of change within the Society. The Society was guided through this period of unrest by his firm and positive leadership, and the confidence engendered was effectively expressed by a simultaneous near doubling of the Society membership to over 1000 by the end of 1989. One could perhaps say in herpetological terms, for the duration of the World Congress at least, that this country rose to become the crossroads between continental Europe, North America and the Commonwealth!

During the 1980s there were other highlights for herpetology in Britain. In 1983, a symposium entitled "The structure, development and evolution of reptiles", was organized by Mark Ferguson in honour of Angus Bellairs, on the occasion of the latter's retirement. This was held at the Zoological Society of London, jointly with the Anatomical Society of Great Britain and Ireland and the British Herpetological Society. The proceedings, edited by Professor Ferguson, constituted a Festschrift for Prof. Bellairs, and were published as No. 52 of the *Symposia of the Zoological Society of London* (1984). 1983 also saw the publication of Deryk Frazer's book in the New Naturalist Series (Frazer, 1983b), constituting a re-write of Malcolm Smith's earlier work.

For good or for bad, the last decade or so of the Society's history has seen a major surge of interest in keeping reptiles and amphibians in captivity. Certainly, what was once the rather genteel occupation of a few distinguished British naturalists has evolved into big business, with many species readily available in pet stores and garden centres. Indeed, one commentator has gone so far as to describe it as a 'craze', which in the long-term may do no good for herpetology as a sphere of interest (Keeling, 1992). Concomitant with this resurgence of interest has been the formation of numerous local herpetological clubs around the country. There is no doubt that people who would have once joined the British Herpetological Society now turn to their local group to further their interest. Intriguingly, however, membership of the Society has remained remarkably stable over the years. This suggests that there has been a shift in the society's membership, away from those simply interested in keeping vivaria to those with a wide range of interests including conservation, captive breeding, education and research.

CONCLUSION

And what of the Society's future? To some extent, I see the Society continuing to evolve in response to need. It is therefore difficult to anticipate the path this will take. Can the Society be reactive or proactive? I see consolidation as an ongoing process; indeed, after the First World Congress of Herpetology, there were certain signs of the Society being stretched, although members inside, and individuals outside, were able to respond well to the demands then made upon them. With such a heavy accent on the academic and professional aspects of herpetology at that time, the aspirations of vivarium keepers were a little muted, although care and breeding of species in captivity was a subject featured, and strongly supported, at the Congress. However, the process of consolidation following the Congress, under Trevor Beebee's carefully judged and effective chairmanship, was exceedingly successful, and I foresee the need for this to continue and be strengthened in the immediate future. The Society should not allow itself to be overridden by one specific interest as has been the case in the past.

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REFERENCES

- Banks, B. & Laverick, G. L. (1986). Garden ponds as amphibian breeding sites in a conurbation in the north east of England (Sunderland, Tyne and Wear). *Herpetological Journal* **1**, 44-50.
- Beebee, T. J. C. (1976). The natterjack toad in the British Isles; a study of past and present status. *British Journal of Herpetology* **5**, 515-521.
- Beebee, T. J. C. (1977). Your opinions needed. *British Herpetological Society Newsletter* **16**, 46-47.
- Bellairs, A. d'A. (1959). Malcolm Smith's contribution to herpetology. *British Journal of Herpetology* **2**, 138-141.
- Braithwaite, A. C., Buckley, J., Corbett, K. F., Edgar, P. W., Haslewood, E. S., Haslewood, G. A. D., Langton, T. E. S. & Whitaker, W. J. (1989). The distribution in England of the smooth snake (*Coronella austriaca* Laurenti). *Herpetological Journal* **8**, 370-376.
- Corbett, K. F. and Tamarind, D. L. (1979). Conservation of the sand lizard, *Lacerta agilis*, by habitat management. *British Journal of Herpetology* **5**, 799-823.

- Cranbrook, Earl of and Lambert, M. R. K. (1983). Future role of the BHS in the Commonwealth. *British Herpetological Bulletin* **8**, 12-14.
- Denton, J. S. (1991). The distribution and breeding site characteristics of newts in Cumbria, England. *Herpetological Journal* **1**, 549-554.
- Frazer, J. F. D. (1949). The reptiles and amphibia of the Channel Isles, and their distribution. *British Journal of Herpetology* **1**, 51-53.
- Frazer, J. F. D. (1977.) The British Herpetological Society, 1947-1977. *British Journal of Herpetology* **5**, 597-600.
- Frazer, D. (1983a). The British Herpetological Society - a reminiscence. *British Herpetological Society Bulletin* **8**, 10-12.
- Frazer, D. (1983b). *Reptiles and amphibians in Britain*. London: Collins The New Naturalist.
- Griffiths, R. A. (1985). A simple funnel trap for studying newt populations and an evaluation of trap behaviour in smooth and palmate newts (*Triturus vulgaris* and *T. helveticus*). *Herpetological Journal* **1**, 5-10.
- Keeling, C. H. (1992). *A short history of British reptile keeping*. Guildford, Surrey: Clam Publications.
- Lambert, M. R.K. (1980). From the beginning - BHS publications and organisation announcements. *British Herpetological Society Bulletin* **1**, 4-6
- Lambert, M. R. K. (1983a). Herpetological societies of Europe and the Commonwealth. *British Herpetological Society Bulletin* **7**, 18-29.
- Lambert, M. R. K. (1983b). Herpetological activity in Britain: Universities I. *British Herpetological Society Bulletin* **7**, 29-42.
- Moore, H. J. (1954). Some observations on the migration of the toad (*Bufo bufo bufo*). *British Journal of Herpetology* **1**, 194-224.
- Pickett, J. (1976). Captivity and conservation. *British Herpetological Society Newsletter* **14**, 26-33.
- Pickett, J. (1979). Herpetology and the law: a summary of Acts of Parliament as they affect the collection, possession, import, export, and sale of reptiles and amphibians. *British Herpetological Society Newsletter* **20**, 6-12.
- Savage, R. M. (1934). The breeding behaviour of the common frog, *Rana temporaria temporaria* Linn. and the common toad, *Bufo bufo bufo* Linn. *Proceedings of the Zoological Society of London*, 55-70.
- Savage, R. M. (1935). The influence of external factors on the spawning date and migration of the common frog, *Rana temporaria temporaria*. *Proceedings of the Zoological Society of London*, 49-98.
- Savage, R. M. (1937). The ecology of young tadpoles with special reference to the nutrition of the early larvae of *Rana temporaria temporaria* Linn., *Bufo bufo bufo* Linn. and *Bombina variegata variegata*. *Proceedings of the Zoological Society of London* **107A**, 219-260.
- Savage, R. M. (1939). The distribution of the spawn ponds of the common frog, *Rana t. temporaria*, over a portion of the London Clay and associated drift. *Proceedings of the Zoological Society of London* **109A**, 1-19.
- Savage, R. M. (1950). A thermal function of the envelope of the egg of the common frog, *Rana temporaria temporaria*, Linn., with observations of the structure of egg clusters. *British Journal of Herpetology* **1**, 57-66.
- Smith, M. (1951). *British amphibians and reptiles*. London: Collins The New Naturalist.
- Taylor, R. H. R. (1948). The distribution of reptiles and amphibia in the British Isles, with notes on species recently introduced. *British Journal of Herpetology* **1**, 1-38.
- Taylor, R. H. R. (1963). The distribution of amphibians and reptiles in England and Wales, Scotland and Ireland and the Channel Isles. *British Journal of Herpetology* **3**, 95-115.
- Taylor, V. (1987). Education - a bridge between captive breeding and conservation. *British Herpetological Society Bulletin* **21/22**, 2-3.
- Tenison, W. P. C. (1959). Obituary. Dr. Malcolm Arthur Smith, F.L.S., F.Z.S. *British Journal of Herpetology* **2**, 136-137.
- Thailand, His Royal Highness Prince Chula of (1960). Dr. Malcolm Smith: an appreciation. *British Journal of Herpetology* **2**, 186-187.

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THE EFFECTS OF CURRENT VELOCITY AND TEMPERATURE UPON SWIMMING IN JUVENILE GREEN TURTLES *CHELONIA MYDAS* L.

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Young green turtles, *Chelonia mydas* responded to increasing current velocities by swimming upstream for a greater proportion of the time. At temperatures of 21-25°C currents equivalent to 1-2 body lengths s⁻¹ induced continuous upstream swimming. At low current velocity the turtles usually employed 'dog-paddle' (ipsilateral synchronized) swimming. At swimming speeds of 0.8-1.4 body lengths s⁻¹ they switched to synchronized forelimb flapping, with stationary rear limbs. Maximum dog-paddle speed was about 40% of maximum speed using synchronized foreflippers: the latter mechanism is clearly capable of generating far more propulsive power. Maximum sustained swimming speeds at 25°C, 21°C and 15°C were 3.31, 2.96 and 2.09 body lengths s⁻¹ respectively; the speed at 15°C was significantly lower than at the other two temperatures, and could not be sustained for more than 2-4 min before instability in pitch, roll and yaw prevented the animal from swimming upstream. A detailed analysis of the swimming mechanism at different temperatures is presented. This demonstrated a significant degradation of co-ordination of swimming at 15°C, even though the lethal temperature of green turtles is well below 10°C. The significance of this finding is discussed in terms of vulnerability of the species to cold.

INTRODUCTION

The swimming of green turtles (*Chelonia mydas* L.) has attracted much study (Carr, 1952; Walker, 1971; Blake, 1981; Davenport, Munks & Oxford, 1984; Wyneken, 1988; Wyneken & Salmon, 1992). Most attention has been paid to swimming by simultaneous beating of the forelimbs, though green turtles, like other cheloniid sea turtles, use other swimming modes at low speed (Davenport *et al.*, 1984; Davenport & Pearson, 1994).

Hatchling and juvenile sea turtles live in the open ocean, mostly drifting with currents (Caldwell, 1968; Carr & Meylan, 1980; Stoneburner, Richardson & Williamson, 1982), though persuasive recent evidence indicates that they are capable of directional swimming (Lohman & Lohman, 1996) using various cues (magnetic, wave direction). Because they move over great distances, they are likely to encounter changing thermal conditions young turtles may also be swept into cold waters and suffer cold-stunning (e.g. Meylan & Sadove, 1986; Witherington & Ehrhart, 1989; Morreale *et al.*, 1992).

The study reported here was designed to investigate how the swimming mechanism of young green turtles was affected by current speed and by temperature.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Twelve green turtles were sent as recent hatchlings from the Lara Reserve, Cyprus, to the School of Ocean Sciences, University of Wales, Bangor, where they were held in large tanks of sea-water (34‰; 25°C) and fed upon commercially-available floating trout pellets.

They were studied about one month after arrival in the UK; at this time their body lengths (snout to tail) ranged from 105-122 mm and their weights from 33.5-70.5 g. After study the animals were returned to the Mediterranean.

FILMING

The turtles were filmed in a flume giving laminar flow over all of the current velocities employed in the study (Fig. 1). This had a long (3 m) square-section (400x400 mm) perspex trough supplied with sea water by a powerful pump and guarded by a gate that could be used to control water depth. The velocity of water flow was controllable by a valve, though this provided only very coarse control and could not be preset to a given current speed. Water flow rate was estimated by determining the rate of movement of weighted polystyrene floats over known distances within the flume (using video-recording and triplicate measurement). For the present study the flume was used to produce laminar flow without wave action. The flume was housed in a building at ambient temperature (*ca* 12°C), but the flume contents were heated during the present study to one of four nominal experimental temperatures (15°, 21°, 22.5° or 25°C). Temperature control was accurate to ±1°C. A section of the flume 600 mm in length was cordoned off by two very coarse mesh (50 x 50 mm) screens, and a grid of vertical lines set 100 mm apart was marked on it. This section was used in all quantitative studies of turtle swimming.

Turtles were filmed with a Panasonic F10 video-camera directed normally to the side surface of the cordoned-off section of the flume from a distance of 5 m (to minimize parallax problems). The camera was fit-

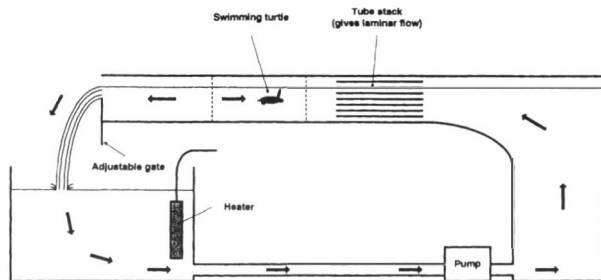


FIG. 1. Flume arrangement.

ted with a high speed (0.001 s) shutter. Film was analysed by freeze-frame and play-back through a Panasonic AG6200 video-recorder and monitor, coupled with drawings made by placing acetate sheets over the monitoring screen. Calculation of foreflipper angles of attack followed the procedure of Davenport *et al.* (1984).

EXPERIMENTAL PROTOCOL

The first objective was to determine the effect of current speed on direction of swimming in the turtles. The flume was first adjusted to temperature and then the pump switched off. A turtle was introduced to the work section of the flume and allowed to acclimate to conditions for 15 min (by this time the initial rapid movement had subsided). The animal was filmed for 5 min, and the proportion of time that the animal swam in the 'up-stream' direction was established. The flume pump was switched on, and a gentle flow along the flume produced. Again the animal was filmed for 5 min. Flow was increased in stepwise fashion, 5 min of filming taking place at each new flow velocity. The experiment was repeated at 15°C, 21°C, 22.5°C and 25°C, using a different turtle in each case.

Davenport *et al.* (1984) established that young green turtles normally used ipsilaterally-synchronized swimming ('dog-paddle') when swimming slowly at 25°C. In the second experiment, at each experimental temperature (15°C, 21°C and 25°C), three turtles, in turn, were each placed in the flume with the flow switched off and allowed to settle down. Water flow was gradually increased until the animals started to use synchronized action of the forelimbs for swimming; the flow rate corresponding to this transition was then measured (in triplicate).

The third experiment consisted of an investigation of the maximum sustained swimming speed at 15°C, 21°C and 25°C. Each turtle was introduced to the flume, and the water velocity gradually increased until the animal just started to lose ground within the working area of the flume, despite swimming continuously. Eleven reliable measurements were made at 25°C, 12 at 21°C and 8 at 15°C; other measurements had to be discarded because animals touched the screens at either end of the working area, or (in the case of animals held at 15°C) yawed sideways and touched the sides of the flume. At 25°C and 21°C the animals swam continuously for at

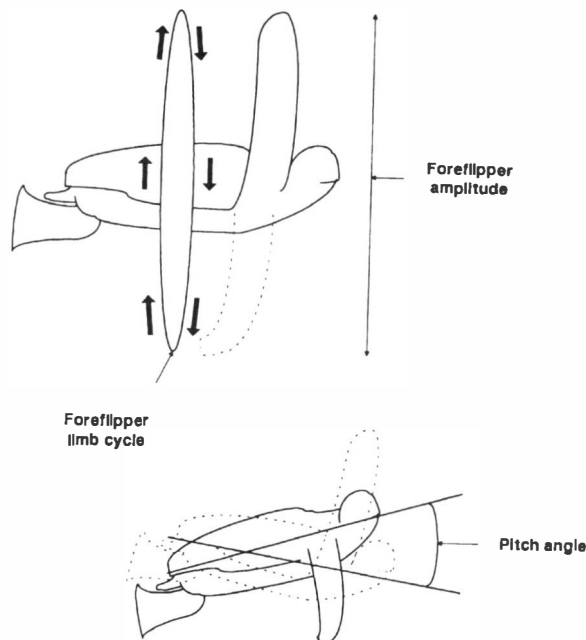


FIG. 2. Diagram illustrating measured features of turtle swimming.

least 10 min during the experiments; at 15°C no more than 2-5 min elapsed before yawing terminated trials. Swimming speed was calculated from the measured water flow and the relative movement of the turtle in that flow. Swimming was periodically interrupted by the turtle taking breaths at the surface, during which they often employed brief dog-paddle; the recorded maximum swimming speeds (transformed to body lengths s^{-1} for comparability) were those observed during immersed swimming, so in most cases were faster than the water velocity, even though the turtle was losing ground overall because of the need to take breaths. During the periods of sustained fast swimming, sufficient videotape was collected to allow detailed analysis of use of the forelimbs, and to measure the degree to which the body of the animal pitched on each swimming stroke (Fig. 2).

RESULTS

EFFECT OF CURRENT SPEED ON DIRECTION OF SWIMMING

From Table 1 it can be seen that, whatever the temperature, the turtles responded to increasing current speed by swimming upstream for more and more of the time. For each animal, the relationship between current speed and proportion of time spent swimming upstream was roughly linear (regression analysis yielded r^2 values between 72% and 89% in each case). By the time that current speed had risen to the equivalent of some 1-2 body lengths s^{-1} , the turtles were swimming directly into the current for almost all of the time at 21°C, 22.5°C and 25°C. At 15°C the situation was rather different; because the animal's swimming was discernibly less efficient, due to pitching and yawing, it was unable to sustain a heading, and was often swept downstream before regaining its position.

TABLE 1. Effect of current speed on direction of swimming in juvenile *Chelonia mydas*. Animals were held in a flume and subjected to gradually-increasing current speed. The proportion of time that they spent swimming in the 'upstream' direction (as opposed to downstream or laterally) was assessed.

| Turtle no. | Temperature (°C) | | | | | | | |
|------------|------------------|-------------------------------------|----|-------|-------|-------|-------|-------|
| 1 | 15.2 | Current speed (m s^{-1}) | 0 | 0.023 | 0.070 | 0.085 | 0.125 | 0.190 |
| | | % time swimming upstream | 7 | 20 | 29 | 57 | 55 | 67 |
| 2 | 21.0 | Current speed (m s^{-1}) | 0 | 0.030 | 0.125 | 0.174 | 0.260 | - |
| | | % time swimming upstream | 8 | 41 | 50 | 66 | 91 | - |
| 3 | 22.5 | Current speed (m s^{-1}) | 0 | 0.026 | 0.060 | 0.088 | 0.200 | 0.225 |
| | | % time swimming upstream | 20 | 27 | 50 | 83 | 95 | 96 |
| 4 | 25.0 | Current speed (m s^{-1}) | 0 | 0.020 | 0.138 | 0.167 | 0.190 | - |
| | | % time swimming upstream | 19 | 26 | 35 | 66 | 86 | - |

TEMPERATURE, SPEED AND SWIMMING MODE

From Table 2 it may be seen that the turtles continued to use dog-paddle until a swimming speed of around 0.8-1.4 body lengths s^{-1} was reached. Dog-paddle swimming was at the surface, and permitted easy breathing as the head was always emersed. Once the turtles had switched to synchronized foreflipper-flapping, all swimming took place with the animal totally immersed, and breathing became an intermittent, rhythmic activity. There was no statistically significant effect of temperature on transition speed.

EFFECT OF TEMPERATURE ON SUSTAINED SWIMMING SPEED

Temperature had a significant effect on swimming speed (Table 3). Although there was no statistically significant difference between swimming speeds recorded at 25°C and 21°C, the turtles held at 15°C were much slower and could only sustain a maximum swimming speed (mean 2.09 body lengths s^{-1}) 63% of that recorded at 25°C (mean 3.31 body lengths s^{-1}). Q_{10} for swimming speed over this temperature range was 1.58. It was also evident that swimming at 15°C was less efficient; the animals showed instability in roll, pitch and yaw, and they often broke the surface with their foreflippers at the top of the limbstroke, unlike the animals studied at the higher temperatures, which were always completely immersed.

