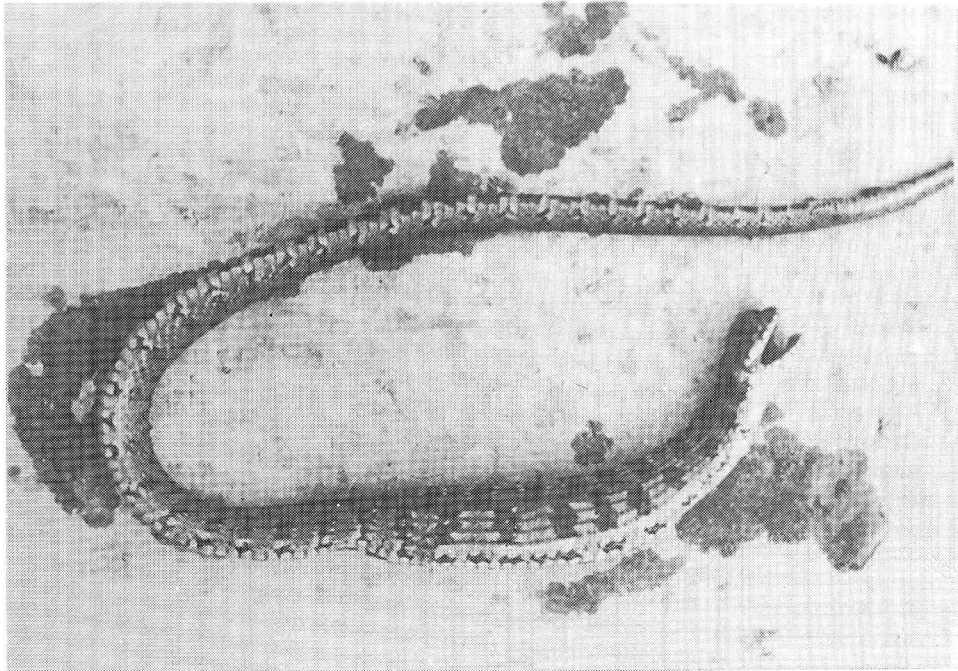


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ANNOUNCEMENTS

OPINIONS FROM THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE.

The following opinions of reference to herpetology were published in the *Bulletin of Zoological Nomenclature*, Vol. 42, Part 4 (September 1985).

- (i) *Kinosternon alamosae* Berry & Legler, 1980 and *Kinosternon oaxacae* Berry & Iverson, 1980 (Reptilia, Testudines): conserved.

REVIEW:

THE STRUCTURE, DEVELOPMENT AND EVOLUTION OF REPTILES

Symposium of the Zoological Society of London No. 52. Co-sponsored by the British Herpetological Society.

PROFESSOR ANGUS D'ALBINI BELLAIRS Festschrift Volume.

Academic Press, London, 1984.

ARMAND J. DE RICQÛES

Université Paris VII, 2 Place Jussieu, 75005 Paris, France.

This thick volume, hardbound under an elegant blue cover with gold lettering, is offered under the usual good publishing standards expected from Academic Press. Even though my own copy had no cover jacket and perhaps suffered from some very minor over inking, making some drawings and photographic plates a little bit too dark, the overall publishing and printing quality is, by and large, excellent.

After the usual general introductory materials, the Introduction chapter itself, by the Editor, Professor M. Ferguson (Manchester) is a lively and informative sketch of Professor d'A. Bellair's career, with many humorous and thought-provoking hints on academic life, past and present. The main content of the book is formed by no less than 27 specialised papers, most of them single-authored. They are arranged under five general themes, forming large chapters or sections, which are successively: Morphology (six papers), Development (six), Physiological Ecology (seven) and Evolution (seven). This provides a sensible framework within which the diversity of the papers could be arrayed, although several papers could easily have been shifted, on logical grounds and content, from one section to another. Such a situation is, to this reviewer, very diagnostic of the current state of the art and trends in Vertebrates Evolutionary Biology, and more will be said on that later.

Because it would not be realistic to try to review uniformly all and every paper in the book, no apologies are due for a more in-depth analysis of some papers than of others, depending on the reviewer's interests and expertise. This admittedly subjective analytical treatment will be balanced, to some extent, by overall synthetic comments on the book as a whole at the end of the review.

Study of the 'Slide-pushing' locomotion, recognised by Carl Gans (Ann Arbor, USA) as a new locomotory process among elongate Squamates, opens the section on morphology. This paper is a clear, concise addition to our knowledge of limbless locomotion.

The study of anterior limb skeleton and musculature in *Varanus* in relation to sprawling gait, by J. M. F. Landsmeer (Leiden, The Netherlands) is an excellent example of the usefulness and relevance of good "classical" anatomy for functional and evolutionary morphology, a fact perhaps too often forgotten in more "fashionable" (i.e. electromicrographic) approaches.

The next paper, by E. N. Arnold (London, England) deals with characters of cloacal and hemipenial musculature among lizards. This paper shows beautifully how the careful comparative study of a complex system can produce important data for the study of relationships. This paper also offers an admirable example of a soft, diplomatic, "cryptoclaicism". While the methodology of inferring relationships is definitely pervaded by a cladistic approach, the paper is "careful" not to offer even one cladogram and rather forcefully concentrates on good empirical data gathering and descriptions.

Next comes a paper by P. C. H. Pritchard (Maitland, Florida, USA) on piscivory of turtles and evolution of long-necked Chelidae. This work offers an interesting methodological contrast with the preceding one.

The Squamate epidermis, as explained in the next paper by P. F. A. Maderson (New York, USA) appears to be an excellent model system for the study of epithelial tissue homeostasis. This most stimulating paper, in fact, brings together many cytological, developmental, physiological and natural history data into mutual interaction, to propose a new synthetic view of squamate skin biology.

The next paper, by R. Presley (Cardiff, Wales) on the problems of tympanic membrane homology closes the section on morphology. Here, Presley offers us, from the point of view of descriptive embryology, a truly admirable piece of work where careful divisions between "Epistemological", historical, descriptive and interpretative sections allows the reader to find its way between Charybde's *anlagen* and Scylla's controversies.

More generally, thanks to works such as this one, it is perfectly clear how and why the good tradition of descriptive, detailed, developmental embryology should be kept alive and healthy within modern evolutionary Biology. Indeed, how could we do without it? Wouldn't it be a good thing for the Universities to keep this beautiful field of knowledge and research alive, even if it is contemptuously labelled a "traditional" one by some potent ignorants?

Section Two, on development, opens with a paper by B. K. Hall (Halifax, Canada) on developmental processes underlying the evolution of cartilage and bone.

The richness of his contribution precludes detailed analysis and comments; it deals especially with the

problems of secondary cartilages, metaplastic bone and (secondary) epiphyseal centres among reptiles. If I fully agree on the all-important issue of timing shifts of developmental processes as a key mechanism in skeletal evolution, I am not fully convinced by the author's contention that reptiles lack secondary cartilages (they appear to be "already" developed among some osseous fishes) and that "reptilian periosteal have limited osteogenic ability".

The next two contributions, one by K. Murreoka and S. Bryant (Irvine, USA) on regeneration and development of vertebrate appendages on the one hand, and the one on pattern formation during development of amniote limbs by L. S. Honig (Los Angeles, USA), on the other, can be treated together. Both papers deal with experimental embryology of vertebrate limbs, the first paper focussing mainly on amphibians, the second one on amniotes, including some reptiles. Elegant experimental approaches, combined with new conceptual frameworks, have both contributed significantly to the recent advances in this fascinating field. But how do cells appear to "know" what they "have to do" at the "right" time and places? This all-important issue of developmental biology is far from settled, as evidenced by these lucid and up to date papers. How relevant and useful the limb development regeneration models are to address the issue meaningfully is also made quite obvious here.

Professor M. Fergusson's paper on craniofacial development in Alligators is the next contribution. This big paper summarises nearly 10 years of work and the author's PhD Thesis. Starting with problems of cleft palate malformations among mammals (a problem with obvious medical and social importance), he went on to realise that the crocodylian secondary palate could be used as a most satisfactory model to understand normal and pathological palate morphogenesis. This, in turn, led to an intensive research project on crocodile development and growth, in order to fully master the model's characteristics. These efforts have been successful enough to push the crocodylians from a position of poorly-known reptiles, as far as development was concerned, to the status of a well standardised, operational model for modern development biology, a not inconsiderable achievement. Fergusson's paper gives much new information on normal and pathological developments of palatal regions and related structures. Although photographic illustrations are numerous and adequate, I would have liked to find some line drawings, for an easier follow up of the descriptions.

The next paper, on amelogenesis in Reptilia and evolutionary aspects of enamel gene products, is co-authored by six scientists, including H. C. Slavkin (Los Angeles, USA) and M. Fergusson. It is perhaps one of the most fascinating papers of the Volume, as it so beautifully blends together the most recent advances of molecular biology and the insights of phylogeny conveyed by the comparative morphologists' tradition. It seems that enamel synthesis is the end result of a single multi-gene family consisting of multiple structural genes coding for enamelin and amelogenin (enamel proteins) throughout the vertebrate phylum, with a high degree of conservation of sequences.