TABLE 2. Effect of temperature on speed at which young green turtles switch from 'dogpaddle' swimming to synchronized foreflipper flapping. ANOVA showed that temperature did not have a significant effect on transition speed ($P=0.294$). Means \pm SD based on $n=3$.

| Temperature (°C) | Mean transition swimming speed (body lengths s^{-1}) | SD |
|------------------|--|------|
| 25 | 1.32 | 0.29 |
| 21 | 1.44 | 0.50 |
| 15 | 0.83 | 0.52 |

EFFECT OF TEMPERATURE ON SWIMMING MECHANISM

From Tables 4 and 5 it is evident that temperature affects several features of the swimming mechanism. At 25°C the turtles showed little body pitch (Table 4) and employed high frequency limbstrokes of lower amplitude than at 21° or 15°C. At 21°C the amplitude of limb beat was significantly greater ($P<0.05$), but the frequency of beat was not significantly reduced; the mean angle of body pitch was greater, but not to a statistically significant extent. At 15°C the amplitude of limb beat was similar to that employed at 21°C, but the frequency of limb beat was much lower ($P<0.05$) and the pitch angle much greater ($P<0.05$). Study of the calculated angles of attack of the foreflippers (Table 5) at the midpoints of the up and down strokes showed no significant differences between 21°C and 25°C (downstroke $P=0.261$; upstroke $P=0.685$), but the mean downstroke angle of attack at 15°C was greater to a highly significant extent ($P=0.000$) than at the other study temperatures. The mean angle of attack at 15°C on the upstroke was also quite different (and much less) than at the other temperatures ($P<0.01$).

DISCUSSION

The finding that young green turtles swim into currents is neither unexpected or novel - many aquatic animals automatically swim into currents provided that cues (visual or non-visual) are available to inform them

TABLE 3. Effect of temperature on sustained swimming speed in juvenile *Chelonia mydas*. ANOVA showed that temperature had a significant effect on swimming speed ($P=0.002$).

| Temperature (°C) | Mean maximum swimming speed (body lengths s^{-1}) | SD |
|------------------|---|-----------------|
| 25 | 3.31 | 0.66 ($n=11$) |
| 21 | 2.96 | 0.78 ($n=12$) |
| 15 | 2.09 | 0.53 ($n=8$) |

TABLE 4. Effect of temperature on foreflipper flap frequency, vertical amplitude of foreflipper movement and angle of body pitch in juvenile *Chelonia mydas* swimming at maximum sustained speed in a flume. ANOVA revealed significant temperature effects on foreflipper flap frequency ($P=0.012$), pitch angle ($P=0.000$) and vertical amplitude of foreflipper movement ($P=0.000$). Means \pm SD based on $n=4$.

| Temperature (°C) | Mean foreflipper flap frequency (limb cycles s ⁻¹) | SD |
|---------------------|--|------|
| 25 | 1.47 | 0.33 |
| 21 | 1.32 | 0.21 |
| 15 | 1.05 | 0.20 |
| | Mean foreflipper amplitude (mm) | SD |
| 25 | 64.3 | 11.9 |
| 21 | 72.3 | 6.9 |
| 15 | 73.5 | 6.5 |
| | Pitch angle (°) | SD |
| 25 | 2.6 | 3.4 |
| 21 | 6.4 | 5.5 |
| 15 | 11.9 | 6.9 |

that they are moving in relation to the earth's surface (e.g. fish; Bainbridge, 1975). In the flume situation many visual cues were available to the turtles from all directions (screens in front and behind, flume walls with markings on either side, the ceiling above and floor below); in the open ocean this would not be true, but there will be circumstances when visual cues are available (shoreline, clouds, starfields etc). For young green turtles of the size studied here, they swim constantly upstream when current velocities reach about 0.5 km h⁻¹. Maximum sustained swimming speeds corresponded to about 1.4 km h⁻¹, so it is clear, that ability to fight currents is limited - off Florida, Gulf Stream velocities are as high as 14 km h⁻¹ (Raymont, 1963).

This study is the first to give some indication of the relative efficiency of different swimming modes in *Chelonia mydas*. If it is assumed that young green turtles switch from dog-paddle to synchronized foreflipper flapping when they are travelling as fast as possible using the former mode, then the maximum dog-paddle speed is about 40% of the maximum speed using synchronized foreflippers. Superficially, since drag increases roughly with the square of the swimming speed, this would suggest that turtles develop around six times as much power when swimming with synchronized foreflippers as when dog-paddling. However, the increase in maximum speed will not simply result from the greater propulsive efficiency of synchronized foreflipper flapping, but will involve a component of avoidance of the high-drag zone at and near the air-water interface. Hertel (1966) studied the drag of a spindle-shaped object of thickness t' , and

TABLE 5. Effect of temperature on angle of attack (°) of the foreflipper blade at the midpoint of the down or upstroke when swimming continuously using synchronized foreflipper flapping. Angles were calculated as described by Davenport *et al.* (1984). ANOVA revealed significant temperature effects on both downstroke angles ($P=0.000$) and upstroke angles ($P=0.004$).

| Temperature (°C) | Downstroke | | Upstroke | |
|---------------------|------------|-----|----------|-----|
| | Mean | SD | Mean | SD |
| 25 | 40.2 | 9.1 | -17.0 | 6.2 |
| 21 | 46.7 | 5.1 | -18.5 | 2.9 |
| 15 | 73.7 | 6.8 | -3.2 | 5.2 |

found that drag started to increase from the normal deeply submerged value at a depth of 3 t' and rose to a maximum at 0.5 t' below the water surface (when the upper surface was in contact with the underside of the surface film). When moving from a deeply submerged position to the maximum-drag zone, the drag on a moving object will rise by a factor of about 5. Obviously turtles are not spindle-shaped, but by switching from surface dog-paddle to submerged synchronized foreflipper flapping, young turtles will encounter less drag.

At 15°C the turtles were not only substantially slower in their swimming than at 21°C or 25°C, (the Q_{10} of 1.56 is in the range that would be expected from an ectothermic species), but were also less efficient, implying a thermal effect on co-ordination. As well as rolling and yawing (not investigated quantitatively here), they showed greatly increased body pitch (Table 4), and calculations indicate that the foreflipper beat was less effective; at 21°C and 25°C the mean distance travelled per forelimb cycle was 2.25 body lengths, while at 15°C it was only 2 body lengths. Particularly interesting were the angles of attack of the foreflipper blades. At 21°C and 25°C the mean angles of attack on the downstroke were 46.7° and 40.2° respectively; corresponding mean angles on the upstroke were -18.5° and -17° respectively. These angles of attack are slightly greater than those reported by Davenport *et al.* (1984) for rather larger young green turtles (200-300 g; experimental temperature 25°C), but imply that forward propulsion was being generated on both up and downstrokes. At 15°C the picture was very different: on the downstroke the calculated mean angle of attack was high (73.7°), implying a flipper at, or close to, a stalled condition (see Davenport *et al.*, 1984 for discussion) generating much drag and little lift; a strong upward pitch component would be predicted. On the other hand the very low mean angle of attack on the upstroke (-3.2°) indicates that little or no propulsion was being produced on the upstroke. This analysis only applies to the midpoints of the strokes, and it should be remembered that the calculated angles of attack do not take into account induced water velocity (Weis-Fogh, 1973)

which reduces the effective angle of attack (whether positive or negative). However, it is clear that the young turtles use their flippers in a very different fashion at 15°C than at the two higher temperatures.

The finding that young green turtles exhibit substantially degraded swimming at 15°C is of interest in the context of vulnerability to cold. Green turtles have a lower lethal temperature well below 10°C (Schwartz, 1978), and temperatures below 10°C have been implicated in cold-stunning (Morreale *et al.*, 1992). However, there is evidence that feeding is impaired at temperatures below 20°C (e.g. Bjørndal, 1979) and will cease at 15-16°C (Davenport *et al.*, 1989). Felger *et al.* (1976) reported onset of torpidity at this temperature (though they worked on the 'black' variant, sometimes classified as a separate species, *Chelonia agazzizi*), so it seems likely that *Chelonia mydas* loses effective control over its ability to respond to currents in its environment at around 15°C, and will soon passively float downstream. However, the data presented in this study are for very small animals. Larger turtles may be capable of generating metabolic heat and sustaining effective swimming until rather lower temperatures are reached. It is also the case that the turtles were given relatively little time to acclimate to 15°C; their response was an acute one. Ideally, a longer acclimatory period would have been desirable, but it was feared that such long-term exposure to low temperatures might compromise the animals' subsequent growth and survival.

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REFERENCES

- Bainbridge, R. (1975). The response of fish to shearing surfaces in the water. pp.529-540 In *Swimming and Flying in Nature Volume 2* (ed. Wu, Y-T. T., Brokaw, C. J. & Brennan, C.). New York: Plenum Press.
- Bjørndal, K. A. (1979). Cellulose digestion and fatty acid production in the green turtle *Chelonia mydas* L. *Comparative Biochemistry & Physiology* **63A**, 127-133.
- Blake, R. J. (1981). Mechanics of drag based mechanisms of propulsion in aquatic vertebrates. *Symposia of the Zoological Society of London* **48**, 29-52.
- Caldwell, D. K. (1968). Baby loggerhead turtles associated with sargassum weed. *Quarterly Journal of the Florida Academy of Science* **31**, 271-272.
- Carr, A. (1952). *Handbook of Turtles*. New York: Comstock.
- Carr, A. & Meylan, A. (1980). Evidence of passive migration of green turtle hatchlings in sargassum. *Copeia* **1980**, 366-368.
- Davenport, J., Antpas, A. & Blake, E. (1989). Observations of gut function in young green turtles *Chelonia mydas* L. *Herpetological Journal* **1**, 336-342.
- Davenport, J., Munks, S. & Oxford, P. J. (1984). A comparison of swimming in marine and freshwater turtles. *Proceedings of the Royal Society of London* **B220**, 447-475.
- Davenport, J. & Pearson, G. A. (1994). Observations on the swimming of the Pacific ridley, *Lepidochelys olivacea* (Eschscholtz, 1829): comparisons with other sea turtles. *Herpetological Journal* **4**, 60-63.
- Felger, R. S., Clifton, K. & Regal, P. J. (1976). Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. *Science* **191**, 283-285.
- Hertel, H. (1966). *Structure-form-movement*. New York: Reinhold.
- Meylan, A. B. & Sadove, S.S. (1986). Cold-stunning in Long Island Sound, New York. *Marine Turtle Newsletter* No. **37**, 7-8.
- Lohmann, K. L. & Lohmann, C. M. F. (1996). Orientation and open-sea navigation in sea turtles. *Journal of Experimental Biology* **199**, 73-81.
- Morreale, S. J., Meylan, A. B., Sadove, S. S. (1992). Annual occurrence and winter mortality of marine turtles in New York waters. *Journal of Herpetology* **26**, 301-308.
- Raymont, J. E. G. (1963). *Plankton and Productivity in the Oceans*. Oxford: Pergamon Press.
- Schwartz, F.J. (1978). Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. *Florida Marine Research Publication* No. **33**, Florida Department of Natural Resources.
- Stoneburner, D. L., Richardson, J. I. & Williamson, G. K. (1982). Observations on the movement of hatchling sea turtles. *Copeia* **1982**, 963-965.
- Walker, W. F., Jr. (1971). Swimming in the sea turtles of the family Cheloniidae. *Copeia* **1971**, 229-233.
- Weis-Fogh, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *Journal of Experimental Biology* **59**, 169-230.
- Witherington, B. E. & Ehrhart, L. (1989). Hypothermic stunning and mortality of marine turtles in the Indian River lagoon system, Florida. *Copeia* **1989**, 696-703.
- Wyneken, J. (1988). Functional innovations in swimming: analyses of sea turtle locomotor patterns. *American Zoologist* **28**, 13A [Abstract].
- Wyneken, J. & Salmon, M. (1992). Frenzy and postfrenzy swimming activity in loggerhead, green and leatherback hatchling sea turtles. *Copeia* **1992**, 478-484.

MICROENVIRONMENTAL EFFECTS ON COMPETITION BETWEEN *RANA* AND *BUFO* LARVAE, AND ON THE ABUNDANCE OF *PROTOTHECA RICHARDSI*, IN SMALL FISH-PONDS

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Previous laboratory and replicated pond experiments have implicated *Prototheca richardsi*, a unicellular alga, in interference competition within larval anuran assemblages. We investigated the extent of interspecific competition between *Rana temporaria* and *Bufo bufo* larvae, and the occurrence of *P. richardsi*, in small fish-ponds where initial tadpole densities were high. Mortality of both *R. temporaria* and *B. bufo* larvae was high during the early stages of development, and interspecific competition was negligible in these ponds and in mesh cages suspended in them. However, growth of *B. bufo* larvae was reduced when they were raised with *R. temporaria* larvae at natural densities in plastic cages within the ponds. *P. richardsi* was positively associated with the plastic cage treatments, but was much less frequent in the ponds outside or in the mesh cage treatments. Predation appears to be a much more important structuring force than either resource competition or *Prototheca*-mediated interference competition in the anuran communities inhabiting these fish-ponds.

INTRODUCTION

Assemblages of larval anurans offer an ideal opportunity to study competitive interactions between species with high degrees of niche overlap. Inter- and intra-specific competition have been demonstrated between anuran larvae under both laboratory and field conditions (e.g. Heusser, 1972; Dash & Hota, 1980; Morin, 1981, 1983; Griffiths, 1991). This competition may be mediated by both resource and interference mechanisms (e.g. Griffiths, Denton & Wong, 1993; Beebee, 1996). Over the past 40 years microscopic organisms have been implicated as mediators of interference competition in a number of anuran species (e.g. Richards, 1958; 1962; Steinwascher, 1979; Petranka, 1989). Beebee (1991) demonstrated that a species of unpigmented unicellular alga, *Prototheca richardsi*, mediated growth inhibition of anuran larvae under laboratory conditions. Growth inhibition was also induced in replicated artificial ponds by rearing small *Bufo* tadpoles in water containing *Rana temporaria* faeces (Griffiths, Edgar & Wong, 1991), again implicating *P. richardsi* in interference competition between anuran larvae kept at moderate densities. There is some doubt, nevertheless, as to whether *Prototheca*-mediated competition is significant in the field and Petranka (1995) and Biesterfeldt, Petranka & Sherbondy (1993) provided evidence that although *Prototheca* cells were present in the natural breeding habitat of *R. sylvatica*, they were not involved in growth inhibition.

The two widespread British anurans *R. temporaria* and *Bufo bufo* exhibit a high degree of sympatry in their geographical distributions (Arnold, 1995) and frequently breed in the same water bodies. However, the common toad *B. bufo* generally spawns days or weeks later than the common frog *R. temporaria*, and the former species may therefore be competitively disad-

vantaged during larval development. In southeast England, small garden fish-ponds are important breeding sites for both species (Beebee, 1979). Population densities in these ponds are often higher than in their rural counterparts due to the inherent limitations in size of garden pools. These ponds thus provide interesting sites for examining interspecific competition between *R. temporaria* and *B. bufo* at high but natural breeding densities. This study was designed to assess the extent of any such competition and the relative strengths of resource and interference (*P. richardsi*-mediated) components in garden fish-ponds.

MATERIALS AND METHODS

STUDY PONDS

Three garden ponds (S, C and R) with naturally-occurring populations of *R. temporaria* and *B. bufo* were chosen as replicates from a data bank of such ponds in the Brighton (Sussex, UK) area. All ponds contained substantial numbers of goldfish (*Carassius auratus*) and similar percentages of submergent and emergent vegetation, but differed in size and depth. Pond R had a perimeter of 22.6 m, mean depth of 10 cm and held about 1770 litres of water; corresponding values for pond C were 9.7 m, 30 cm and 700 litres, and for pond S, 7.4 m, 30 cm and 410 litres.

TADPOLE DENSITY, SURVIVAL AND GROWTH

Spawn clumps of *R. temporaria* and strings of *B. bufo* were counted in each pond within one week of oviposition. The latter species spawned at least two weeks after the former in ponds R and C, but some four weeks after *R. temporaria* in pond S. *R. temporaria* egg numbers were estimated by multiplying the number of spawn clumps by 1300 (Cooke, 1975a). *Bufo bufo* egg numbers were calculated by counting the average

number of eggs present in 20 random 10 cm string sections and multiplying by the total estimated string length. Egg density was calculated by dividing total egg numbers by the volumes of the ponds to give an estimate of eggs/litre. Mark-recapture (Banks & Beebee, 1988) was carried out on *R. temporaria* tadpoles to estimate numbers in the ponds three and six weeks after hatching. When still present, *B. bufo* tadpole numbers were estimated by mark-recapture five weeks after hatching. In pond R, frog tadpole numbers were too high to mark-recapture on week three, so densities were estimated by counting tadpoles in five 50 cm x 50 cm areas of the pond and multiplying by the total area in which tadpoles were present.

GROWTH CONDITION TREATMENTS

Six 10-litre cages were placed in each pond in February 1996, several weeks prior to the arrival of anurans. Each cage was an open-top nylon mesh cylinder which reached from the bottom of the pond to 5 cm above the surface. Three of these cages were placed directly in the pond, whilst the other three were first placed into plastic bags filled with pond water, also open-topped, and then into the pond. Water and organisms < 1 mm² in cross section could pass between the main pond and the mesh cylinders, but plastic-coated cylinders were essentially impermeable to water and organisms from the rest of the pond. Each cage was filled with representative quantities of pond sediment and vegetation.

As soon as *R. temporaria* and *B. bufo* larvae were free-swimming in the study ponds, samples were placed at natural initial densities (as gauged from viable spawn estimates) into treatment cages. Each pond contained six cages, three of mesh only and three with plastic liners. Within each set of three, one cage had *R. temporaria* only, one *B. bufo* only, and one both species. Tadpole densities in the treatment cages were altered twice during the course of the experiment to mimic changes in natural densities in the main ponds, as gauged by later mark-recapture estimates. Each pond thus contained six different treatments, and each treatment was replicated three times (once in each of the three ponds). Replicates were in separate ponds to minimize individual pond effects in subsequent data analysis.

Free-swimming tadpoles in the main body of the pond acted as references against which treatments were compared. The treatments were divided into two groups: mesh cages and plastic cages. Each of these groups was divided into three treatments comprising one mixed species cage and two single species cages. The mixed-species cages contained larvae of both species at densities similar to those in the pond outside, and were thus controls for cage effects. The single-species cages each contained either *R. temporaria* or *B. bufo* larvae at their individual natural densities in the pond outside. Total tadpole densities in the single-species cages were therefore lower than those in the exterior

pond. Mesh cage treatments allowed free interchange of micro-organisms and were designed to permit interference but not resource competition to persist at levels similar to those in the pond outside. Plastic cage treatments were designed to preclude microorganisms and thus to relieve both interference and resource competition. Tadpole growth rates were monitored by measuring total lengths (snout-tail tip) and body lengths (snout-vent) of 3-10 randomly-chosen individuals from the ponds ("free-swimmers") and from all treatment cages on a weekly basis.

PROTOTHECA TITRES

Faecal samples from two tadpoles from each treatment cage and from free-swimmers in the ponds were collected on a weekly basis from five weeks after hatching until metamorphosis. Each tadpole was placed in 20 ml water in a mesh cage for one hour, under field conditions. Faeces were then spun down in a bench centrifuge and re-suspended in 2 ml of water and shaken vigorously. 50 µl samples were placed on a haemocytometer slide and numbers of *Prototheca* cells counted under a phase contrast microscope (Beebee, 1991). The average number from each pair of tadpoles was used as the datum point.

STATISTICAL ANALYSIS

Statistical analysis was carried out on MINITAB Version 8.1 using an IBM PC. Mean tadpole length within a cage was treated as a datum point to ensure independence between measurements. The effects of treatment on body length were analysed by ANOVA (standard or repeated-measures with time and species composition as independent variables). The association of *Prototheca* with particular treatments was analysed using *G*-tests (Fowler & Cohen, 1990).

RESULTS

SURVIVAL IN THE PONDS

Mortality rates of both *R. temporaria* and *B. bufo* were high and six weeks after hatching less than 1% of *R. temporaria* larvae (relative to numbers of viable eggs) survived in all three ponds (Fig. 1). *B. bufo* bred two weeks later in pond S than in the other two ponds, while in pond R *B. bufo* larvae were not found more than three weeks after hatching. In pond C *B. bufo* survival was monitored successfully by mark-recapture and 5% of larvae survived five weeks after hatching. *R. temporaria* metamorphs were seen at all three ponds, but *B. bufo* metamorphs were only seen in pond C.