Obviously, much further work of considerable interest is likely to follow.

The last paper in the section on development is a rather short review by K. W. Jones (Edinburgh, Scotland) of the problem of evolution of sex chromosomes in reptiles and mammals, with emphasis on snakes. The paper mainly introduces a model which would account, in evolutionary terms, for the diversity of mechanisms of sex determination within groups, and from one group to another. I have the feeling that the literature coverage, especially regarding the problems of environmental sex determinism among reptiles, is rather on the light side.

The next section, dealing with physiological ecology, starts with an interesting work of G. J. Webb (Kensington, Australia) and A. M. Smith (Canberra, Australia) on sex ratios and survivorship in the Australian freshwater *Crocodylus johnstoni*.

The study seems to me a model of careful naturalist work spanning from extensive field surveys to theoretical computations, *via* histological gonad analysis. It is clear, however, that the "advantages" (if any), in terms of classical selective/evolutionary theories of "epigenetical" sex determinism, still seem far from being clearly understood.

V. Lance's (New Orleans, USA) paper on endocrinology of reproduction in male reptiles seems to me to be a clear, up to date, synthesis review of an interesting problem, much more orientated, however, towards histo-endocrinology than towards physiological ecology itself. My only reservation is that, perhaps, not enough emphasis is put on the relationships between reproductive cycles and the various environmental ones, such as climatic cycles, that male reptiles find in their actual environments.

The next paper, by H. R. Bustard (Alyth, Scotland) reviews the captive breeding behaviour of the gharial. This is part of a major UN and Government of India conservancy project, the aim of which is to save the Ganges gharial from extinction. This lively report is a true piece of natural history, full of practical experiences, political, managerial and ethological. It happily ends with reasonably optimistic prospects for gharial survival.

Thermoregulation, energetics, metabolism and growth are interrelated fields which pervade modern researches on reptiles, and have far-reaching consequences for our understanding of vertebrate evolutionary biology in general. It is thus not surprising that these themes are touched upon by at least five papers, spread under chapters on physiological ecology and evolution.

R. A. Avery's (Bristol, England) paper on the role of thermoregulation in lizard growth, as exemplified by *Lacerta vivipara*, is a case in point. The experiments reported show that thermoregulation *per se* has no influence on growth physiology, growth rates being increased under behavioural thermoregulation only because this allows an increase in food intake. This seems to be a reasonable conclusion but the paper amply demonstrates the difficulties in getting experimental results with good statistical reliability in such kinds of researches.

R. A. Coalson's (New Orleans, USA) contribution, on how metabolic rate and anaerobic glycolysis

determine the habits of reptiles, is an intriguing paper, worth studying in detail. This work encourages controversy as some definitions and physiological interpretations offered would probably not match those used by other specialists.

Next comes a paper on thermoregulation in the Nile crocodile by J. P. Loveridge (Harare, Zimbabwe). It is surprising that this common species among crocodylians had not been subjected to modern analysis in terms of its ecological physiology. This paucity of data is now ending, thanks to these detailed field studies, which bring new results, for instance on the significance of evaporative cooling by gaping.

I have little to comment on F. E. Russell's (Tucson, USA) paper on snake venoms. It seems to me that this paper may be an excellent and helpful general introduction to the subject, notably for clinicians. The paper is deeply pervaded by the author's personal experience and overall humanistic feeling for the subject, rather than being really an in-depth technical-analytical review of it. Some acid comments on the current state of the art "gadgetisation" of research are excellent. I would have liked to find more in-depth discussions in this work on venom chemistry as possibly interesting biochemical "trade marks" of snake phylogeny.

The last section, on evolution, opens with G. Underwood's (London, England) work on scleral ossicles of lizards: an exercise in character analysis. The title of the paper expresses admirably the aim of the work. Explicit statements and formalisation at all steps of the analysis are provided. This kind of approach is exceedingly useful because the procedures, both intellectual and practical, are crystal clear and encourage possible "tests" and discussions. However, I have the feeling that what is *not* explicit in the paper are basic "philosophical" issues on relationships between classifications and phylogeny, between phenetics and cladistics, even if both turn-out to be quantitative; hence, perhaps, an overall feeling of "stoic, lucid, desperation" in the general discussion.

O. Rieffel (Zurich, Switzerland) gives an excellent account on miniaturisation of the lizard skull and on its functional and evolutionary implications. D. B. Norman (Oxford, England) starts the more palaeontological section of the book with an account on cranial morphology and evolution of dinosaurs. This is essentially a progress report which provides, nevertheless, a clear introductory account of the current concepts on interrelationships in this important group. The paper offers one of the very few cladograms found in the whole book.