TREATMENT EFFECTS

Starting densities of *R. temporaria* and *B. bufo* tadpoles within the experimental cages, calculated to reflect those in the ponds, ranged from 6-20 per litre. Tadpole survival was substantially higher in treatment cages than in the main body of the pond. Tadpole densi-

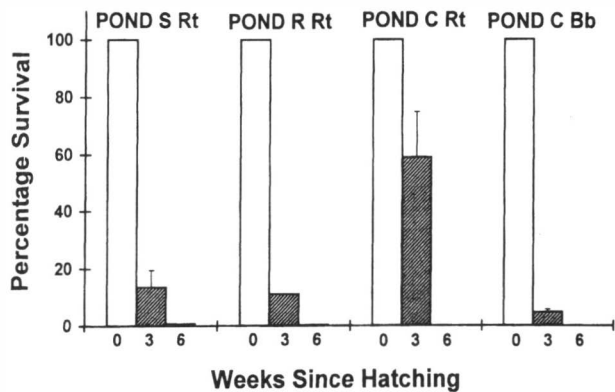


FIG.1 Percentage survival of *R. temporaria* (Rt) and *B. bufo* (Bb) larvae in all three study ponds. Estimates were made 3 weeks and 5/6 weeks after hatching, relative to numbers of viable eggs laid (week 0). Standard deviations of the estimates, where large enough are shown by error bars.

TABLE 1. Larval growth under different treatment regimes. n= no. treatment replicates (ponds or cages in which larvae were measured).

| (A). SIZES (SNOUT-VENT LENGTHS) AT DAY 63 AFTER HATCH OF <i>R. TEMPORARIA</i> SPAWN | | | | |
|---|------------------------|--------------------|------------------|--------------------|
| Treatment | <i>Rana temporaria</i> | | <i>Bufo bufo</i> | |
| | n | Mean size mm (±SD) | n | Mean size mm (±SD) |
| Free swimming | 3 | 12.8 ±1.3 | 2 | 10.9±1.3 |
| In mesh cage | 2 | 13.0 ±1.4 | 2 | 9.9±2.6 |
| In plastic cage | 3 | 12.3 ±0.9 | 2 | 10.3±1.1 |
| In mesh + competitor | 1 | 15.0 | 2 | 10.5±2.1 |
| In plastic + competitor | 2 | 12.7±0.9 | 2 | 9.6±2.0 |

| (B). ANOVA OF GROWTH TO DAY 63 UNDER DIFFERENT TREATMENT REGIMES | | | | | |
|--|----|-------|------|------|-------|
| <i>B. bufo</i> | | | | | |
| Source: | DF | SS | MS | F | P |
| Factor | 4 | 2.14 | 0.54 | 0.17 | 0.947 |
| Error | 6 | 19.10 | 3.18 | | |
| Total | 10 | 21.25 | | | |

| <i>R. temporaria</i> | | | | | |
|----------------------|----|------|------|------|-------|
| Source: | DF | SS | MS | F | P |
| Factor | 3 | 0.79 | 0.26 | 0.21 | 0.887 |
| Error | 6 | 7.54 | 1.26 | | |
| Total | 9 | 8.32 | | | |

ties in treatment cages were therefore reduced at regular intervals to mimic densities in the main pond, and by the end of the experiment were at around 0.3 tadpoles per litre. Because free-swimming *B. bufo* larvae disappeared from pond R within 2-3 weeks of hatch, numbers of this species in cages in pond R were adjusted to densities comparable with those in pond C during the course of the experiment. Also, fish attacked the mesh cages in pond R and no useful data were obtained from this treatment group in that pond.

Tadpole size 63 days after the hatch of *R. temporaria* spawn is summarized in Table 1A for the various treatments. This was an arbitrary time point late during development and reflected cumulative growth rates. In almost all cases, data were available for only two out of the three replicates rather than the full set. This was due to various factors, including fish attack on the mesh cages in pond R and late spawning by *B. bufo* in pond S. ANOVA of the growth attained at day 63 indicated no gross differences between any of the treatments for either species (Table 1B), and little evidence of cage effects relative to free-swimming tadpoles. Nevertheless, there was an indication that *B. bufo* larvae in plastic cages with *R. temporaria* grew more slowly than under any other conditions. This was confirmed by closer analysis of growth rates in plastic cage treatments (Fig. 2). *B. bufo* alone in plastic cages (in ponds R and C) grew at rates indistinguishable from those free-swimming in pond C, the only pond in which *B. bufo* was available as a control from early enough in the experiment. However, *B. bufo* in plastic cages with *R. temporaria* grew consistently more slowly than those either caged alone or free-swimming. The effects of both time and competition (presence of *R. temporaria*) in plastic cages, but not of interactions between them, were highly significant as judged by repeated measures ANOVA (Table 2). No comparable effects on *R.*

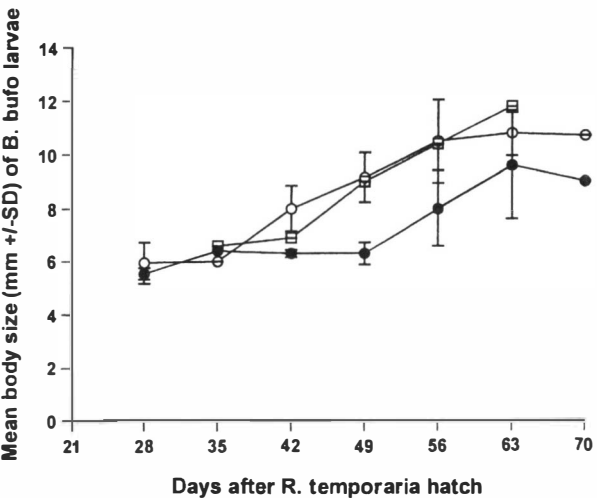


FIG 2. Growth rate of *B. bufo* larvae in the presence of and absence of *R. temporaria* in closed plastic cages. Open squares, tadpoles free-swimming in pond C; open circles, averages of tadpoles caged alone in ponds R and C; filled circles, averages of tadpoles caged with *R. temporaria* in ponds R and C.

TABLE 2. Repeated-measures of ANOVA of growth of *B. bufo* larvae in a plastic cage

| Source: | DF | SS | MS | F | P |
|-------------|----|-------|-------|-------|--------|
| Competition | 1 | 14.42 | 14.42 | 20.50 | <0.001 |
| Time | 5 | 67.34 | 13.47 | 19.15 | <0.001 |
| Comp.x time | 5 | 4.04 | 0.81 | 1.15 | 0.388 |
| Error | 12 | 8.44 | 0.70 | | |
| Total | 23 | 94.23 | | | |

temporaria larvae were observed in plastic cage treatments (data not shown).

PROTOTHECA TITRES

Table 3 shows the proportion of faecal samples containing *Prototheca* in each treatment group and the average numbers of *Prototheca* observed. Titres of *Prototheca*, when the organism was found, were comparable with those seen under laboratory conditions. The majority of free-swimming tadpoles and tadpoles in mesh cages had few or no protothecans in their faeces, but about one third of the samples examined from tadpoles in plastic cages contained *Prototheca*. This frequency was significantly higher than in mesh cages or the main ponds (*G*-test *P* < 0.05). There was, however, no specific association between growth inhibition and the occurrence of *Prototheca* in the plastic cage treatments. Growth-inhibited animals in mixed cages did not differ significantly in their production of *Prototheca* from the single species controls.

TABLE 3. *Prototheca* titres (*P.r.*) in faecal samples. *excluding one sample yielding 2.3×10^7 protothecans / tadpole/hr. Figures in parentheses are proportions of total samples in each species-treatment in which protothecans were detected. Third column shows mean no. cells/tadpole/hr in positive samples.

| Treatment/ Species | No. samples with <i>P.r.</i> | No. samples without <i>P.r.</i> | No. <i>P.r.</i> / tadpole/hr |
|-------------------------------|---------------------------------|------------------------------------|---|
| <i>R. temporaria</i> | | | |
| Free-swimming | 1(0.09) | 10 | 1.0×10^5 |
| In mesh | 0(0) | 8 | - |
| In plastic | 4(0.31) | 9 | 2.7×10^5 |
| In mesh+ <i>B. bufo</i> | 1(0.14) | 6 | 2.2×10^5 |
| Plastic+ <i>B. bufo</i> | 5(0.38) | 8 | 4.7×10^6 (* 1.8×10^5) |
| Total | 11(0.21) | 41 | 2.3×10^6 |
| <i>B. bufo</i> | | | |
| Free-swimming | 0(0) | 7 | - |
| In mesh | 0(0) | 9 | - |
| In plastic | 4(0.33) | 8 | 3.4×10^5 |
| In mesh+ <i>R. temporaria</i> | 0(0) | 7 | - |
| Plastic+ <i>R. temporaria</i> | 5(0.45) | 6 | 4.0×10^5 |
| Total | 9(0.20) | 37 | 3.5×10^5 |

TABLE 4. Correlation coefficients of body versus total length for *R. temporaria* and *B. bufo* larvae before and after six weeks from hatching.

| Conditions | <i>R. temp.</i> <wk. 6 | <i>R. temp.</i> >wk. 6 | <i>B. bufo</i> <wk. 6 | <i>B. bufo</i> >wk. 6 |
|---------------|---------------------------|---------------------------|--------------------------|--------------------------|
| In cages | 0.946 | 0.917 | 0.932 | 0.957 |
| Free-swimming | 0.978 | 0.682 | 0.970 | 1.000 |

EVIDENCE OF LARVAL PREDATION IN THE PONDS

Vertebrate predator attacks frequently leave surviving tadpoles with mutilations, especially tail bites. Evidence of such attacks was apparent from examination of tadpoles within cages (protected from fish) and those free-swimming and exposed in the main ponds. Comparisons of tadpole total (including tail) and body lengths demonstrated that in the latter stages of development the correlation between these two measurements was weak for free-living *R. temporaria* but high for young larvae, caged animals of all ages, and for *B. bufo* under all conditions (Table 4). These data suggested that *R. temporaria* larvae were more prone to fish attack than were those of *B. bufo*, and that such predation occurred at a substantial level in all three ponds. The high length correlation in small *R. temporaria* larvae was unsurprising, because prior to the attainment of a size refuge predator attacks generally result in complete consumption rather than mutilation.

DISCUSSION

POPULATION DYNAMICS OF ANURAN LARVAE IN SMALL FISHPONDS

R. temporaria and *B. bufo* spawn densities were several-fold higher in small garden ponds than is normal in larger rural sites, including (for example) sand dune ponds (Banks & Beebee, 1987). Mortality of hatchlings was, however, very great. On average, less than 15% of *R. temporaria* survived for three weeks and by six weeks only 0.6-1.0% remained. Five percent of *B. bufo* hatchlings survived to five weeks post-hatching in the single pond where comparative measurement was possible. These survival rates were much lower than those found for *R. temporaria* and *B. bufo* in a sand dune ecosystem (Banks & Beebee, 1987), and low by comparison with most other studies of anuran development (reviewed in Davis, 1985). In all three garden ponds there were large numbers of vertebrate predators, predominantly goldfish (*Carassius auratus*). Carnivorous invertebrates, such as odonate larvae (*Anax* spp.) and backswimmers (*Notonecta* spp.) were also present. *R. temporaria* larvae are heavily predated by fish (e.g. Cooke, 1975b) and this probably explains the low numbers of *R. temporaria* surviving through to metamorphosis as well as the extensive tail damage seen in larger larvae. In the first few weeks after hatch-

ing, *R. temporaria* are suitable prey for gape-limited predators such as goldfish. Once the larvae are a few weeks old they become too large to be consumed by these predators, but many lose large sections of their tails instead (Cooke, 1974). *B. bufo* tadpoles are unpalatable to most (though not all) vertebrate predators (e.g. Reading, 1990) but are attacked by many invertebrates (Banks & Beebee, 1988). The widespread occurrence of predatory insects may explain the high mortality of *Bufo* larvae in garden ponds. Survival of both species was substantially higher in treatment cages than in the main ponds, implicating predation of some kind as the major cause of mortality.

EFFECT OF TREATMENT ON TADPOLE GROWTH RATE AND *PROTOTHECA* ACCUMULATION

Caged tadpoles in single-species treatments relieved from direct (resource) or direct and indirect (interference) competition from tadpoles free-swimming in the main pond grew at rates indistinguishable from those outside the cages. Interspecific competition between *R. temporaria* and *B. bufo* in these fish-ponds was therefore apparently insignificant in treatments that mimicked natural pond conditions and densities. This was presumably because of the rapid fall in tadpole numbers due to high levels of predation. Competition was however induced by placing tadpoles at natural densities in plastic cages with no flow-through of water. In this microenvironment *B. bufo* exhibited significant levels of growth inhibition in the presence of *R. temporaria*. There was however no evidence of intraspecific growth inhibition in *B. bufo* in plastic single species cages (relative to those outside or in mesh), and no effects on *R. temporaria* under any circumstances.

A number of experiments in the laboratory and using replicated ponds have implicated *P. richardsi* in the growth inhibition of competitively inferior anuran larvae (e.g. Richards, 1958; Beebee, 1991; Griffiths *et al.*, 1993). In this study, however, the relationship was unclear. Plastic cages were associated with growth inhibition and high *Prototheca* titres, but inhibited and uninhibited (single-species treatment) *B. bufo* larvae had equally high frequencies of *Prototheca* in their faeces. Plastic cages were designed to reduce the number of growth inhibitors available to the tadpoles from the external pond, but may actually have served to concentrate protothecans produced within them. It is possible that *P. richardsi* accumulation was induced by raising tadpoles in closed cages, with no natural flow-through of water or nutrients. The majority of experiments on the role of micro-organisms in interference competition between anurans have employed glass or plastic containers (e.g. Richards, 1958; Beebee, 1991; Biesterfeldt *et al.*, 1993). However, Griffiths *et al.* (1993) found high numbers of protothecans in tadpoles raised in open mesh cages and Wong *et al.* (1994) found high levels of *Prototheca* in tadpoles from two natural ponds. It seems likely that some aspect of microenvironment quality, as yet undetermined, influences both competi-

tion intensity and *Prototheca* accumulation although it remains uncertain as to whether or how these phenomena are causally related under natural conditions.

Biesterfeldt *et al.* (1993) attempted to induce *Prototheca* accumulation in closed cages of tadpole-crowded pond water in the laboratory and in the field. Cages left for five days in the field consistently failed to produce inhibitors, whilst cages kept in the laboratory accumulated inhibitors within a few days. Their results suggested that *Prototheca* accumulation is inhibited by biotic and abiotic factors not present in the laboratory, such as UV light, low pH or competition with other micro-organisms. In our study, plastic cages contained water, sediment and vegetation from the main body of the pond and were exposed to the same levels of UV light and other environmental variables as the rest of the pond. Densities of tadpoles in these cages were low in comparison to laboratory stocks. Nevertheless, *Prototheca* accumulated in the faeces of tadpoles raised in these cages to levels similar to those seen in the laboratory. This evidence confirms that *P. richardsi* can attain high titre under natural levels of UV light and in the presence of other micro-organisms present in pond sediments. Manipulation of the plastic cage microenvironment should therefore provide a useful approach for further investigations of interference competition in nature.

CONCLUSIONS

We draw two conclusions from this study. Firstly, it seems clear that neither resource nor interference competition was a significant structuring force on *B. bufo* and *R. temporaria* populations in fish-ponds where predation pressure was high. *R. temporaria* tadpole densities had fallen by over 50% by the time *B. bufo* larvae were free-swimming, and continued to decrease rapidly thereafter. Top-down predation effects in such ecosystems are thus probably more important than competition in moulding the community structure of these anuran assemblages, despite the very large initial densities of eggs laid. Nevertheless, high levels of *Prototheca* may increase vulnerability of tadpoles to predation (Lefcort & Blaustein, 1995), and as suggested by Werner & Anholt (1996), it is probably futile to study competition and predation in isolation from one another. Secondly, competition can be induced in fishponds by constraining *B. bufo* with *R. temporaria* at natural densities in plastic cages. Further study is clearly required to determine how microenvironment affects competition and *P. richardsi* titres, and whether these two phenomena are causally related in the field as they appear to be in the laboratory.

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REFERENCES

- Arnold, H. R. (1995). *Atlas of Amphibians and Reptiles in Britain*. ITE Research Publication 10, HMSO, London.
- Banks, B. & Beebee, T. J. C. (1987). Spawn predation and larval growth inhibition as mechanisms for niche separation in anurans. *Oecologia* **72**, 569-573.
- Banks, B. & Beebee, T. J. C. (1988). Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *J. Animal Ecol.* **57**, 475-492.
- Beebee, T. J. C. (1979). Habitats of the British amphibians (2): Suburban parks and gardens. *Biol. Conserv.* **15**, 241-256.
- Beebee, T. J. C. (1991). Purification of an agent causing growth inhibition in anuran larvae and its identification as a unicellular unpigmented alga. *Can. J. Zool.* **69**, 2146-2153.
- Beebee, T. J. C. (1996). *Ecology and Conservation of Amphibians*. Chapman & Hall, London.
- Biesterfeldt, J. M., Petranka, J. W. & Sherbondy, S. (1993). Prevalence of chemical interference competition in natural populations of wood frogs, *Rana sylvatica*. *Copeia* **1993**, 688-695.
- Cooke, A. S. (1974). Differential predation by newts on anuran tadpoles. *Brit. J. Herpetol.* **5**, 386-390.
- Cooke, A. S. (1975a). Spawn clumps of the common frog *Rana temporaria*: number of ova and hatchability. *Brit. J. Herpetol.* **5**, 505-509.
- Cooke, A. S. (1975b). Spawn site selection and colony size of the frog (*Rana temporaria*) and toad (*Bufo bufo*). *J. Zool. (Lond.)* **175**, 29-38.
- Dash, M. C. & Hota, A. K. (1980). Density effects on the survival, growth rate and metamorphosis of *Rana tigrina* tadpoles. *Ecology* **61**, 1025-1028.
- Davis, C. A. (1985). *The population dynamics of the natterjack toad (Bufo calamita, Laurenti) in the North Merseyside sand-dune system*. PhD thesis, Liverpool Polytechnic.
- Fowler, J. & Cohen, L. (1990). *Practical Statistics for Field Biology*. Open University Press, Milton Keynes, UK.
- Griffiths, R. A. (1991). Competition between common frog, *Rana temporaria*, and natterjack toad, *Bufo calamita*, tadpoles: the effect of competitor density and interaction level on tadpole development. *Oikos* **61**, 187-196.
- Griffiths, R. A., Denton, J. & Wong, A. L-C. (1993). The effect of food level on competition in tadpoles: interference mechanisms mediated by protothecan algae? *J. Anim. Ecol.* **62**, 274-279.
- Griffiths, R. A., Edgar, P. W. & Wong, A. L-C. (1991). Interspecific competition in tadpoles: Growth inhibition and growth retrieval in natterjack toads, *Bufo calamita*. *J. Anim. Ecol.* **60**, 1065-1076.
- Heusser, H. (1972). Intra- and interspecific crowding effects in tadpoles of *Bufo calamita* Laur. *Oecologia* **10**, 93-98.
- Lefcort, H. & Blaustein, A. R. (1995). Disease, predator avoidance and vulnerability to predation in tadpoles. *Oikos* **74**, 469-474.
- Morin, P. (1981). Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. *Science* **212**, 1284-1286.
- Morin, P. (1983). Predation, competition and the composition of larval anuran guilds. *Ecol. Monog.* **53**, 119-138.
- Petranka, J. W. (1989). Chemical interference competition in tadpoles: Does it occur outside laboratory aquaria? *Copeia* **1989**, 921-930.
- Petranka, J. W. (1995). Interference competition in tadpoles: Are multiple agents involved? *Herpetol. J.* **5**, 206-207.
- Reading, C. J. (1990). Palmate newt predation on common frog, *Rana temporaria*, and common toad, *Bufo bufo*, tadpoles. *Herpetol. J.* **1**, 462-465.
- Richards, C. M. (1958). Inhibition of growth in crowded *Rana pipiens* tadpoles. *Physiol. Zool.* **31**, 138-151.
- Richards, C. M. (1962). The control of tadpole growth by alga-like cells. *Physiol. Zool.* **35**, 285-296.
- Steinwascher, K. (1979). Host-parasite interaction as a potential population-regulating mechanism. *Ecology* **60**, 884-890.
- Werner, E. E. & Anholt, B. R. (1996). Predator-induced behavioural indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* **77**, 157-169.
- Wong, A. L-C., Beebee, T. J. C. & Griffiths, R. A. (1994). Factors affecting the distribution and abundance of an unpigmented heterotrophic alga *Prototheca richardsi*. *Freshw. Biol.* **32**, 33-38.