Next contribution is J. W. Osborn's (Edmonton, Canada) on the evolution of dentitions from reptiles to mammals, with emphasis on tooth attachment. This paper proposes a very detailed evolutionary scenario, trying to encompass the various changes required, starting from a plesiomorphic acrodont, haplodont, polyphriodont dentition, to reach the highly derived thecodont, plexodont diphodont condition found among most mammals. I found some difficulty in following the details encompassed into the numerous, small and complex sketch drawings. Is the task involved in making such detailed evolutionary

scenarios worth the work? I think that, in this actual case, the answer may be yes, because the scenario can be tested. Indeed detailed comparative palaeohistological analyses of teeth and dentigerous bones among the full array of pelycosaurs and therapsids may constitute an effective test of the scenario. It would practically involve, however, at least a several-year full time programme by an experienced palaeohistologist, always provided the material was available.

M. J. Benton's (Oxford, England) paper on the relationships and early evolution of the Diapsida, certainly an up-to-date and useful overview of a most important and complex theme of reptilian phylogeny. An especially original contention of the work is that *no* competition need be invoked to explain the substitution of therapsids by archosaurs from the most prominent terrestrial niches during the mid-upper Triassic.

This very point is taken up as the subject of the next contribution, by A. Charig (London, England), which deals with competition between archosaurs and therapsids during the Triassic, with a review and synthesis of the current theories. In this paper, which is in substantial disagreement with the preceding one by Benton, a competition phenomenon is clearly advocated. Charig's overview is a most interesting and useful one, as it makes the debate clear, proposes a taxonomy of opinions and reviews many contributions.

Last but not least, R. E. H. Reid's (Belfast, Ulster) paper on the histology of dinosaur bone, and its possible bearing on dinosaurian physiology will be commented upon here as it so obviously deals with this reviewer's favourite studies. Dr. Reid with this paper, offers the most modern analytical review of dinosaurian bone histology, with a great number of new and interesting data. To what extent do these new data change the functional interpretations of dinosaur bone histology? Briefly, even though the issue of thermal and metabolic physiology of dinosaurs must remain an open one, I regard Reid's contribution as definitely one of the most careful, reliable and fairly balanced ones published in this "hot" field.

The closing address, by Professor d'A. Bellairs (London, England) deals with the organ of Jacobson, intermandibular connection and evolution of squamates. This paper aptly describes and comments on rather complex structures, which may be importantly involved in discussions on squamate evolution. They are dealt with by Professor Bellairs in his usual pleasant style.

After these analytical comments, some sort of synthetic overview on the book should be finally added. First, it might be felt that the crocodylian part of the book (five papers and relatively more in terms of pages), relative to turtles (one paper) and squamates, is on the heavy side, but this feeling is not warranted and the balance between various topics, and various reptilian groups, is, by and large, a good one. The book will be of interest to all kinds of herpetologists and to biologists more generally.

Second, there is a feeling of healthy excitement and enthusiasm to discover in this book; vertebrate evolutionary biology is fresh and alive, perhaps more so than some other fields of "classical" biology. Especially commended are the apparently good

interrelationships between various approaches devoted to different levels of biological integration. From molecular biology, gene products, genetics and chromosomes through cytology, histology, developmental biology, descriptive embryology, functional and comparative anatomy, physiology, ethology, ecology to systematics, phylogeny and evolution, the whole array of approaches is there, happily cooperating and interacting towards, at the same time, a more precise and a more general understanding of reptilian evolutionary biology.

For the scientists of some countries, where it appears that progress in a given scientific field can be achieved only if other fields are first killed for good, the apparent healthy situation of cooperation and open-mindedness conveyed by the book between various "classical" and "modernist" approaches in Biology will appear as a most refreshing and encouraging hope. But on the gloomy side, and even if, as a Festschrift, and hence dedicated to one outstanding scientist by his friends and former students, I regret that a book of such importance and magnitude has not better

conveyed the truly international aspects of current researches on reptiles. It seems to me hard to believe that major scientific countries like the Soviet Union, Italy, Germany, Spain (which is currently performing a dramatic scientific come back in vertebrate evolutionary biology), South American countries, and many others, not to mention my own, should not have contributed more, at least at the level of cited bibliography, to the exciting content of this book.

To conclude, the Editor, Professor Marc Fergusson should be congratulated for a splendid job well done. This massive volume is a fitting monument dedicated to the scientific and teaching achievements of Professor d'A. Bellairs. It is obviously a "must" for the libraries of all universities, museums and similar institutions actively working in vertebrate evolutionary biology, and not only on reptiles. Shelves should be emptied again, for this magnificent book to secure a place proudly with such classics as C. Gans' *Biology of the Reptilia* and *Morphology and Biology of Reptiles* of B. Cox and . . . A. d'A. Bellairs.

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GARDEN PONDS AS AMPHIBIAN BREEDING SITES IN A CONURBATION IN THE NORTH EAST OF ENGLAND (SUNDERLAND, TYNE AND WEAR)

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ABSTRACT

A survey of the distribution of amphibians was carried out in Sunderland (Tyne and Wear). Five species were present in the area, but *Triturus cristatus* and *T. helveticus* were uncommon. All the amphibian species were declining or apparently extinct in wild ponds. Garden pools were less common than in other parts of England that have already been surveyed, and as a result of the low density of ponds many had not been colonised by amphibians. There was an encouraging number of colonies that had been started by deliberate introduction however. *Rana temporaria* and *T. vulgaris* were the only species that had colonised the ponds to any great extent. Both were found to be very susceptible to fish predation, and mechanisms for surviving in fish ponds are discussed. Another danger was the destruction of garden ponds which was astonishingly common.

INTRODUCTION

It is a well known fact that while amphibian breeding sites have been declining in the countryside, garden ponds have increased in popularity and are becoming important refuges for some species (Mathias, 1974; Beebee, 1979 and 1981; Cooke and Scorgie, 1983). In particular the common frog *Rana temporaria* and the smooth newt *Triturus vulgaris* seem to have been the most successful in this respect, while the common toad *Bufo bufo* has been less adaptable.

The palmate newt *T. helveticus* has also been recorded in garden ponds, although Cooke and Scorgie stated that it was less common in these habitats by virtue of its being most common in areas that are less susceptible to urbanisation. The crested newt *T. cristatus*, however, has not been very successful in colonising this relatively new habitat.

Mathias reported a recent increase in the number of garden ponds being built, while Beebee found that 16.5 per cent of gardens in Brighton had one or more. In Scotland, according to Cooke and Scorgie, the idea

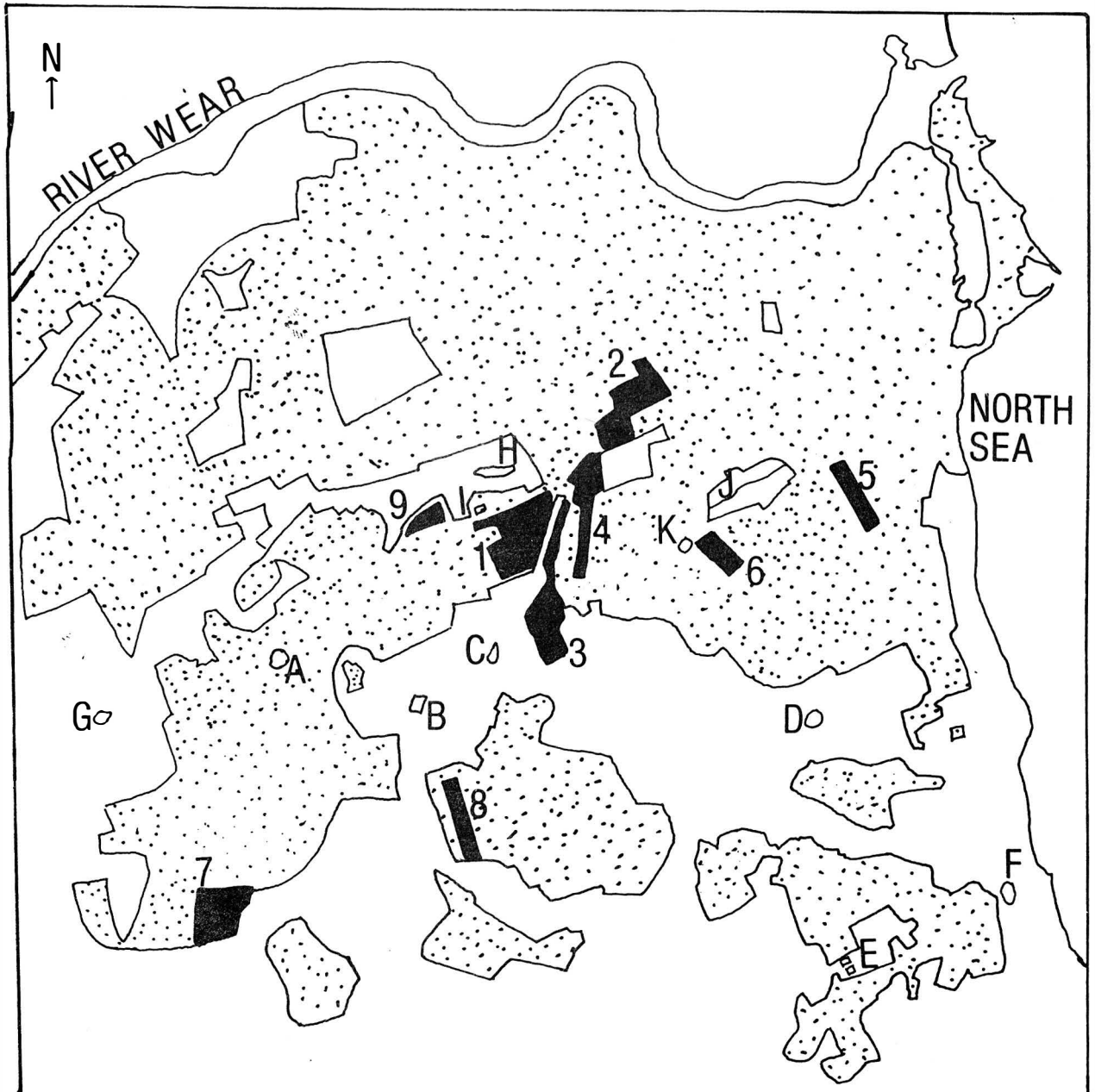
has been less favourable, and this was our initial impression of the situation in north east England. We therefore carried out a survey in Sunderland to determine the extent of amphibian breeding sites, public attitudes to garden ponds, and to see which (if any) of the amphibian species had succeeded in the urban environment. In addition we attempted to assess the status of wild populations living on undeveloped land in the survey area.