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A TAXONOMIC REVIEW OF THE *VARANUS (POLYDAEDALUS) NILOTICUS* (LINNAEUS, 1766) SPECIES COMPLEX

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The status of the two nominal subspecies of *Varanus niloticus* (Linnaeus, 1766), viz. *V. n. niloticus* and *V. n. ornatus* (Daudin, 1803) is re-evaluated based on morphological (colour pattern, scalation, dimensions, outer genitals), ecological, and distributional data. Evidence is presented that both forms have markedly surpassed the subspecific level and have to be treated as two distinct, though closely related, species.

INTRODUCTION

In his subgeneric classification of the genus *Varanus*, Mertens (1942) placed the two tropical African monitor lizard species *V. exanthematicus* and *V. niloticus* in two different subgenera. Whereas he assigned the former together with the Indian *V. flavescens* to a joint subgenus *Empagusia* Gray, 1838 (type: *V. flavescens*), he accommodated the latter in a monotypic subgenus *Polydaedalus* Wagler, 1830. This largely phenetic classification has not been supported by subsequent studies. *V. flavescens* turned out to be unrelated to the African steppe monitors (see Ziegler & Böhme, 1997 and references therein), which, in turn, actually consist of three species: *V. exanthematicus* s. str., *V. albigularis* and the SW-Arabian *V. yemenensis*. Moreover, they turned out to be rather closely related to their largely sympatric congener *V. niloticus* and are therefore now jointly accommodated in the subgenus *Polydaedalus* (for a summary of these changes and an updated review of varanoid lizard classification in general see Böhme, 1988, and Ziegler & Böhme, 1997).

Varanus niloticus has a vast distribution area covering most of the African continent, with the exception of the Mediterranean zone in the north-west and the extreme south, as well as the huge desert areas of the northern and south-western part of the continent (cf. the sketch maps in Buffrénil, 1993, and Lenz, 1995). Due to a different colour pattern, Mertens (1938, 1942) distinguished two subspecies:

- *V. n. niloticus* (Linnaeus, 1766), characterized by 6-9 light crossbands or rows of light ocelli between fore- and hindlimbs, and inhabiting the open areas outside the West and Central African rain forest;

- *V. n. ornatus* (Daudin, 1803), characterized by normally only 5 light cross-bands or oblique rows of light ocelli between the extremities, and inhabiting the western and equatorial forest block.

Mertens (1942) mentioned an additional distinguishing character, viz. the colour pattern of the tail which has broader – and therefore fewer – light crossbands in *V. n. ornatus* (12) than in *V. n. niloticus* (16-18). He further assumed craniological differences between both forms, but due to scarce skull material with partly insuffi-

cient locality data he was unable to demonstrate them. His scale counts proved to be a little more conclusive, but he finally considered both subspecies to be distinguished only by their colour pattern.

If one considers the numerous papers dealing with *V. niloticus* from different viewpoints, it seems that Mertens' (1938, 1942) concept of these two subspecies has been largely accepted until present (e.g. Dunger, 1967; Branch, 1988; Buffrénil, 1993; Bennett, 1995; Lenz, 1995). The differences in colour pattern as described by Mertens (1942) are, however, not the only distinguishing features between the two forms of the Nile monitor. As well as biological differences, we are aware of additional morphological distinguishing characters (see our personal communications in Lenz, 1995: p. 10) that have been reiterated already in popular articles (see Faust & Bayless, 1996). In view of our very new genital-morphological results (Ziegler, 1996; Ziegler & Böhme, 1997), it seems appropriate to reconsider the taxonomic status of the two *V. niloticus* forms on the basis of new morphological and distributional analyses.

MATERIAL AND METHODS

Our study is based on material kept in the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK), the Zoologische Staatssammlung, Munich (ZSM), the Natural History Museum, London (BM), and the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main (SMF). From literature data we refer also to voucher specimens kept in the Zoologisches Museum, Hamburg (ZMH).

In the course of preliminary investigations, we evaluated only locality and tongue colour data following a first assignment based on colour pattern. Here we were greatly supported by B. Hughes, London, who provided data from more than 80 *V. niloticus* specimens deposited in the BM and some additional specimens from his own collection. The metric and meristic values are derived from 69 ZFMK and ZSM specimens; we incorporated only a few SMF specimens in our investigations, as the numerous data of Mertens (1942) that

TABLE 1. Morphological characteristics of *V. n. niloticus* and *V. n. ornatus*.

| | <i>V. n. niloticus</i> | | | <i>V. n. ornatus</i> | | |
|--|------------------------|---------------------------|---------|----------------------|-------------------------|---------|
| | <i>N</i> | Range | Mean±SD | <i>N</i> | Range | Mean±SD |
| Light dorsal cross-bands between the extremities | 36 | 6–11 | 7±1.2 | 33 | 4–6 (1x4, 31x5, 1x6) | 5±0.3 |
| Light cross-bands of the tail | 32 | 10–18 | 13±2.3 | 33 | 9–12 | 10±0.9 |
| Colour of tongue | 97 | pigmented (blueish-black) | | 57 | light (whiteish-pink) | |

are incorporated in our study are already based on SMF material.

The genital-morphological findings and terminology are based on the works of Ziegler (1996) and Ziegler & Böhme (1997).

The distribution maps were plotted on the basis of the specimens investigated by the authors and B. Hughes and supplemented by unambiguous data from the literature.

RESULTS

MORPHOLOGICAL CHARACTERS

Colour pattern. Sorting the studied Nile monitor material by the number of light dorsal cross-bands or oblique rows of light ocelli resulted in a separability of nearly 100%, in juveniles as well as in adults: 5 rows in *ornatus*, and markedly more in the nominate form; a similar situation is found concerning the light cross-bands of the tail (Table 1).

Tongue colouration. We found a highly consistent correlation between these colour pattern characters and the colouration of the tongues (we excluded artefacts such as a later depigmentation due to alcohol storage for several decades). Whereas specimens of the nominotypic form constantly have fully pigmented,

dark tongues, all *ornatus* specimens studied had unpigmented, light, whitish to pink tongues. Only in very rare cases were some small dark flecks observed on these tongues, and if so, only in their hindparts (e.g. ZSM 140/1975 from Yaoundé, Cameroon: 5 light dorsal bands, 9 light tail bands, 158 midbody scales). In view of this constant, additional distinguishing character we are able to assign the 2 specimens of *ornatus* with a slightly deviating colour pattern (ZSM uncatalogued: Mundame, 4 light dorsal bands, 11 light tail bands; ZSM 619/0: Gabon, 6 light dorsal bands, 10 light tail bands, 161 midbody scales: see also Table 1) clearly to *ornatus*.

Differing from this character combination is only a Nile monitor photographed near Mombasa, Kenya. This specimen (available only as a photograph) has a colour pattern similar to typical *V. n. niloticus*; it shows, however, a light, whitish tongue which is otherwise typical of *ornatus*. Another specimen, likewise from eastern Africa (BM 1969. 404: Condocuanza, Mozambique) has also a light (faded?) tongue, as does a specimen from NE Africa (BM 1906.7.25.3: Egypt, Luxor) (Hughes, pers. comm.). For a discussion of these and other exceptional specimens see further below.

TABLE 2. Scalation characteristics of *V. n. niloticus* and *V. n. ornatus*.

| | <i>V. n. niloticus</i> | | | <i>V. n. ornatus</i> | | |
|---|------------------------|---------|----------|----------------------|---------|---------|
| | <i>N</i> | Range | Mean±SD | <i>N</i> | Range | Mean±SD |
| Scales across the head from rictus to rictus (after Mertens, 1942) | / | 43–56 | / | / | 50–60 | / |
| Oblique ventral scale rows from gular fold to insertion of hindlegs (after Mertens, 1942) | 11 | 77–94 | 88±5.6 | 16 | 80–95 | 90±4.5 |
| Scales around midbody (after Mertens, 1942) | 12 | 137–165 | 154±8.1 | 15 | 146–175 | 90±4.5 |
| Scales around midbody (own data) | 32 | 136–183 | 153±10.3 | 31 | 149–174 | 161±5.4 |
| Scales around midbody (own data + Mertens, 1942) | 44 | 128–183 | 153±9.8 | 46 | 146–175 | 162±6.7 |

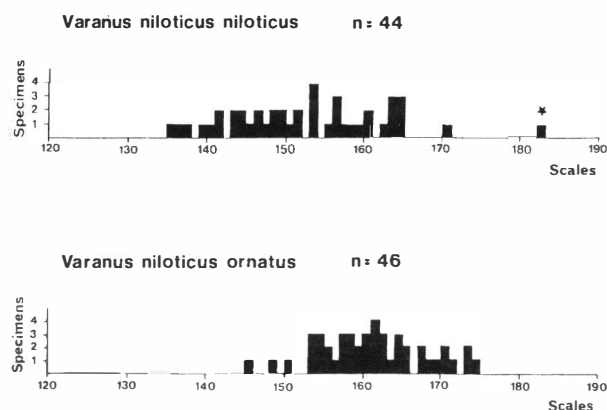


FIG. 1. Histogram of scales around midbody, based on Mertens' (1942) and own data. * = *V. n. niloticus* (ZFMK 2784) from Egypt, surroundings of Cairo (black tongue, 8 light dorsal crossbands between the extremities, 14 light crossbands of the tail).

Scalation. The results of the scale counts done by us are summarized in Table 2, where we incorporated also the scalation data published by Mertens (1942). However, he did not give the sample sizes on which his values relied (oblique ventral scale rows from gular fold to insertion of hindlegs for *V. n. niloticus* 75-94, mean = 88, for *V. n. ornatus* 80-97, mean = 89; scales around midbody for *V. n. niloticus* 128-165, mean = 153, for *V. n. ornatus* 146-175, mean = 164). Therefore, we compiled the raw data from Mertens' (1942) paper – as far as possible – in our Table 2 and calculated their mean values and standard deviations. The most useful scale character to separate both forms is the midbody scale count which we illustrated by a histogram (Fig. 1).

Head proportions and dimensions. Like Mertens (1942), we did not have sufficient skull material with reliable data available to carry out a comparative craniological study. Nevertheless, it became evident from our material that adult *V. n. ornatus* have a much more massive skull architecture than equal-sized adults of the nominotypic form (see also Mertens, 1942: pl. 27; Dunger, 1967: pl. 1). Fig. 2 documents this situation by

illustrating the heads of two roughly equal-sized males, the *ornatus* male having a markedly more compact, higher and blunter head (and consequently also skull) than the *V. n. niloticus* male.

Here we can report also on an extremely large (though partly damaged) *V. n. ornatus* skull of unknown sex from Ureca, Bioko Island, Equatorial Guinea (ZFMK 14889). It measures from tip of snout to occiput 14.2 cm, from tip of snout to the hindmargin of the squamosum 15.0 cm; the lower jaw (from tip of snout to the posterior end) measures no less than 15.2 cm (cf. the data published by Haacke & Groves, 1995).

Genital morphology. Available were the everted organs of several representatives of both sexes of the nominotypic form (ZFMK 17521, 32389, 35565-6, 61141-2, 2 specimens ZFMK uncatalogued) as well as of *V. n. ornatus* (ZFMK 9399, 58217, 61132, 61137, 61140). Detailed descriptions of these organs can be found in Ziegler (1996) and in Ziegler & Böhme (1997). We restrict ourselves here only to highlight the differences between the two taxa in question.

The outer genital organs (of both males and females) of *V. n. niloticus* tend to have fewer (5-10) paryphasmata (versus 8-12 in *V. n. ornatus*). These are completely divided in the longitudinal axis in the former, and not completely divided in the latter, the most proximal 1-2 paryphasmata being uninterrupted.

DISTRIBUTION

The locality data of the museum specimens used in this study have been plotted on a map of Africa – separately for each of the two taxa – and have been supplemented by locality records for both *V. n. niloticus* and *V. n. ornatus* according to literature data (see legend of Fig. 3). For a better documentation of para- resp. sympatry, we provided an additional map for west and western central Africa, where we numbered each locality and gave the voucher references in the legend (Fig. 4).

From these maps it is evident that *V. n. niloticus* inhabits the extended savanna areas of Africa except the

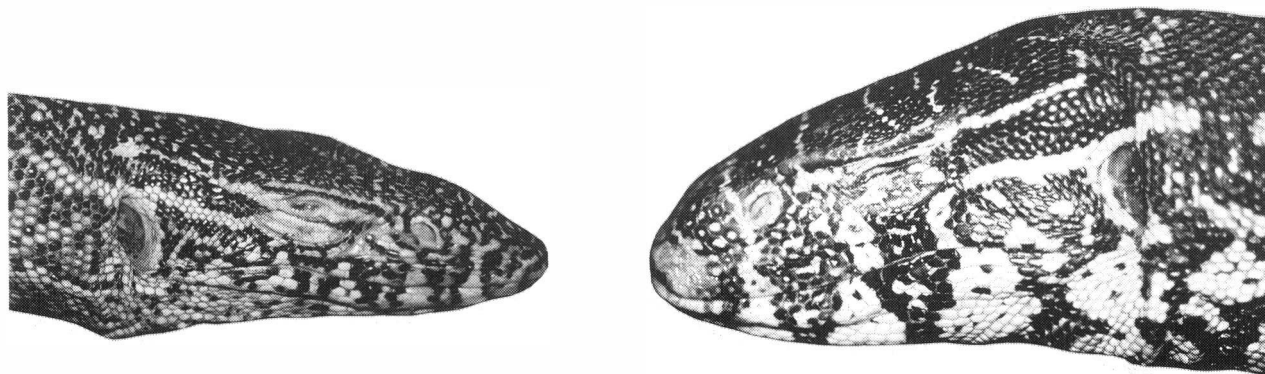


FIG. 2. Head proportions of two roughly equal-sized adult males of *V. n. niloticus* and *V. n. ornatus*. Left: *V. n. niloticus* (ZFMK 17521) Senegal, Diattacounda, leg. W. Böhme, 10.-26. 12. 1975 (1.65 m); right: *V. n. ornatus* (SMF 49832) "French Congo, Province Orientale", Epulu, leg. B. Grzimek, 4.3.1954 (1.60 m).

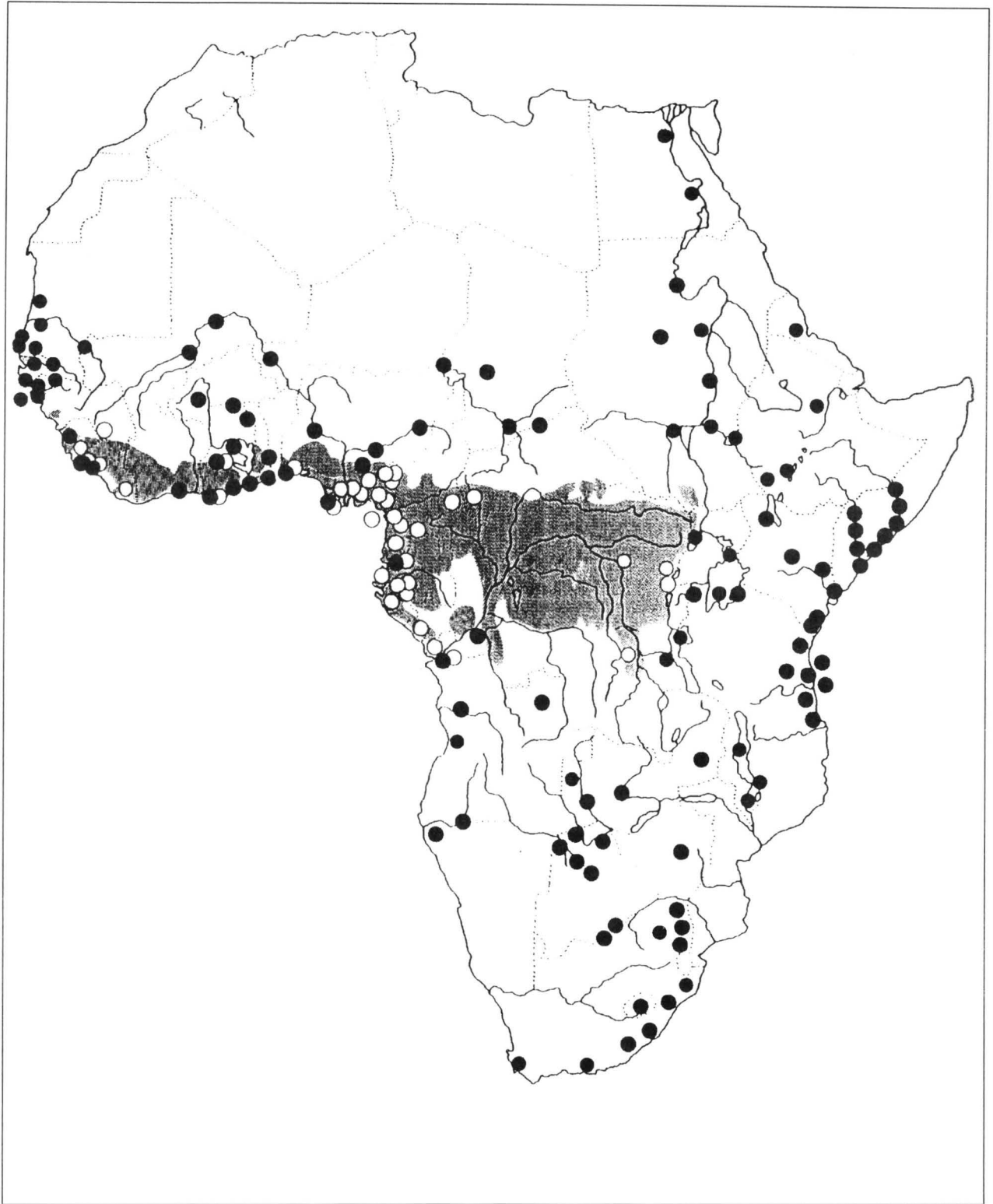


FIG. 3. Rough distribution of *Varanus n. niloticus* (black circles) and *Varanus n. ornatus* (white circles) in Africa; marked area: tropical rain forest, swamp forest and mangrove, modified after Martin (1989). Locality data from examined specimens of BMNH, SMF, ZFMK and ZSM and according to Mertens (1942, 1971), Laurent (1964), Dunger (1967), Papenfuss (1969), Pienaar (1978), Auerbach (1987), Branch (1988), Lanza (1990) and Böhme et al. (1996); for more detailed information see overview in Buffrénil (1993).