METHODS

A door-to-door survey was carried out between October 1981 and December 1982 in nine estates in different parts of Sunderland. Participants were asked if they had a garden pond, or if they had ever filled one in on their present property, and if they would ever consider creating one in the future. Prejudices against ponds were also recorded. If a pond did exist we enquired to see if fish or amphibians were using the pool, and the origin of the latter group was investigated. When amphibians were present we checked to ensure that they had been identified correctly. In addition any records of amphibians in garden ponds outside the estates surveyed, or of wild populations, were investigated. This was added to our knowledge of the area, gained by deliberate survey in recent years.

Fig. 1 The Study Area

- Study estates, numbered as described in the text.
- ▨ Built-up areas.
- Open countryside/parkland.
- Ponds, labelled A-K (see also Table 1).



Finally the first edition of Ordnance Survey maps (1853-1857) were examined, and the number of ponds within 1km of area 1 (see Fig. 1) was noted. These maps show the positions of many small ponds (some of which still existed in areas), and were regarded as being more accurate than their modern counterparts in this respect.

THE STUDY AREA: — A HISTORICAL PERSPECTIVE.
AND THE PRESENT STATE

All the surveys were carried out in estates to the south of the River Wear, but records of amphibians in garden ponds were collected from all over Sunderland. At the turn of the century Sunderland was a much smaller town, and much of the survey area was rural with scattered pit villages. Small scale quarrying activities, gravel extraction, and mining activities resulted in the production of many man made ponds.

The 1853 maps revealed no less than 28 ponds within 1km of estate 1. Since then the town has expanded rapidly, especially since 1930, with many large council and private housing estates being built, and this has resulted in the loss of many wetlands (Dunn, 1980). Further losses of ponds have also occurred on agricultural land surrounding the town.

The geology of the area probably has some influence on the abundance of *T. helveticus*, as will be discussed later. The bed rock of the area is Permian Magnesian limestone, overlaid by stagnogleyic brown earth (poorly drained calcareous soil), (Dunn, 1980). Fig. 1 shows the estates that were visited, these were as follows: 1. Humbledon Hill; 2. Thornhill area; 3. Silksworth Lane and Elstob estate; 4. Alexandra Road-St. Nicholas Avenue; 5. Grangetown; 6. Ashbrooke; 7. East Herrington; 8. Vicarage Estate; and 9. Plains Farm North. The first eight estates were privately owned, while the latter was a council estate.

Pool	Species present	+/- G.a.	Site description	Present status/fate
A.	Tc, Tv, Rt, Bb	?	Sand/gravel pits.	Built on before 1955.
B.	Rt, Bb, Tv.	+	Colliery pond.	Recently turned into boating/fishing pond.
C.	Rt, Bb, Tv.	+	Colliery Pond.	Recently turned into boating/fishing pond.
D.	Rt, Bb.	-	Pond.	Drained in 1983.
E.	Rt, Bb, Tv.	-	Cooling ponds.	Bb extinct since 1982, Rt very scarce.
F.	Rt, Bb, Tv.	?	Quarry ponds.	Apparently filled in.
G.	Rt.	-	Pasture ponds.	Still present in 1978.
H.	Rt.	+	Park pond.	Spawn present only in recent years, possibly introduced.
I.	Tv.	-	School pond.	Large population of unknown origin.
J.	Rt	+	Pools on edge of stream.	Present in low densities up to 1982, possibly colonised from adjacent gardens.
K.	Rt, Tv + ?	?	Pasture pond.	Drained in 1950's.

Summary

Species.	Number of populations recorded.	Number still extant.
Rt.	10	3 - 6
Bb.	6	0 - 2
Tv.	7	2 - 4

TABLE 1: Known breeding sites (past and present) in the study area

Abbreviations: Tc = *Triturus cristatus*, Tv = *T. vulgaris*, Rt = *Rana temporaria*, Bb = *Bufo bufo* and G.a. = *Gasterosteus aculeatus*. Variations in the numbers of populations still extant refer to the cases where species had not been recorded at some sites during the last two years, and there continued survival was in doubt.

Area	Age of estate	n.	Number of: Existing ponds (%)	Ponds being built	Ponds filled in
1.	post 1955	262	24 (9.1)	0	3
2.	pre 1939	84	9 (10.7)	1	3
3.	pre 1955	168	11 (6.5)	3	13
4.	pre 1955	86	6 (6.9)	0	1
5.	pre 1955	62	8 (12.9)	0	2
6.	pre 1955	200	7 (3.5)	0	3
7.	post 1955	200	3 (1.5)	0	3
8.	post 1955	126	4 (3.1)	0	0
9.	pre 1955	100	4 (4.0)	0	0
Total		1288	76 (5.9)	4	25

TABLE 2: Numbers of ponds in various estates

n. = the number of houses surveyed. (%) = the percentage of houses in each estate with garden ponds.

RESULTS

DISTRIBUTION AND STATUS OF WILD AMPHIBIANS IN THE STUDY AREA

Four amphibian species have definitely been recorded in the study area since the 1930s. The only record for *T. cristatus* was from site A (Fig. 1, Table 1), a series of ponds that were filled in before 1955. *R. temporaria*, *B. bufo* and *T. vulgaris* were still present in the area up until 1981, but as summarised in Table 1, all three species had suffered declines. These were due to drainage, human recreation (i.e. children fishing in pools B and C), and the cleaning of pool E shortly after the spawning season of *B. bufo*, for a series of years in the late 1970s. This pond also used to be notable for a population of *T. vulgaris* that contained many neotenus individuals, but these were also affected by the cleaning operations.

It should be noted however that the presence of *R. temporaria* at two sites was believed to be due to stock either spreading from garden ponds, or being translocated there as spawn.

NUMBERS AND SIZES OF GARDEN PONDS IN THE STUDY ESTATES, AND THE ATTITUDES OF THE PUBLIC

Questionnaires were completed for a total of 1288 households, resulting in the location of 76 gardens with ponds, and a further four in the process of being excavated. This yielded a total of 6.2 per cent of gardens with ponds. Of these 80 gardens, 78 contained only one pond, while the remainder had two and five ponds respectively. The estates varied widely in terms of the percentage of houses with ponds, with the highest value being 12.9 per cent (Table 2). It was noticed that there was a distinct neighbour effect, with the few gardens that had ponds often being close together. Table 3 illustrates the fact that when comparing the numbers of ponds expected and observed, in estates built before and after 1955, there was no significant difference when a chi squared test was applied (i.e. new estates contained just as many ponds as older ones).

Age of estate	n.	Number of existing ponds:		χ^2	p	Number of ponds destroyed:		χ^2	p
		O.	E.			O.	E.		
Pre 1955	700	45	41.3	0.70	>0.1	22	13.5	11.63	<0.001
Post 1955	588	31	34.6			3	11.5		

TABLE 3: χ^2 analysis of the effect of the age of the garden on the numbers of ponds existing, and drained
n = number of houses sampled belonging to each age group. O = number of ponds observed, E = number of ponds expected in each age group.

A total of 25 ponds were found to have been filled in. As this was probably an underestimate (ponds may have been destroyed by previous occupants), at least 24 per cent of all the ponds ever made were subsequently lost. This time there was a significant difference between estates built before and after 1955, with more ponds than would be expected being lost in the older houses.