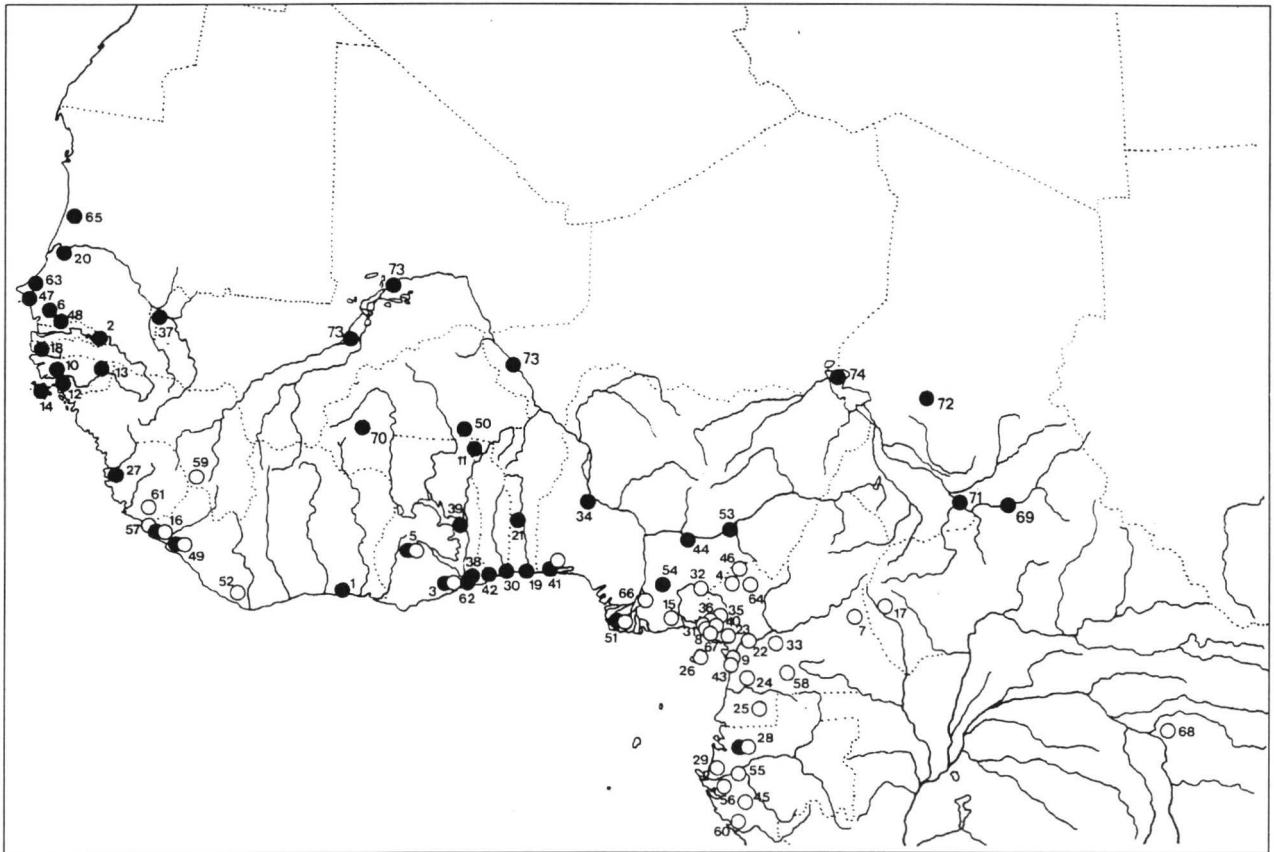


FIG. 4. Rough distribution of *Varanus n. niloticus* (black circles) and *Varanus n. ornatus* (white circles) in West Africa (for origin of localities see caption of Fig. 1). 1 Abidjan / 2 Abuko National Park / 3 Accra / 4 Akwu / 5 Ashantee / 6 Bandia / 7 Batouri / 8 Bibundi / 9 Bipindi / 10 Bissau / 11 Bogou / 12 Bolama / 13 Boughari / 14 Bubaque / 15 Calabar / 16 Cape Mount / 17 Carnot / 18 Casamance / 19 Cotonou / 20 Dagana / 21 Dahomey / 22 Dibongo / 23 Duala / 24 Ebolowa / 25 Evinayong / 26 Bioko / 27 Freetown / 28 Gabon / 29 "Gabon City" = Libreville / 30 Great Popo / 31 Idenau / 32 Ikom / 33 Yaoundé / 34 Jebba / 35 Johann Albrechts Hill / 36 Cameroon Mountain / 37 Kayes / 38 Keta / 39 Kete / 40 Mt. Kupe / 41 Lagos / 42 Little Popo / 43 Longji / 44 Makurdi / 45 Malimba / 46 Mamfe / 47 Mbour / 48 Medina / 49 Monrovia / 50 National Park W / 51 Niger Delta / 52 Nyaake / 53 Numan / 54 Obubra / 55 Ogooue / 56 Rembo / 57 Robert Port / 58 Sangmélina / 59 Sérédou / 60 Sette Kama / 61 Sumbuya / 62 Teshie / 63 Thiès / 64 Tinto / 65 Trarza / 66 Umuahia / 67 Victoria / 68 Wanie Rukula. Addendum: 69 Bahr Aouk / 70 Bobo Dioulasso / 71 Chari / 72 Fitri / 73 Niger / 74 Chad.

true deserts, whereas *V. n. ornatus* has a distributional pattern restricted to the Upper Guinean and western Lower Guinean forest block, with some records also at the eastern margin of the latter. Numerous localities document sympatric overlap of the two forms not only at the joint margins of their respective distribution areas, but also within them (e.g. Liberia, Ghana, Nigeria, Gabon and SW Zaire).

There are some doubtful or problematic localities of voucher material studied by us which have not been included in our maps. These are:

– ZSM 7/1953: Lake Chad. This specimen has a white tongue (being darkened only in its hindpart), 5 light dorsal crossbands, 11 light tail bands and 166 scales around midbody, being thus a typical *ornatus*. We therefore consider its locality to be incorrect. – ZSM 618/0: "Kilwa, E Africa", having a white tongue, 5 light dorsal crossbands, 12 light tail bands and 168 scales around midbody, and thus being a typical *ornatus*, too. "Kilwa" may refer to a locality on the SW bank of Lake Mweru in Zaire, or to a locality of the same name south

of Dar es Salam in Tanzania. We suspect the first locality to be the correct one but this is not certain.

– SMF 49832: "Epulu, Province Orientale, French Cong". This specimen has been illustrated by us above (Fig. 2) and is a typical *ornatus*. We did not map it because we are not aware of a locality Epulu in the ex-French Congo (today People's Democratic Rep. Congo), although there is an Epulu in the Province Orientale of Upper Zaire (= ex-Belgian Congo). Both possibilities would fit the distribution area of *V. n. ornatus*, but we cannot yet decide upon the correct one.

DISCUSSION

MORPHOLOGICAL DIFFERENCES

Our results clearly show that the two forms of Nile monitors are not only separable by their colour pattern, as supposed by Mertens (1942), but also by (1) the colouration of their tongues; (2) by different (though overlapping) scale counts; (3) by head and skull proportions; and (4) by marked differences in the morphology of their outer genital organs.

(1) The tongue colouration is strongly related to the body colour pattern, being always dark in the savanicolous *niloticus* and pinkish-whitish in the forest form *ornatus*. This drastic difference in tongue colouration in two closely related monitors is reminiscent of the situation in *Varanus indicus* and its sibling species *V. doreanus* in New Guinea (Böhme, Horn & Ziegler, 1994), where a functional significance in specific recognition has even been hypothesized, as an aggressive "threatening tongue-flicking" does play a role in ritual combats (Horn, Gaulke & Böhme, 1994). Böhme *et al.* (1994) consider the light tongues as the plesiomorphic condition, in which case *ornatus* would be the most primitive form within the Nile monitor complex.

(2) Although the scale counts show a broad overlap (Table 2, Fig. 1), there is a clear tendency in *ornatus* for increased values in all 3 parameters checked (i.e. across the head from rictus to rictus, ventral rows from gular fold to insertion of hind legs, and scales around midbody). As higher scale counts are generally considered to be more primitive than lower counts (see e.g. Hellmich, 1951, Peters, 1962: 456), also in this respect *ornatus* is the less advanced form.

(3) Already Mertens (1942) had observed that despite similar body proportions in both Nile monitor forms, the heads of *ornatus* were relatively larger and more robust, particularly in very old males. Although he assumed subsequently that also very old *niloticus* (s. str.) males should be able to achieve similar head proportions, our material suggests that indeed *ornatus* has a relatively much more robust head (see Fig. 2). The huge *ornatus* skull from Bioko Island reported on here seems to belong to the largest Nile monitor ever recorded (cf. Haacke & Groves, 1995).

(4) The differences in the structure of the outer genitals, in fact of the hemipenes as well as of the hemiclitores, have to be given particular weight as to the taxonomic distinctness of their semaphoronts, as they most likely play a role in sexual selection (Ziegler, 1996; Ziegler & Böhme, 1997). The constant existence of a largely closed lower paryphasman row strongly argues for a plesiomorphic condition of this character in *ornatus*.

ECOLOGICAL DIFFERENCES

In addition to the morphological differences discussed above, there are important differences in the ecology of both forms in respect of (1) habitat selection, and (2) phenology.

(1) As stated above, *V. n. niloticus* typically inhabits savanna biotopes in rather close association with water bodies (rivers), and is able to penetrate even desert areas along large river systems (e.g. Senegal river, Nile and others). However, it avoids deserts without sufficient permanent water (see Figs. 3 and 4). *V. n. ornatus*, in contrast, is a rain-forest form restricted to the African forest biota as far as they still exist (see Figs. 3 and 4).

(2) Obviously connected with this adaptation to two different biota, there is an important phenological difference between the two forms, pointed out for the Cameroon populations by Buffrénil (1993): "In the north of the country, north of Ngaoundéré, where the dryness of the soil is very marked from December to (inclusively) April, the Nile monitors aestivate in burrows, hollow trees or termite mounds for several months ('diapause estivale'). On the contrary, in the southern half of the country, where there is a very humid equatorial climate, the Nile monitors (probably the subspecies *V. n. ornatus*) do not undergo a 'diapause'" (our translation). An aestivation during the dry season has also been reported for Senegalese populations by Cissé (1976). We consider it unlikely that this ecological difference, which requires a very different physiological basis, should be simply due to an adaptational modification. Rather, we consider it to be selectively, i.e. genetically, induced. This view is corroborated by the map provided by Buffrénil (1993: p. 126), showing the distribution of estivating vs. non-estivating populations in Cameroon.

DISTRIBUTIONAL PATTERN

The answer to how to estimate and possibly reassess the taxonomic status of the two forms of *Varanus niloticus* relies largely on their distributional pattern: i.e. whether they occur in sympatry or not. Already the morphological differences, in particular those of the genital organs and the tongues, lead to the suspicion that both forms are exceeding the subspecies level. This is corroborated by the phenological differences which argue for a selectively induced divergent evolution into different biota. But the question of whether they should be regarded as semispecies within a superspecies *Varanus niloticus*, or as incipient (= *in statu nascendi*) species, can – apart from conceptual problems – be judged only from the biological criterion of unmixed sympatry (resp. syntopy) in nature. The distributional situation as documented here demonstrates a general broad parapatry, but gives several examples of true sympatry at various places of their ranges, and this not only at the periphery of the *ornatus* range. This rather complicated distributional pattern, particularly in West Africa and in Gabon/southern Zaire, reflects the dramatic climatic history of the African tropics. The shrinking of the rain forest belt as seen today is a rather recent phenomenon, i.e. only 6000–7000 years old (Martin, 1989; Kingdon, 1990; Maley, 1996). This enabled the savanna-inhabiting populations to penetrate the forest block at various places where they met with the forest-inhabiting *ornatus* populations, obviously without any indication of intergradation or hybridization, as would be expected from conspecifics. On the other hand, the forest block which reached its maximum extension only 7000 years ago (see above) had its minimum extension during the Pleistocene only 18 000 years ago, when the forest was reduced to very small

relict patches in West Africa, southern Cameroon, eastern Zaire and possibly a narrow coastal strip in southern Kenya. So the recolonization of the entire Zaire basin by the rain forest is also a rather recent event (between 18 000 and 7000 ybp.). Interestingly, we failed to find literature records for the central Zaire basin. This could indicate that the forest fauna, including the Nile monitor, is slow in recolonizing the forest. Indeed, there are numerous faunal examples of a similar distributional pattern (Martin, 1989; Kingdon, 1990, and others).

It is, however, interesting to note that *V. n. niloticus* has also not been recorded from the Zaire basin, this "evolutionary whirlpool" (Kingdon, 1990), where savannas and forests replaced one another several times. The extant *V. n. niloticus* is therefore not an old pre-Pleistocene savanna relict, but rather a modern, and in most of its characters, derived form, as compared with *ornatus*. This latter form seems to represent the survivor of an older, morphologically plesiomorphic stock. Its disjunct distribution pattern within the lower Guinean forest block discussed above (see also Figs. 3 and 4) fits this assumption. It may be noted that Mertens (1942) considered also the possibility of a "polytopic" origin of the forest-dwelling *ornatus* populations.

CONCLUSION AND FUTURE PROSPECTS

The morphological, ecological and distributional evidence presented here leads us to the conclusion that the two traditional subspecies of the Nile monitor have to be regarded as full species:

– *Varanus (Polydaedalus) niloticus* (Linnaeus, 1766)

– *Varanus (Polydaedalus) ornatus* (Daudin, 1803).

As no new forms are currently involved, we refrain from discussing synonyms of both species in this paper. This could, however, well become necessary, when additional material from critical areas becomes available. Problems for future taxonomic research on Nile monitors in Africa are indicated by some single specimens which are currently regarded as aberrant or, in some instances, possibly mislabelled (see above). An additional example is ZMB 18823, labelled as originating from Arafalis Rock, Sinai peninsula, but most likely coming from Arafale, Eritrea (Mertens, 1942). Also a clear *ornatus* (ZSM 7/1953) from Lake Chad, discussed already above, certainly has wrong locality data.

Another problem is the variability of the colour pattern of *V. ornatus*. As can be seen from our Table 1, the number of light dorsal crossbands can be reduced or augmented. Previously Mertens (1942) reported that there were very rarely juvenile *ornatus* with only 3 dorsal bands. Moreover, he mentioned an adult specimen figured by Daudin (1803), also with 3 dorsal light cross-bands. He also reports on a sample from between Idenau and Bibundi (Mt. Cameroon), where next to one specimen with 3 crossbands (SMF 11608) others had

four (SMF 11604, ZMH 2936, 3607, 3990 and 4406). An increase over the number typical of *ornatus*, viz. 5, was observed by Mertens (1942) only once, in a specimen from Molundu (SMF 11600): Due to an asymmetrical pattern it showed 6 light, dorsal cross-bands.

Mertens (1942) considered the low numbers of dorsal cross-bands as being "reduced". If we compare, however, this situation with that of the steppe monitors, which share the subgenus *Polydaedalus* with the Nile monitors, again the forms with higher scale counts and less derived hemipenes (*V. albigularis*) have lower numbers of dorsal oblique rows of ocelli. These are increased in the northern *V. a. microstictus* and *V. exanthematicus* (see Laurent, 1964; Böhme *et al.* 1989). It seems therefore reasonable to consider low numbers of light dorsal cross-bands in *Polydaedalus* as primitive, and increased numbers as derived. For the *V. niloticus* complex this means that *V. niloticus* (s. str.) can also be regarded as the derived form with respect to its colour pattern.

A last point of future taxonomic research in Nile monitors concerns the light-tongued specimens which have been found outside the currently known distribution range of *V. ornatus*, but which have a dorsal pattern like *V. niloticus* (see above). It is therefore questionable whether this is due to individual or to geographical (i.e. taxonomically relevant) variation. The monitor from Luxor, Egypt, with its light (probably faded) tongue is most unlikely to represent a specimen of *ornatus*, as Egypt was not covered by rain forest even during the maximal forest extensions in Africa. The situation of the – also in life – whitish-tongued Nile monitors inhabiting the East African coast between Kenya and Mozambique may, however, well be different, because this East African coastal strip has been a forest refuge during Africa's unstable Plio-/Pleistocene history.

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REFERENCES

- Auerbach, R. D. (1987). *The Amphibians and Reptiles of Botswana*. Mokwepa Consultants (Pty) Ltd., Gaborone, 295 pp.
- Bennett, D. (1995). *A Little Book of Monitor Lizards*. Viperpress, Aberdeen, 208 pp.

- Böhme, W. (1988). Zur Genitalmorphologie der Sauria: funktionelle und stammesgeschichtliche Aspekte. *Bonn. zool. Monogr.* **27**, 1-176.
- Böhme, W., Horn, H.-G. & Ziegler, T. (1994). Zur Taxonomie der Pazifikwarane (*Varanus indicus* - Komplex): Revalidierung von *Varanus doreanus* (A.B. Meyer, 1874) mit Beschreibung einer neuen Unterart. *Salamandra*, Rheinbach, **30**, 119-142.
- Böhme, W., Joger, U. & Schätti, B. (1989). A new monitor lizard (Reptilia: Varanidae) from Yemen, with notes on ecology, phylogeny and zoogeography. *Fauna of Saudi Arabia*, **10**, 433-448.
- Böhme, W., Meinig, H. & Rödel, M.-O. (1996). New records of amphibians and reptiles from Burkina Faso and Mali. *Bull. Brit. Herp. Soc.* **56**, 7-26.
- Branch, W. R. (1988). *Field Guide to the Snakes and other Reptiles of South Africa*. Cape Town (Struik), 328 pp.
- Buffrénil, V. de (1993). Les varans africains. *Varanus niloticus* et *Varanus exanthematicus*. Données de synthèse sur leur biologie et leur exploitation. Programme des Nations Unies pour l'environnement (PNUE), CITES secrétariat, 162 pp.
- Cissé, M. (1976). Le cycle génital des Varans du Sénégal (Reptiles Lacertiliens). *Bull. de l'I.F.A.N.* **38**, A(1), 188-205.
- Daudin, F. M. (1803). Description du *Tupinambis* orné. *Ann. Mus. natn. Hist. nat.* **2**, 240-243.
- Dunger, G. T. (1967). The lizards and snakes of Nigeria. Part 3: The monitors and a plated lizard. *The Nigerian Field* **32**, 170-178.
- Faust, R. J. & Bayless, M. K. (1996). Nile monitors: ecology, morphology and husbandry. *Reptiles* **4**, 68-83.
- Haacke, W. D. & Groves, D. (1995). *Varanus niloticus niloticus*. Nile monitor. Size. *African Herp News* **22**, 45-46.
- Hellmich, W. (1951). On ecotypic and autotypic characters, a contribution to the knowledge of the evolution of the genus *Liolaemus* (Iguanidae). *Evolution* **5**, 359-369.
- Horn, H.-G., Gaulke, M. & Böhme, W. (1994). New data on ritualized combats in monitor lizards (Sauria: Varanidae) with remarks on their function and phylogenetic implications. *Zool. Garten, Jena, N.F.*, **64**, 265-280.
- Kingdon, J. (1990). *Island Africa - The Evolution of Africa's Rare Animals and Plants*. Collins, London, 287 pp.
- Lanza, B. (1990). Amphibians and reptiles of the Somali Democratic Republic: check list and biogeography. *Biogeographia* **14**, 407-465.
- Laurent, R. F. (1964). Reptiles et amphibiens de l'Angola. Diamang, Publicações Culturais No. 67, Museu do Dundo, 165 pp.
- Lenz, S. (1995). Zur Biologie und Ökologie des Nilwarans, *Varanus niloticus* (Linnaeus 1766) in Gambia, Westafrika. *Mertensiella* **5**, Bonn, 256 pp.
- Maley, J. (1996). The African rain forest - main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proc. Roy. Soc. Edinburgh*, **104B**, 31-73.
- Martin, C. (1989). *Die Regenwälder Westafrikas: Ökologie, Bedrohung, Schutz*. Birkhäuser Verlag, Basel, 235 pp.
- Mertens, R. (1938). Amphibien und Reptilien aus Angola, gesammelt von W. Schack. *Senckenbergiana* **20**, 425-443.
- Mertens, R. (1942). Die Familie der Warane (Varanidae). *Abh. Senck. naturf. Ges.* **462**, 1-116, **465**, 117-234, **466**, 235-391.
- Mertens, R. (1971). Die Herpetofauna Südwest-Afrikas. *Abh. Senckenb. naturforsch. Ges.*, Frankfurt a. Main **529**, 1-110.
- Papenfuss, T. J. (1969). Preliminary analysis of the reptiles of arid central West Africa. *The Wasmann Journal of Biology* **27**, 249-325.
- Peters, G. (1962). Die Zwergeidechse (*Lacerta parva* Boulenger) und ihre Verwandtschaftsbeziehungen zu anderen Lacertiden, insbesondere zur Libanon-Eidechse (*L. fraasii* Lehrs). *Zool. Jb. Syst.* **89**, 407-478.
- Pienaar, U. de V. (1978). *The reptile fauna of the Kruger National Park*. National Parks Board, Sigma Press (Pty) Ltd., Pretoria, 222 pp.
- Ziegler, T. (1996). *Zur Genitalmorphologie der varanoiden Reptilien (Squamata: Sauria: Platynota) unter besonderer Berücksichtigung der Hemiclitoris*. Unpubl. MSc thesis, Univ. Bonn, 246 pp.
- Ziegler, T. & Böhme, W. (1997). Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. *Mertensiella* **8**, (in press).

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EFFECTS OF LARVAL HISTORY AND MICROTAGS ON GROWTH AND SURVIVAL OF NATTERJACK (*BUFO CALAMITA*) METAMORPHS

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The metamorphic success of larval cohorts and the post-metamorphic growth of toadlets were studied in a large metapopulation of natterjack toads (*Bufo calamita*) in the Rhinelands, Germany. Larval density was greater in the cohorts studied in 1991 than in those studied in 1992 and metamorphs were smaller in 1991 than in 1992, indicating short-term carry-over effects. Metamorphic success and average snout-vent length were larger in the cohort originating from the early breeding period than in those from the main breeding period in the previous year. The further terrestrial development of three metamorph cohorts was followed until adulthood using commercial fish marks (microtags) for batch-tagging. Microtags are small pieces of wire which are injected below the skin. Their presence is determined using a hand-wand metal detector. The short- and long-term effects of this new marking technique on growth and survival of almost 2000 free-ranging toadlets are reported. The results obtained indicate that microtagging is a useful and harmless technique for the study of metamorphs.

INTRODUCTION

Studies on the ecology and behaviour of free-ranging anuran metamorphs are severely limited whenever the identification or tracing of recaptured individuals or cohorts is required. For example, carry-over effects of larval history on the early terrestrial stage of life history have been demonstrated experimentally in natterjack toads *Bufo calamita* (e.g. Golay & Durrer, 1995; Golay, 1996), but their significance for survival in the field remains to be evaluated. Any attempt to do this requires an adequate tagging method for metamorphs. Presently, the size of metamorphs (mostly < 10 mm SVL, snout-vent length) impedes the application of most techniques available for adults (Sinsch, 1992a; Richards *et al.*, 1994). The only exception I am aware of is toe-clipping for individuals or batch-tagging of *Rana* and *Bufo* metamorphs (e.g. Blair, 1953; Dole, 1971; Breden, 1987; Berven & Grudzien, 1990; Reading *et al.*, 1991; Tejedo *et al.*, 1997). However, its usefulness is controversial as regeneration and accidental toe loss may interfere with the permanency and the individuality of the mark, and the removal of up to four toes may influence survival and thus interfere with conservation measures (e.g. Clarke, 1972; Golay & Durrer, 1994). Therefore, in a pilot project on the recruitment of natterjack metamorphs from different larval cohorts and their postmetamorphic dispersal, a new tagging method based on commercial fish marks (microtags) was tested (Sinsch, 1992a,b). Microtags consist of small pieces of wire which are injected below the skin and allow for batch recognition. This paper reports on (1) differential metamorphic success of larval cohorts during the prolonged breeding period, and on (2) the short- and long-term effects of the new marking technique on the growth and survival of almost 2000 toadlets tagged in 1991 and 1992. Results obtained indicate that microtagging is a useful and harmless

technique for the identification of anuran metamorphs in long-term ecological studies.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in St. Augustin near Siegburg (northern Rhineland, Germany) at altitudes between 52 and 58 m. An area of about 4 km² inhabited by several thousands of natterjack toads (*Bufo calamita*) has been monitored regularly since 1986. Capture and release of the metamorphs was performed in an area with six ponds labeled as breeding area III in other papers dealing with this natterjack metapopulation (Sinsch 1988a,b; 1992a,b; Sinsch & Seidel, 1995).

LARVAL DENSITY

Tadpole density was studied in two ponds from which metamorphs were recruited for tagging. Fluctuations of density were monitored weekly in one pond during the breeding period of 1992, whereas in 1991 larval density in another pond was determined only on two occasions. To estimate the numbers of tadpoles, all those captured during a one-hour-census were stained for 15 minutes in a 0.005% solution of neutral red (method adapted from Viertel, 1980) and immediately released again at three localities in their native pond. Control experiments showed that this procedure does not cause any mortality during a period of 48 hr following staining. One day after staining, another one-hour census was performed to determine the tadpole numbers and the corresponding standard deviation using the method of Rüst (1969). The fluctuations in water volume were measured using a permanent grid (1 m x 1 m) to estimate the surface area and the corresponding depth at any point of the grid (Wenzel, 1993). Finally,

mean larval density was calculated as the number of tadpoles per litre of water volume.

TAGGING PROCEDURE

In this study, natterjack metamorphs were batch-marked with sequentially coded microtags. Microtags (standard CWT 10-99K FFTEN30) are pieces of wire 1.1 mm long with a diameter of 0.25 mm (mass: < 1 mg) which were injected below the skin using modified syringes (single shot fish I.D. tag injectors). The presence and position of a microtag in a toadlet were detected using a hand-wand style metal detector (S/N35). This equipment was manufactured by Northwest Marine Technology, Inc., Shaw Island, Washington, USA. In this study, microtags served exclusively as batch marks because individual recognition would have required the surgical removal of the microtags.

In 1991, the pond in which larval density had been monitored, was surrounded completely with a drift fence seven days before the onset of metamorphosis. Traps integrated into the fence and the area within the fence were checked daily for metamorphs. A total of 710 metamorphs which emerged from the spawn strings of the early breeding period were batch-tagged immediately after leaving the pond, between 5-24 July. The microtags were placed between cranium and skin and the metamorphs were kept in the laboratory with unlimited food supply (*Drosophila*) until release. The toadlets of the first cohort were released on 27 July, within their natal area. Another 263 metamorphs which emerged from the spawn strings of the main breeding period were provided with tags injected into the abdominal region (28 July - 7 August). They were also kept in the laboratory with unlimited food supply and released on 9 August.

In 1992, the pond studied in the previous year had been destroyed and another pond (150 m distant) was chosen for the monitoring of larval density and recruitment of metamorphs. Again, a drift fence was used to assess the number of emerging metamorphs. A total of 841 metamorphs from the spawn strings of the early breeding period were batch-tagged in the same way as the toadlets of the early cohort of 1991, when they emerged from the pond, between 30 June and 8 July. The survival of these toadlets during the first 48 hr after tagging was recorded in the laboratory (with unlimited food supply) and compared with that of a control group

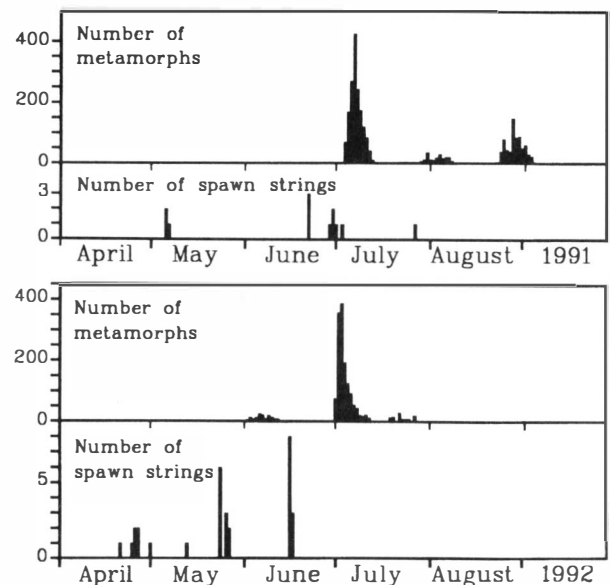


FIG. 1. Time course of spawning and metamorphosis in two permanent ponds of breeding area III. Further data are given in Table 1.

of 845 metamorphs of the same cohort without further treatment. These metamorphs were released in the vicinity of their natal pond on 10 July.

MONITORING OF METAMORPHS IN THE FIELD

Following the release of microtagged toadlets on 27 July 1991, their growth and dispersal were monitored by checking potential daytime shelters (e.g. below stones, planks or in burrows) mainly within their natal area, but also within a radius of 2 km around. Nine censuses were performed, each lasting 6-9 person-hours, on 6, 13, 20/21, 27/28 August; 2, 12, 19, 27 September and 14 October. Capture site, SVL (to the nearest 0.5 mm) and presence of microtag were recorded for each individual captured. Toadlets from the first cohort could not be confused with those of the second cohort because of the size and the position of the tag. Growth and dispersal of the group released on 10 July, 1992, were monitored by the same procedure as in 1991, in 9 censuses on 14, 23, 29 July; 5, 15, 19, 25 August; 3, 9 September.

The presence of microtagged natterjacks was monitored during 50-70 night and day censuses per year in the period from April to September during the years 1991 - 1994. The night censuses began about 30 min

TABLE 1. Metamorphic success of natterjack tadpoles and size of metamorphs originating from spawn strings of different temporal breeding assemblages. Size is presented as mean SVL \pm SE.

| Cohort | Spawn strings | 1991 Metamorphs | | Spawn strings | 1992 Metamorphs | |
|-----------------------|---------------|--------------------|----------------|---------------|--------------------|----------------|
| | | number | SVL (mm) | | number | SVL (mm) |
| Early breeding period | 3 | 1626 | 8.6 \pm 0.03 | 16 | 1568 | 9.4 \pm 0.02 |
| Main breeding period | 8 | 263 | 8.3 \pm 0.06 | 11 | 118 | 9.3 \pm 0.07 |
| Late breeding period | 1 | 695 | 8.3 \pm 0.03 | / | / | / |

after sunset and lasted about 2-4 person-hours each, depending on general reproductive activity (Sinsch & Seidel, 1995). The day censuses in the years 1993 and 1994 consisted of searches in potential shelters and lasted about 3 person-hours each.

RESULTS

METAMORPHIC SUCCESS OF LARVAL COHORTS

In 1991, the number of spawn strings laid into the monitored pond varied considerably among the early, main and late breeding periods (Fig. 1, Table 1). The density of tadpoles hatching from the spawn strings of the early breeding period was estimated at 8.5 per litre on 6 June, whereas density of the second larval cohort was 4.3 per litre on 18 July. The recruitment of metamorphs was higher from spawn of the early breeding period than from that of the main breeding period (Table 1). The largest 710 metamorphs of the first cohort, and all 263 metamorphs of the second cohort, were batch-tagged, but at distinct parts of the body to distinguish between the two groups.

In 1992, there was little difference between the number of spawn strings laid during the early and main breeding period (Fig. 1, Table 1). The density of tadpoles was low during the whole breeding period, ranging from 0.1 to 3.9 per litre (Table 2). However, metamorphic success differed dramatically among the larval cohorts (Table 1): the cohort resulting from the early spawning period produced far more metamorphs than the second cohort. Due to substantial post-tagging mortality in 1991, the 1568 metamorphs of the first cohort were randomly allocated to an untreated control group ($N = 845$) and a batch-tagged experimental group ($N = 841$) to check for treatment effects. Because of the low number of metamorphs recruited from spawn laid during the main breeding period, no further metamorphs were marked in 1992.

TABLE 2. Estimates of the number of natterjack tadpoles in the study pond during 1992 and the corresponding tadpole density per litre water. Estimates are given as means \pm standard deviation except for the estimates in early May which are based on one sample.

| Date | Number of tadpoles (N) | Density of tadpoles (N/l) |
|---------|----------------------------|-------------------------------|
| 18 May | 1220 | 0.4 |
| 25 May | 633 | 0.6 |
| 31 May | 332 \pm 7 | 0.2 |
| 17 June | 11 117 \pm 2550 | 3.9 |
| 29 June | 8824 \pm 763 | 1.9 |
| 8 July | 3460 \pm 536 | 0.4 |
| 15 July | 504 \pm 51 | 0.2 |
| 21 July | 4074 \pm 14 | 0.7 |
| 28 July | 141 \pm 14 | 0.1 |

TABLE 3. Mortality in tagged and untagged metamorphs during 48 hr following capture.

| Temporal population | Tagged toadlets | Control toadlets |
|---------------------|---------------------------|-------------------------|
| Early cohort 1991 | 14.8% (105 out of 710) | / |
| Main cohort 1991 | 4.6% (12 out of 263) | / |
| Early cohort 1992 | 0% (0 out of 841) | 1.8% (10 out of 845) |

SIZE AT METAMORPHOSIS

The average snout-vent-length of the metamorphs was significantly lower in 1991 than in 1992 (Table 1, ANOVA, $P < 0.001$). Within one year, metamorphs of the early cohort tended to be larger at metamorphosis than those of the later, but only in 1992 was the difference significant (ANOVA, $P < 0.01$).

MORTALITY RATES OF RECENTLY METAMORPHOSED TOADLETS

The mortality rate of microtagged metamorphs during the first 48 hr following treatment varied among the years and ranged from 0% to 14.8% (Table 3). The post-metamorphic mortality of untreated metamorphs was in the same range as that of the microtagged individuals when tested in 1992. No further mortality was observed between the third day following tagging and the day of release.

GROWTH OF METAMORPHS

The growth of microtagged toadlets, i.e. the increase of SVL, following release in the field was compared with that of untagged individuals captured simultaneously (Fig. 2). In 1991, only the fate of tagged toadlets

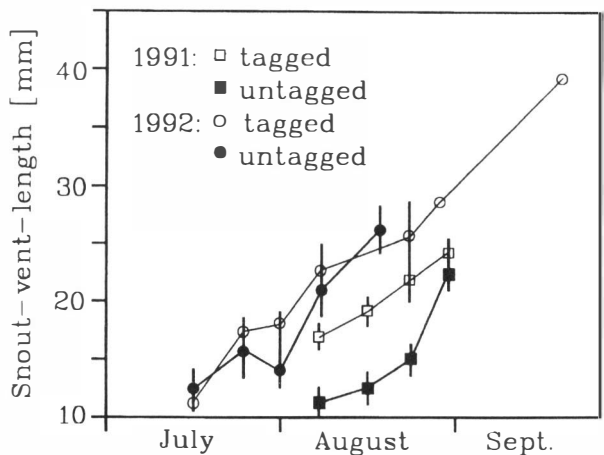


FIG. 2. Growth of tagged and untagged metamorphs of the early cohort in the year of release. Data are given as means with the corresponding 95% confidence interval. The number of observations per mean ranged between 13 and 446 in the control group and 1 and 36 in the experimental group.

TABLE 4. Recaptures of microtagged individuals as reproductive adults.

| Origin | Initial no. in 1991-2 | No. found 1993 | No. found 1994 |
|-------------------|--------------------------|-------------------|-------------------|
| Early cohort 1991 | 605 | 5(0.8%) | 1(0.2%) |
| Main cohort 1991 | 251 | 4(1.6%) | 1(0.4%) |
| Early cohort 1992 | 841 | / | / |

pertaining to the early cohort was followed. At the date of release, they were significantly larger than the untagged toadlets of the same cohort which were found in the field (ANOVA, $P < 0.001$). This difference is an experimental artefact due to (1) the selection of the larger metamorphs for tagging and (2) their prolonged stay under laboratory conditions (unlimited food supply and higher temperatures than in the field). However, the mean growth rate during the first month after release was identical in the two groups: 0.32 mm increase of SVL per day.

In 1992, tagged metamorphs were released after two days in the laboratory and size differences between these and untagged individuals remained insignificant until mid-July (ANOVA, $P > 0.05$). The mean growth rate during this period was 0.39 mm increase of SVL per day. The massive appearance of new metamorphs from neighbouring ponds in mid-July rendered the mean size of the untagged toadlets meaningless for comparison after this time with the few recaptured tagged individuals, which continued to grow at about the same rate as before.

SURVIVAL RATES OF MICROTAGGED METAMORPHS TO ADULTHOOD

The numbers of microtagged individuals which were recaptured as breeding adults in 1993 and in 1994 are summarized in Table 4. All recaptured individuals were males advertising at the ponds of the breeding area from which they originated. Despite thorough censuses in neighbouring breeding areas over a radius of 2 km, neither microtagged females nor additional males advertising in other than their natal site were found. Moreover, all microtagged adults originated from the two cohorts marked in 1991, whereas no individual of the 1992 cohort was recaptured later than October 1992.

DISCUSSION

In this study, microtags have been used for the first time to permanently tag toadlets of 6-11.5 mm SVL and to follow their fate until adulthood in the field. As there has been no previous experience with the short-term and/or long-term effects of this method in toads, a critical evaluation of tagging as a potential additional source of juvenile mortality is necessary before assessing the significance of carry-over effects from larval history on the fitness of adults.

EFFECTS OF MICROTAGS

Severe short-term effects should result in an increased mortality within two days after handling. Yet mortality rates in tagged and untagged metamorphs of 1992 were at the same low level, indicating that the treatment did not directly affect survival. Still, mortality of tagged metamorphs was substantial in the 1991 cohorts (no data were collected on untreated controls). Two factors probably increased mortality over the level found in 1992: (1) the skill of placing the microtags without harming the toadlets certainly improved in the course of the study; (2) larval density in the pond of origin was much higher in 1991 than in 1992, a factor shown to correlate with postmetamorphic mortality in *Bufo bufo* (Goater, 1994) and *Bufo calamita* (Golay, 1996). Moreover, the time immediately following metamorphosis is a period of high natural mortality because metamorphs are more vulnerable to desiccation (unfavourable surface/volume-ratio), to predation and to intraspecific competition (high densities occur in the vicinity of ponds) than are larger juveniles and adults (Licht, 1974; Cohen & Alford, 1993).

Sublethal effects of the tagging procedure could influence growth and reduce the probability of long-term survival. Mean growth rates of natterjack juveniles during their first summer of life in the field did not significantly differ between tagged and untagged individuals, and the increase in overall size ranged from 2.4 to 3.4-fold. These values closely correspond to those measured in *Bufo bufo* (2.0-2.8; Goater, 1994), in *Bufo calamita* (1.5-2.2; Golay, 1996), in *Bufo fowleri* (3.4; Labanick & Schlueter, 1976), and in *Bufo hemiophrys* (2.2; Breckenridge & Tester, 1961). An experimental analysis of growth in *Bufo bufo* metamorphs suggests that a size increase of about a factor of three indicates *ad libitum* feeding conditions (Goater, 1994). Thus, the growth of the tagged natterjack toadlets in the study area was probably neither influenced by tagging nor limited by the availability of food.

Finally, long-term survival of tagged individuals could have been modified by other effects than growth retardation. Such effects, if they exist, would be difficult to detect as local environmental factors are the main determinants of survival. Comparisons among different study areas or even among different species can only yield ideas about the order of magnitude of survival. There have been few attempts to estimate the rates of survival between metamorphosis and adulthood by toe-clipping: in *Bufo bufo* Reading *et al.* (1991) found 0.6% survival of males and 0.1% survival of females out of 5158 toadlets marked in 1984, and 0.2% male and 0% female out of 2101 toadlets marked in 1985 at the same site. In *Bufo fowleri*, Breden (1987) found 0.4% unsexed adults out of 8539 toadlets and in *Bufo valliceps*, Blair (1953) found 5.6% males and 1.4% females out of 357 toadlets. The survival rates es-

timated from the recaptures of microtagged *Bufo calamita* as breeding adults (this study) were in the same range: 0.8% as males from 605 toadlets, 1.6% as males from 263 toadlets and 0% out of 841 toadlets, but no female from any of the three cohorts of metamorphs. These rates are still two or three times higher than those found in the same species marked by toe-clipping in Spain: Tejedo *et al.* (1997) recaptured only seven adults (0.3%) out of 2500 toadlets marked in 1992 after two years, and another seven after three years. The exceptionally high survival rate in *Bufo valliceps* is due to the fact that they attain sexual maturity within one year, whereas in the *Bufo* species studied here males need at least two years, and females three or more years (Hemelaar & Van Gelder, 1980; Gittins *et al.*, 1985; Reading, 1991).

The sex-specific difference in the duration of the juvenile stage probably accounts for generally lower recapture rates of females. In the study population, there is no indication that females suffer a significantly higher mortality than males and the failure to recapture microtagged females may more probably be due to the fact that the vagility of females is far larger than that of males (Sinsch, 1992b; Sinsch & Seidel, 1995). The monitored area was probably too small to adequately cover their range of activity. Thus, the number of the 1991 metamorphs reaching adulthood was probably greater than suggested by the recaptures in 1993 and 1994, and it seems reasonable to assume that approximately the same numbers of immature females and males survive from year to year. Furthermore, an unknown, but probably very small, proportion of individuals may have joined breeding assemblages at sites which have not been intensely monitored. Based on these assumptions, an overall survival rate of 2-3% in the 1991 metamorphs until 1993 seems realistic. This estimate agrees remarkably well with the corresponding survival rates averaging 2% (range: 0.3-6.0%) determined in the Woolmer natterjack population over 15 years (Banks & Beebee, 1988; Banks *et al.*, 1993). Survival rates of this magnitude imply annual mortality rates in the range of 80-85%, lower than larval mortality (e.g. Kadel, 1975; Banks & Beebee, 1988).

In contrast, the reasons for the absence of any recapture of adults originating from the microtagged early cohort of 1992 are completely obscure. Similar disappearances of cohorts have also been noticed in the Woolmer population (Beebee, personal communication). Yet, the 1992 generation of toadlets was not lost completely, as evidenced by a number of untagged juveniles captured in 1993 before the emergence of new metamorphs. The origin of these juveniles, i.e. breeding pond and tadpole cohort, is unknown because the 1992 generation of this area included metamorphs originating from the early, main and late tadpole cohort. A contribution of tagging to the cohort disappearance cannot be excluded, but does not seem probable. Still, the available data do not indicate any adverse effect of

microtagging on the short- or long-term survival of juveniles. In conclusion, microtags have proved to be a useful tool to study small-sized anurans.

CARRY-OVER EFFECTS

As observed from experimental plots (Golay & Durrer, 1995), the size of metamorphs in the field was inversely related to the density the tadpoles experienced before metamorphosis. However, the average SVL obtained under field conditions was up to 4 mm lower than under experimental conditions, indicating that food availability in the natural ponds was far from optimal (Banks & Beebee, 1988). Mortality within four weeks after metamorphosis was also demonstrated to be higher in metamorphs raised in high tadpole densities than in those originating from low density conditions (Golay, 1996). Remarkably, even optimal food supply after metamorphosis did not compensate for this carry-over effect on post-metamorphic mortality, but only reduced mortality from about 50% to 35% (Golay, 1996). Consequently, in 1991 a substantial contribution of a carry-over effect resulting from high larval density to post-metamorphic mortality seems probable. The data presented here are in agreement with the hypothesis that the larval history influences important life history parameters during the early terrestrial stage of life.

In contrast, there was no indication of effects on the probability of long-term survival during the terrestrial stage. Larval history was apparently more favourable in 1992, but survival to adulthood was certainly lower than in the two 1991 cohorts. Even comparing only the fate of first and the second 1991 cohort, the significantly larger toadlets of the early breeding period apparently did not perform better than the smaller ones of the main breeding period. This is remarkable not only because of the size difference at metamorphosis, but also because the first cohort was fed far longer in the laboratory and had a longer feeding period in the field before hibernating. Effects of body size on toadlet survival over winter were also absent in the Woolmer population (Denton & Beebee, 1996). In conclusion, it seems doubtful that carry-over effects from the aquatic life history stage have long-term consequences for the performance of toads during the juvenile stage or even for the fitness of adults.

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REFERENCES

- Banks, B. & Beebee, T. J. C. (1988). Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *Journal of Animal Ecology* **57**, 475-492.
- Banks, B., Beebee, T. J. C. & Denton, J. (1993). Long-term management of a natterjack toad (*Bufo calamita*) population in southern Britain. *Amphibia-Reptilia* **14**, 155-168.
- Berven, K. A. & Grudzien, T. A. (1990). Dispersal in the wood frog (*Rana sylvatica*). Implications for genetic population structure. *Evolution* **44**, 2047-2056.
- Blair, W. F. (1953). Growth, dispersal and age at sexual maturity of the Mexican toad (*Bufo valliceps* Wiegmann). *Copeia* **1953**, 208-212.
- Breckenridge, W. J. & Tester, J. R. (1961). Growth, local movements and hibernation of the Manitoba toad, *Bufo hemiophrys*. *Ecology* **42**, 637-646.
- Breden, F. (1987). The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* **1987**, 386-395.
- Clarke, R. D. (1972). The effect of toe-clipping on survival in Fowler's toad (*Bufo woodhousei fowleri*). *Copeia* **1972**, 182-185.
- Cohen M. P. & Alford, R. A. (1993). Growth, survival and activity patterns of recently metamorphosed *Bufo marinus*. *Wildlife Research* **20**, 1-13.
- Denton, J. S. & Beebee, T. J. C. (1996). Habitat occupancy by juvenile natterjack toads (*Bufo calamita*) on grazed and ungrazed heathland. *Herpetological Journal* **6**, 49-52.
- Dole J. W. (1971). Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* **1971**, 221-228.
- Gittins, S. P., Kennedy, R. I. & Williams, R. (1985). Aspects of the population age-structure of the common toad (*Bufo bufo*) at Llandrindod Wells Lake, Mid-Wales. *British Journal of Herpetology* **6**, 447-449.
- Goater, C. P. (1994). Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology* **75**, 2264-2274.
- Golay, N. (1996). Die Kreuzkröte (*Bufo calamita*) Laur. als Pionierart. *PhD Thesis, University of Basel*, 180 pp.
- Golay, N. & Durrer, H. (1994). Inflammation due to toe-clipping in natterjack toads (*Bufo calamita*). *Amphibia-Reptilia* **15**, 81-83.
- Golay, N. & Durrer, H. (1995). Zur Variabilität der Metamorphosegröße bei Kreuzkröten (*Bufo calamita*). *Zeitschrift für Feldherpetologie* **2**, 3-15.
- Hemelaar, A. S. M. & Van Gelder, J. J. (1980). Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Netherlands Journal of Zoology* **30**, 129-135.
- Kadel, K. (1975). Freilandstudien zur Überlebensrate von Kreuzkrötenlarven (*Bufo calamita* LAUR.). *Revue Suisse de Zoologie* **82**, 237-244.
- Labanick, G. M. & Schlueter, R. A. (1976). Growth rates of recently transformed *Bufo woodhousei fowleri*. *Copeia* **1976**, 824-826.
- Licht, L. E. (1974). Survival of embryos, tapoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Canadian Journal of Zoology* **52**, 613-627.
- Reading, C. J. (1991). The relationship between body length, age and sexual maturity in the common toad, *Bufo bufo*. *Holarctic Ecology* **14**, 245-249.
- Reading, C. J., Loman, J. & Madsen, T. (1991). Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology* (London) **225**, 201-211.
- Richards, S.J., Sinsch, U. & Alford, R. A. (1994). Radio-Tracking. In: *Standard Methods for Measuring Biological Diversity: Amphibians*, 155-158. Donnelly, M., Heyer, W. R., Inger, R. F., & McDiarmid, R. W. (eds.). Smithsonian Institution Press.
- Rüst, H. (1969). Schätzung der Amphibienbestände in einem Teich durch ein Wiederfangverfahren. *Vierteljahresschrift der naturforschenden Gesellschaft Zürich* **114**, 279-291.
- Sinsch, U. (1988a). Temporal spacing of breeding activity in the natterjack toad, *Bufo calamita*. *Oecologia* **76**, 399-407.
- Sinsch, U. (1988b). Auskiesungen als Sekundärhabitate für bedrohte Amphibien und Reptilien. *Salamandra* **24**, 161-174.
- Sinsch, U. (1992a). Zwei neue Markierungsmethoden zur individuellen Identifikation von Amphibien in langfristigen Freilanduntersuchungen: erste Erfahrungen bei Kreuzkröten. *Salamandra* **28**, 116-128.
- Sinsch, U. (1992b). Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). *Oecologia* **90**, 489-499.
- Sinsch, U. & Seidel, D. (1995). Dynamics of local and temporal breeding assemblages in a natterjack metapopulation (*Bufo calamita*). *Australian Journal of Ecology* **20**, 451-461.
- Tejedo, M., Reques, R. & Esteban, M. (1997). Actual and osteochronological estimated age of natterjack toads (*Bufo calamita*). *Herpetological Journal* **7**, 81-82.
- Viertel, B. (1980). Überlebensraten und Mortalität bei Erdkrötenlarven (*Bufo bufo* L.) im Freiland. *Salamandra* **16**, 19-37.
- Wenzel, S. (1993). Zeitliche Variabilität des Wachstums und der Metamorphoserate von Kreuzkröten-Kaulquappen im Freiland. *Unpubl. Diplom-thesis, Zoological Institute of the University of Bonn*, 89 pp.

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SHORT NOTES

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THE TAXONOMIC STATUS OF THE BANDED NEWT (*TRITURUS VITTATUS*) IN SOUTHERN TURKEYKURTULUS OLGUN¹, VAROL TOK², J. W. ARNTZEN³ AND OGUZ TÜRKÖZAN⁴¹Adnan Menderes Üniversitesi, Fen-Edebiyat Fakültesi, Biyoloji Bölümü, 09010 Aydın, Turkey²Ege Üniversitesi, Fen Fakültesi, Biyoloji Bölümü, İzmir, Turkey³School of Biological Sciences, Brambell Building, University of Wales, Bangor LL57 2UW, UK⁴Dokuz Eylül Üniversitesi, Eğitim Fakültesi, Biyoloji Bölümü, İzmir, Turkey

The range of the banded newt, *Triturus vittatus* (Gray, 1835) falls into two parts. In northern Turkey, the species is distributed along the Black Sea coast from Bursa in the west to Ardahan in the east (Baran & Yilmaz, 1986). The range continues into and across the Caucasus mountains to Stavropol in the north and Telavi in the east (Djanashvili, 1956; Visotin & Tertyshnikov, 1988; Tuniyev, Bakradze & Beregovaya, 1987; Tarkhnishvili, 1996). In southern Turkey, the species is found in the provinces of Icel, Adana, Gaziantep and Hatay (Steinitz, 1965; Schmidtler & Schmidtler, 1967; Atatür, 1974). The southern range continues into Israel as far south as Nahr Rubin (Bodenheimer, 1926) and the easternmost recorded locality is Berisa in Iraq (Kennedy, 1937). Groups of populations are generally attributed to different subspecies: *T. v. ophryticus* in the north and *T. v. vittatus* in the south (Thorn, 1968; Griffiths, 1996). Alternatively, the southern group of populations is subdivided into four or more subspecies: *vittatus* from Syria; *excubitor* Wolterstorff, 1905 from Antakya, Turkey; *cilicensis* Wolterstorff, 1906 from Adana, Turkey; *chuldaensis* Bodenheimer, 1926 from Chuida, Israel and a newly indicated form from Akantu in northern Cyprus. The recorded presence on Cyprus, although accepted by Corbett (1989), probably goes back to an unpublished report by Dr. F. Boglu and H. Hayman (1978), that is of unknown reliability (Schmidtler, 1984; Schaetti & Sigg, 1989). Along with the latter authors, one of us (KO) has been unable to find *T. vittatus* on Cyprus, despite the presence of apparently suitable aquatic habitat for newts.

In a taxonomic revision Steinitz (1965) places *excubitor*, *cilicensis* and *chuldaensis* under *vittatus*, arguing that the diagnostic features used by previous

authors were mere individual variations. This opinion is not shared by Schmidtler & Schmidtler (1967) or Atatür (1974) who, on the basis of newly collected material from southern Anatolia, recognise *T. v. cilicensis* as a separate taxon that is characterized by interrupted dark stripes bordering the silver-grey lateral bands, whereas these stripes are continuous and wider in *T. v. vittatus*. Furthermore, males of *T. v. cilicensis* in breeding condition possess a dorsal crest with a larger number of spikes than the nominate subspecies. We collected material with the aims of describing and testing for morphological differences between the forms.

Thirty-two male and 25 female newts were caught at Ciftlik Köjü near Icel and 20 males and 25 females were caught at Antakya, representing nominal *T. v. cilicensis* and *T. v. vittatus*, respectively (Fig. 1). All were collected in spring 1995 and were in breeding condition. The dark lateral stripes bordering the silver-grey band from fore-leg to hind-leg were scored as either interrupted or uninterrupted. In males the number of spikes in the crest was counted over the length from the snout to the vent, and over the tail. Freshly killed specimens were measured with dial callipers (0.1 mm precision) as follows: snout-vent length (SVL) from the tip of the snout to the anterior end of the cloacal slit, tail length (TL) such that TL equals total length minus SVL, inter-limb length (ILL), head length (HL) from the tip of the snout to the throat-fold and head width (HW) at the widest part of the head. A principal component analysis (PCA) was performed on the standardized residuals of the regression of log-transformed data for each of the variables versus log-transformed SVL, with the software SYSTAT-5 (Wilkinson, 1989). The preserved material is kept in the private collection of K. Olgun.

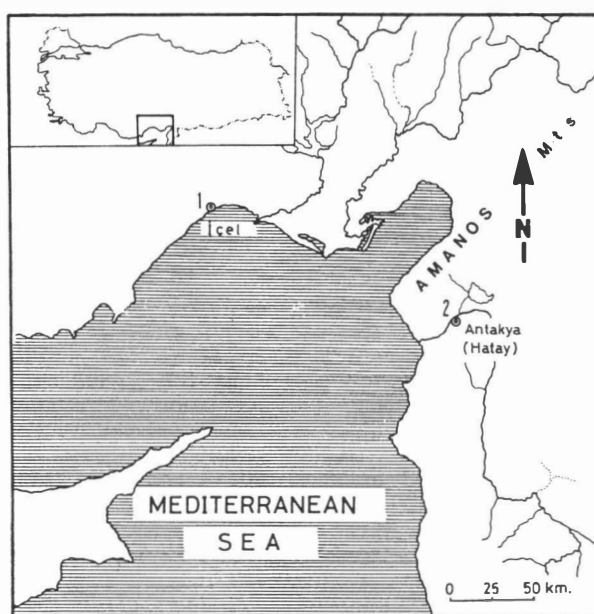


FIG. 1. Localities Icel and Antakya from which specimens of *Triturus vittatus* were studied. The population from Icel is identified as belonging to *T. v. cilicensis* and that from Antakya as belonging to *T. v. vittatus*.

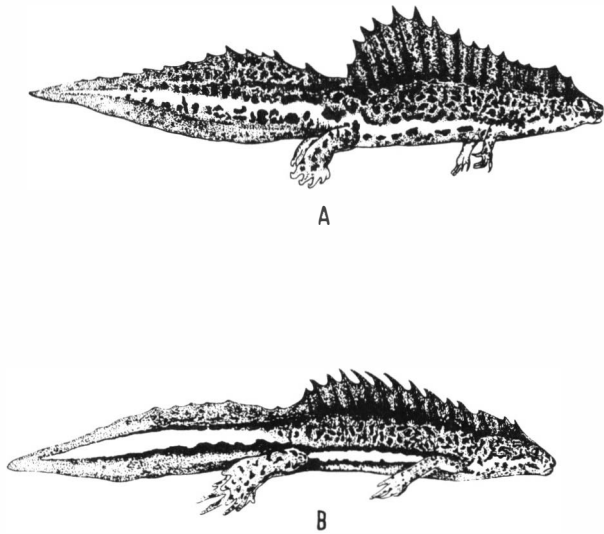


FIG. 2. Typical specimens of *Triturus vittatus cilicensis* from Icel (A) and *T. v. vittatus* from Antakya (B). The male from Icel has 15 crest spikes over the snout-vent length and several, more or less pronounced spikes in the tail crest. The upper and the lower dark stripes bordering the lateral silver-grey band are both interrupted. The male from Antakya has 14 crest spikes while the tail crest is smooth with almost no spikes. The dark lateral stripes are both uninterrupted.

TABLE 1. Results of principal component analysis of the morphometric data.

| | Icel | | Antakya | |
|----------------|----------------------|----------|----------------------|----------|
| | 32 males, 25 females | | 20 males, 25 females | |
| | 1st axis | 2nd axis | 1st axis | 2nd axis |
| <i>Males</i> | | | | |
| mean | 0.54 | -0.17 | -0.25 | 0.49 |
| SD | 0.743 | 0.801 | 1.162 | 2.169 |
| min. | -1.51 | -1.91 | -1.28 | -0.84 |
| max. | 1.82 | 1.32 | 0.88 | 2.86 |
| <i>Females</i> | | | | |
| mean | -0.28 | -0.50 | -0.21 | 0.32 |
| SD | 1.902 | 2.467 | 1.209 | 1.845 |
| min. | -3.03 | -2.25 | -1.90 | -1.75 |
| max. | 1.85 | 1.14 | 1.05 | 2.07 |

In male newts from Icel the dorsal crest had 14 or 15 spikes as counted over the snout-vent, while fewer but clearly distinct spikes were observed over the tail. In the population from Antakya the number of spikes in the crest over the snout-vent was 13 or 14, while spikes over the tail were few and less pronounced or almost absent (Fig. 2). Variation was also observed between

TABLE 2. Morphological data for eight external characters in *Triturus vittatus* from Icel and Antakya. Morphometric data include mean, standard deviation, and range in mm. The indices [character] / SVL are shown for comparative purposes. For abbreviations used see text.

| Population | | SVL | TL | ILL | HL | HW | no. spikes in crest | upper stripe interrupted | lower stripe interrupted |
|----------------------------------|-------|-------|-------|-------|-------|-------|---------------------|--------------------------|--------------------------|
| Icel, males <i>n</i> =32 | mean | 89.4 | 47.5 | 24.2 | 11.5 | 8.0 | 14.7 | 38% | 100% |
| | SD | 9.19 | 6.06 | 1.59 | 1.08 | 0.63 | 0.58 | - | - |
| | min. | 73.6 | 38.3 | 20.7 | 9.5 | 6.9 | 14 | - | - |
| | max. | 108.8 | 61.2 | 27.5 | 14.2 | 9.3 | 15 | - | - |
| | index | - | 0.531 | 0.271 | 0.129 | 0.089 | - | - | - |
| Icel, females <i>n</i> =25 | mean | 72.9 | 35.0 | 22.5 | 10.4 | 7.5 | - | 88% | 100% |
| | SD | 5.93 | 3.59 | 1.69 | 0.87 | 0.60 | - | - | - |
| | min. | 62.4 | 28.2 | 19.4 | 8.7 | 6.1 | - | - | - |
| | max. | 85.8 | 42.7 | 25.2 | 11.8 | 8.5 | - | - | - |
| | index | - | 0.480 | 0.309 | 0.143 | 0.103 | - | - | - |
| Antakya, males <i>n</i> =20 | mean | 88.3 | 44.1 | 25.2 | 11.4 | 8.1 | 13.5 | 0% | 35% |
| | SD | 7.66 | 4.69 | 2.03 | 0.78 | 0.66 | 0.51 | - | - |
| | min. | 76.3 | 36.6 | 22.9 | 9.9 | 7.6 | 13 | - | - |
| | max. | 108.5 | 55.6 | 30.9 | 12.9 | 10.5 | 14 | - | - |
| | index | - | 0.499 | 0.285 | 0.129 | 0.092 | - | - | - |
| Antakya, females <i>n</i> =25 | mean | 78.4 | 37.8 | 24.1 | 10.6 | 8.1 | - | 0% | 20% |
| | SD | 7.99 | 4.56 | 2.26 | 0.99 | 0.72 | - | - | - |
| | min. | 64.4 | 30.3 | 20.3 | 9.3 | 6.7 | - | - | - |
| | max. | 93.0 | 45.4 | 27.8 | 12.3 | 9.2 | - | - | - |
| | index | - | 0.482 | 0.307 | 0.135 | 0.104 | - | - | - |

populations in the frequency with which the lateral stripes were interrupted. The upper stripe was interrupted in 34 specimens out of 57 (60 %) from Icel while the lower stripe was interrupted in all specimens. The upper stripe was uninterrupted in all specimens from Antakya while the lower stripe was uninterrupted in 33 specimens out of 45 (73 %). A principal component analysis on the data that are summarized in Table 1 indicated that morphometric variability within the Icel and Hatay populations largely exceeded inter-populational variability. Similarly, no consistent morphometric differences were found between males and females (Table 2).

The results of the present study confirm the notion that in the banded newt from southern Turkey two different forms can be recognized (Schmidtler & Schmidtler, 1967; Atatür, 1974). One form typically has 14 or more spikes in the male dorsal crest and has a discontinuous lower lateral stripe while the upper lateral stripe may also be interrupted. The other form typically has 14 or fewer spikes in the crest and has a continuous upper lateral stripe while the lower lateral stripe may also be uninterrupted. The first form is found in Icel and conforms to *T. v. cilicensis*. The second form was found in Antakya and conforms to *T. v. vittatus*. No consistent morphometric differences were observed between the forms. Populations from many more localities will have to be investigated in order to document the geographical distribution of the two subspecies. The available data suggest that the two forms may be geographically separated by the Amanos mountains (Fig. 1).

REFERENCES

- Atatür, M. K. (1974). Morphological and taxonomical investigations on *Triturus vittatus* (Salamandridae) populations in southern Anatolia. *Scientific Reports Faculty Science, Ege University* no. 188, 1-22, Izmir (in Turkish with English summary).
- Baran, I. & Yilmaz, I. (1986). On the distribution of *Triturus vittatus ophryticus* in northern Anatolia. In: *Zoology in the Middle East*. Volume 1, pp. 105-107. R. Kinzelbach & M. Kasperek (eds). Kasperek Verlag, Heidelberg.
- Bodenheimer, F. S. (1926). *Triton vittatus chuldaensis* n. subsp. aus Palastina. *Arch. Naturgesch. Berlin* 91, 7679.
- Boglu, F. & Hayman, H. (1978). *Aufstellung der lebenden urodelen in der Turkey*. Typescript pp. 1-8, October 1978, translated by the [sic] 'Göthe Institut, Ankara'.
- Corbett K. (ed.) (1989). *Conservation of European reptiles and amphibians*. Christopher Helm, London.
- Djanashvili, A. G. (1956). *Guide to the amphibians of Georgia*. Tbilisi Univ. Publishers, Tbilisi (in Georgian).
- Griffiths, R. (1996). *Newts and salamanders of Europe*. Poyser, London.
- Kennedy, W. P. (1937). Some additions to the fauna of Iraq. *J. Bombay Nat. Hist. Soc.* 39, 745-749.
- Schaetti, B. & Sigg, H. (1989). Die Herpetofauna der Insel Zypern, Teil 1: Die Herpetologische Erforschung/ Amphibien. *Herpetofauna* 11, 9-18.
- Schmidtler, J. F. (1984). Zur Bestandsituation der Amphibien und hydrophilen Reptilien auf der Insel Zypern. *Salamandra* 20, 43-49.
- Schmidtler J. J. & Schmidtler, J. F. (1967). Über die Verbreitung der Molchgattung *Triturus* in Kleinasien. *Salamandra* 3, 15-36.
- Steinitz, H. (1965). *Triturus vittatus* (Jenyns), geographic distribution and taxonomic subdivision. *Israel J Zool.* 14, 234-240.
- Tarkhnishvili, D. N. (1996). The distribution and ecology of the amphibians of Georgia and the Caucasus: a biogeographical analysis. *Zeitschrift Feldherpetol.* 3, 167-196.
- Thorn, R. (1968). *Les salamandres d'Europe, d'Asie et d'Afrique du Nord*. Lechevalier, Paris.
- Tuniyev, B. S., Bakradze, M. A. & Beregovaya, S. Y. (1987). On the distribution and ecology of the banded newt, *Triturus vittatus* (Jenyns, 1835). *Proc. Zool. Inst., Leningrad* 158, 161-169 (in Russian).
- Visotin, A. G. & Tertyshnikov, M. F. (1988). Amphibians of Stavropol district. In: *Animals of northern Caucasus and adjacent territories*, pp. 87-121. Tertyshnikov, M. V. (ed.). Pedagogical Institute Publishers, Stavropol (in Russian).
- Wilkinson, L. (1989). *SYSTAT: The system for statistics*. Computer programme. SYSTAT Inc., Evanston, Illinois.

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REDESCRIPTION AND ILLUSTRATION OF THE TADPOLE OF *PLECTROHYLA DASYPUS* (ANURA: HYLIDAE)

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McCranie & Wilson (1981) described the hylid frog *Plectrohyla dasypus* and included a description of the tadpole presumed to belong to that species. In July 1996, we collected tadpoles, metamorphosing froglets, recent metamorphs, and adults that form a definite link between the tadpoles and adults of *P. dasypus*. This material was collected from a small stream and associated streamside vegetation at the species' type locality (El Cusuco, Departamento de Cortés, Honduras). Although the tadpole described as *P. dasypus* by McCranie & Wilson (1981) was correctly identified, the material is poorly preserved and several errors occur in the description. As a result of these errors, the keys purporting to identify the *P. dasypus* tadpole in Campbell & Kubin (1990), Duellman & Campbell (1992), and Wilson & McCranie (1993) will not do so. Additionally, the *P. dasypus* tadpole has not been illustrated. The purpose of this report is to redescribe and illustrate the tadpole of *P. dasypus*.

A typical tadpole (lot USNM 513859) in stage 40 (Gosner, 1960) has a body length of 15.6 mm, a tail length of 33.2 mm, and a total length of 48.8 mm. The tadpoles in this lot may be described as follows (Fig. 1): body slightly depressed, slightly wider than high; snout semicircular in dorsal aspect, rounded in profile; eyes small (eye length/body height ca. 0.24), directed dorsolaterally; interorbital distance ca. 3.8 mm; nostrils

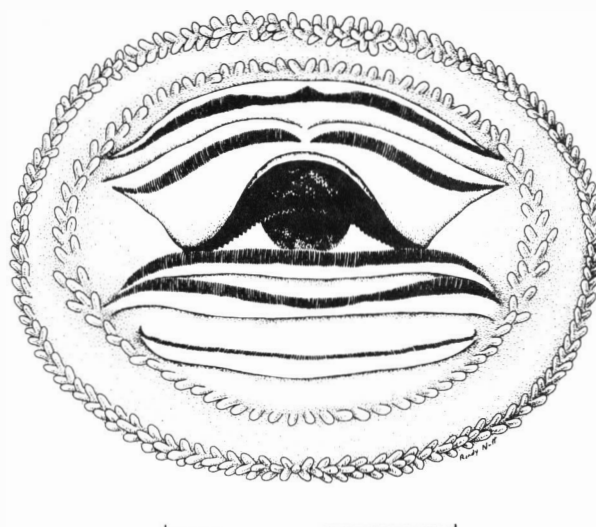


FIG. 2. Oral disc of the tadpole of *Plectrohyla dasypus* (lot USNM 513859) in Gosner stage 40. Scale bar = 3 mm.

situated at point slightly closer to eyes than tip of snout, directed anterolaterally; spiracle sinistral, directed posteriorly, situated near midline at about midbody; vent tube long, dextral; tail musculature robust, extending nearly to tip of rounded tail, with height of tail musculature much greater than height of either fin at midlength of tail; dorsal fin terminating at posterior end of body.

Oral disc (Fig. 2) large (oral disc width/snout width ca. 0.83), ventral, completely bordered by two to three rows of large marginal papillae (ca. 10/mm); single row of larger submarginal papillae present on both labia just inside marginal papillae; few additional submarginal papillae present laterally; oral disc not emarginated; keratinized jaw sheaths medium-sized, bearing short, somewhat pointed to blunt serrations; upper jaw sheath widely arched with long, slender lateral processes; lower jaw sheath widely V-shaped; labial tooth rows 2/3 with second anterior row narrowly interrupted medially; anterior tooth rows long, subequal, extending to lateral portion of oral disc; posterior tooth rows slightly shorter than anterior rows; first and third posterior tooth rows subequal, second posterior row slightly longer than first and third posterior rows; third posterior tooth

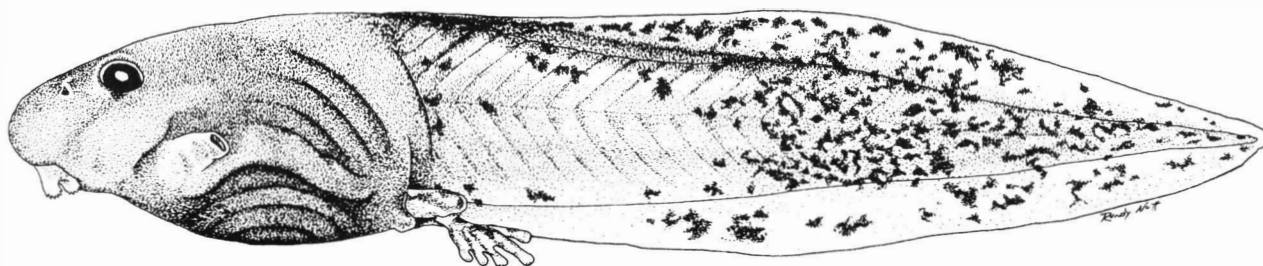


FIG. 1. Lateral view of the tadpole of *Plectrohyla dasypus* (lot USNM 513859) in Gosner stage 40. Scale bar = 5 mm.

row sometimes with smaller teeth than first and second posterior rows. Variation in oral features is negligible.

Colour in life (stage 40): dorsum of head and body Citrine (colour 51 in Smithe, 1975); tail musculature Olive-Yellow (52) with Citrine (51) spots; tail fins transparent with Citrine (51) spots; iris coppery red.

Colour in life of a tadpole (lot USNM 513861) in stage 41: dorsum of head and body Citrine (51) with heavy Greenish Olive (49) mottling; dorsum of limbs Greenish Olive (49) with Olive-Yellow (52) mottling; tail musculature Olive-Yellow (52) with Citrine (51) spotting; iris coppery red.

Colour in life for two nearly metamorphosed froglets (lot USNM 513862) in stage 44: dorsum of head, body, and limbs bronze with Greenish Olive (49) spots; iris coppery red.

Colour in life for a frog that is clearly *P. dasypus* and had recently completed metamorphosis (snout-vent length 16.3 mm; lot USNM 513862): dorsum of head, body, and limbs bronze with Greenish Olive (49) spots; iris coppery red.

Metamorphosing froglets and a recently metamorphosed frog (lots USNM 513860, 513862) of *P. dasypus* were collected at night sitting on low vegetation immediately above a small tributary of the Río de Cusuco at 1550 m elevation. A search of the leaves on the bottom of the stream below the point where these metamorphs were sitting revealed the tadpoles in lots USNM 513859, 513861.

Plectrohyla dasypus tadpoles are very similar morphologically to those of *P. guatemalensis*. In fact, McCranie & Wilson (1981) identified several lots of *P. dasypus* tadpoles as *P. guatemalensis*. The most reliable way to distinguish *P. dasypus* tadpoles from those of *P. guatemalensis* is iris colour in life (coppery red in *dasypus*, pale brown in *guatemalensis*). Additionally, *P. guatemalensis* does not occur at any of the known *P. dasypus* localities located in a small area of the Sierra de Omoa in the western portion of Departamento de Cortés, Honduras, nor is *P. guatemalensis* known from any locality in Cortés.

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REFERENCES

- Campbell, J. A. & Kubin, T. M. (1990). A key to the larvae of *Plectrohyla* (Hylidae), with a description of the tadpole presumed to be *Plectrohyla avia*. *Southwestern Naturalist* **35**, 91-94.
- Duellman, W. E. & Campbell, J. A. (1992). Hylid frogs of the genus *Plectrohyla*: systematics and phylogenetic relationships. *Misc. Publ. Mus. Zool., Univ. Michigan* **181**, i-vi, 1-32.
- Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**, 183-190.
- McCranie, J. R. & Wilson, L. D. (1981). A new hylid frog of the genus *Plectrohyla* from a cloud forest in Honduras. *Occas. Pap. Mus. Nat. Hist., Univ. Kansas* **92**, 1-7.
- Smithe, F. B. (1975). *Naturalists color guide*. New York: American Museum of Natural History.
- Wilson, L. D. & McCranie, J. R. (1993). Preliminary key to the known tadpoles of anurans from Honduras. *Royal Ontario Mus. Life Sci. Occas. Pap.* **40**, 1-12.

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BOOK REVIEWS

Ecology and Conservation of Amphibians. T. J. C. Beebee. (1996). 214 pp. Chapman & Hall, London. £35.00 (cloth).

Trevor Beebee has applied his considerable experience to the latest volume in Chapman & Hall's well-received Conservation Biology series. Aimed not only at students of biology, ecology and conservation, but also at professionals in industries and agencies involved with the environment, *Ecology and Conservation of Amphibians* represents a succinct introduction to the wealth of literature hidden away in the depths of university and government libraries. As the author remarks, 'selling' herpetology – especially to the public – is often no easy task. However, to quote him directly "amphibians are fascinating and important, and we must look towards a better understanding and protection of them". Reading this book will surely convince any sceptic of the validity of this statement.

The book is composed of ten chapters. These range from the obligatory 'What...?' and 'Why...?' to well-researched accounts of evolution, behaviour, population and community ecology, distribution, threats, and two chapters dealing specifically with practical conservation. Throughout the book the author has attempted to present a balanced global perspective of amphibian research. However, he has avoided the largely descriptive work of many countries, instead favouring the more experimental approach. This has inevitably led to a bias towards research from Europe and North America.

Within the chapter on 'Why Study Amphibians?' Dr Beebee reviews the debate surrounding global amphibian declines. Although this is a controversial area, he approaches the subject with objectivity, carefully evaluating the available scientific material, but ultimately concluding that amphibian declines are no worse than those currently affecting the rest of our planet's biodiversity.

The three chapters on behaviour, population ecology and community ecology reveal what most enlightened herpetologists already appreciate: amphibians display a fantastic array of life-history adaptations, the study of which can, and indeed has, shed light on wider ecological issues. The author highlights Nelson Hairston's work on plethodontid salamanders, whose population densities are so high that they significantly reduce the flow of energy through the whole ecosystem. These chapters provide valuable insights into many aspects of ecology, from mate choice and kin selection, to competition and predation.

The final chapters describe the various ways in which amphibians may be conserved. In addition to covering the conventional issues, such as legal protection, site acquisition, and habitat management; the more contentious issues of captive breeding and translocations are also presented fairly and concisely. A number of case-studies are used to illustrate the is-

ssues discussed. These include rare species with restricted ranges, such as the Majorcan midwife toad (*Alytes muletensis*); widespread but localized species, including that on which the author must rank as the world authority, the natterjack toad (*Bufo calamita*); and widespread, generalist species. In this latter category the author adds fuel to the debate surrounding current protection measures for the great crested newt (*Triturus cristatus*).

Few books are without flaws, but annoyingly the main problem with this one could so easily have been avoided. Many of the illustrations are taken directly from other journals and articles, but are poorly reproduced. In a couple of cases, the text on the figures is difficult to read at all. With high quality scanning and touch-up facilities now readily available to anyone with a desk-top computer, it is difficult to understand why Chapman & Hall could not have done a more professional job on many of these. The quality of the text deserves better.

In conclusion, this is a book filling a much needed niche in the armoury of any conservationist. It is well-researched, extremely well written and full of interest. Indeed, the user-friendly writing style makes this a book that should appeal to the armchair naturalist as well as the field researcher and professional conservationist. Unfortunately the publisher's quality control leaves a lot to be desired and at £35 per copy this is no small point. Nevertheless, I await the volume on reptiles with great enthusiasm.

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Reptiles and Herbivory. Gillian King (1996). 160 pp. Chapman & Hall, London. £39.00 (cloth).

One of the questions addressed in this unusual and extremely interesting book is why there should be so few herbivorous reptiles in the world today compared either with mammals or with the impressive reptilian radiations of past eras. Apart from tortoises and turtles, very few modern reptiles are herbivores. This is a puzzle, and the question arises as to why a successful and widespread group of animals, such as lizards, has not radiated into herbivorous niches. The major part of the book is concerned with examining a variety of reptilian taxa that exhibit or have exhibited herbivory. Not only are structural features – skulls, jaw articulations and teeth etc. – considered, but also the interplay between feeding and other aspects of adaptation in extant forms, especially their metabolic and thermoregulatory regimes. These are compared with the same physiological systems of birds and mammals.

Mesozoic herbivores enjoyed two major periods of increasing diversity, Triassic-Early Jurassic and Middle-Late Cretaceous. During the first of these, changes in the flora of gymnosperms may have con-

trolled the adaptations of the herbivores through changes in food quality, such as toughness, with which the earlier therapsids had been unadapted to cope. The early dinosaurs were probably more successful as a result of better gut processing. Most of the reptilian herbivore taxa of this period had simple or reduced dentition. In contrast, the Cretaceous increase in reptilian diversity was marked by a corresponding diversity of tooth form and jaw mechanisms. This might well have been the result of coevolution between the herbivorous dinosaurs of the period and the fruiting structures of the later Mesozoic angiosperms. The latter became heavily defended by hairs, thorns, hard outer coverings and so on, which protected them from being eaten before their seeds had matured. No doubt herbivorous reptiles would also have played an important part in seed dispersal.

In the development of her themes, Dr King discusses several interesting topics. She defines herbivory, analyses the classification of reptiles, compares them with birds and mammals, and argues that the gastroliths of sauropods were used in a muscular gizzard to grind vegetation. Later, she argues that Galapagos tortoises and *Sauromalus* lizards which swallow sand and gravel do so for the same reason. Two main theories have been proposed to explain lithophagy – to produce ballast in aquatic animals or to act as grinding stones to break down food. In crocodiles, it seems reasonable to assume that gastroliths have both functions. When items such as eggshell and cuttlebone are ingested by reptiles, they may provide an extra source of calcium prior to egg-laying.

A considerable amount of information is available about feeding in living reptiles, not only on how teeth and jaws work but also on the structure and physiology of the alimentary canal. A few examples of the mummified gut contents of dinosaurs are known. Perhaps the most famous is that of the hadrosaur *Apatosaurus* whose presumed stomach contents comprised conifer needles, twigs, seeds and other parts of land plants. This was one of the early pieces of evidence that showed the duck-billed hadrosaurs to have fed at least partially on land plants and not on soft water vegetation as previously supposed. In addition, a coprolith attributed to an ornithomimid dinosaur apparently contained bits of fibrous undigested plant matter. Finally, footprints have

been preserved with plant matter in such a way that they seem to have been made by dinosaurs browsing on the foliage of both conifers and of angiosperm trees.

Fossilized parallel trackways of dinosaur footprints also provide evidence of herding, as do the mass accumulations of skeletons of dinosaurs, such as *Iguanodon* and *Plateosaurus*. 'However, all these large numbers of skeletons really indicate is that the dinosaurs were common and successful in life. We cannot actually prove that they had any specific association while they were alive. However, in the case of *Iguanodon*, parallel trackways are known as well, which would indicate some kind of herding'. Also described is the fossil evidence for communal nesting among hadrosaurian dinosaurs which shared many similarities with that of *Iguana iguana*. Green iguanas use the same nest sites repeatedly. The mothers guard the nests, the eggs are laid at the beginning of the dry season so that drowning of the eggs is avoided, and hatching takes place with the onset of the rainy season when fresh, nutritious food become available.

The possibility of thermoregulation and aestivation in dinosaurs is also considered, as well as thermoregulation in lizards but, surprisingly, only thermal inertia in tortoises. Comparable treatment is accorded to the mammal-like reptiles as well as to other less well known taxa of extinct reptiles. Finally, the general conclusion is reached, 'that herbivore-plant interactions are liable to be responsible for changing extinction and speciation rates of the two groups cannot be faulted..... Herbivorous lizards perhaps fall between two stools: as ectotherms they would be better off in deserts or highly seasonal environments, but as herbivores they do better in more constant tropical environments. It seems that lizards cannot have their cake and eat it. Modern turtles do a bit better, probably because of their tank-like strategy (which reduces predation) combined with their low metabolic rate'.

As the above quotations indicate, *Reptiles and Herbivory* is a fascinating and well-argued book. It is beautifully illustrated with line drawings by Denise Blagden and the standard of production is high.

J. L. Cloudsley-Thompson
British Herpetological Society

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Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

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

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

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