564 householders who did not have ponds were asked if they would like one in the future. Only 23 (4 per cent) gave a positive response. Of the remainder 328 (58 per cent) did not like, or were indifferent to ponds, while a further 118 (21 per cent) thought that their gardens were unsuitable (mainly too small). A further 95 (17 per cent) were against the idea because of the danger of drowning children or pets, and would fill a pond in if it was in their garden.

Most of the ponds were small, varying in surface area from 0.08m²-18.0m². Only one of the pools had a surface area greater than 9m².

USE OF GARDEN PONDS BY AMPHIBIANS

37 (48 per cent) of the gardens with ponds were owned by fish-keepers, while 31 (40 per cent) of the gardens with ponds were amphibian breeding sites. A total of 21 ponds had neither fish nor amphibians (26 per cent). Table 4 shows that of all the garden ponds where amphibians were recorded (throughout Sunderland), *Rana temporaria* was the most common species, followed by *T. vulgaris*. *B. bufo* was very scarce, while the other two *Triturus spp.* were not recorded. *T. vulgaris* especially, and *R. temporaria* were found less often in ponds containing fish, although when χ^2 tests were applied the results were not significant. Of the 13 ponds that contained both fish and *R. temporaria*, no less than eight of these were close to ponds in adjacent gardens that were fish-free. One of the four ponds containing *T. vulgaris* was in a similar arrangement. When these ponds were eliminated for

both amphibians and the χ^2 test was repeated, there was a significant excess of frog colonies in fish free ponds and a significant relationship also for *T. vulgaris*. In another of the ponds with both fish and *T. vulgaris* it was reported that newt larvae only metamorphosed in years when there was a dense growth of aquatic plants, which had been the case in recent years, following a deliberate introduction attempt.

Only four pond owners with amphibians regarded these amphibians as pests. One thought that the newts would eat her goldfish, and had tried (unsuccessfully) to eradicate them, while three other pond owners thought that the large depositions of frogspawn were unsightly. It seems that more pond keepers were keen to encourage amphibians in their gardens. Table 5 shows that a majority of the *R. temporaria* and *T. vulgaris* records were derived from stock deliberately introduced to their ponds. Further analysis of the data obtained from the study estates revealed that all the colonies of *R. temporaria* in the new estates were derived from introductions, while in the older estates more ponds were colonised naturally. In estates of both age groups *T. vulgaris* tended to be introduced more often, while both of the attempts by *B. bufo* to spawn in garden pools were the results of natural colonisation.

DISCUSSION

It is quite likely that in the past all of the 'commoner' British amphibian species were present in the study area. Although some areas of the magnesian limestone outcrop are quite dry, due to the permeability of the rock (Dunn, 1980), this was clearly not the case in Sunderland (south) in 1853. This situation had no doubt been improved by man's early industrial activities, and so at this time potential breeding sites were abundant.

Species	All known sites				Excluding all pools with fish close to 'reservoir' site					
	Number of records in ponds (+/-) fish		χ^2	p	Number of records in ponds (+/-) fish		χ^2	p		
	+	-			+	-				
<i>R. temporaria</i>	O.	13	23	2.03	N.S.	O.	5	23	10.24	0.01
	E.	17.3	18.7			E.	13.4	14.6		
<i>B. bufo</i>	O.	2	1	N.T.						
	E.	1.5	1.5							
<i>T. vulgaris</i>	O.	4	11	2.73	N.S.	O.	3	11	3.95	0.05
	E.	7.2	7.8			E.	6.7	7.3		

TABLE 4: The effect of fish on the distribution of amphibian species

Expected values were obtained by assuming that fish should be present in 48% of the pools. Too few *B. bufo* records were obtained to allow any χ^2 analysis (i.e. N.T.). N.S. = not significant. A reservoir site was a fish free pool adjacent to pools containing fish.

Species, and age of the estate	n.	Source of parental stock:		
		Introduction	Colonisation	Unknown
<i>R. temporaria</i>				
All records	36	16	13	7
In garden built:				
before 1955		4	11	
After 1955		9	0	
<i>B. bufo</i>				
All records	3	1	2	0
In gardens built:				
Before 1955		0	2	
After 1955		0	0	
<i>T. vulgaris</i>				
All records	15	8	3	4
In gardens built:				
Before 1955		2	1	
After 1955		3	1	

TABLE 5: Origin of amphibians in garden ponds, and the effect of the age of the estate

'All records' refer to data obtained from both the study estates and other garden ponds that were visited in Sunderland. Records in houses built before and after 1955 are from the study estates only.

T. helveticus can still be found in two small pools 5km south of Sunderland, but it is generally rather uncommon, and this is in keeping with information on this species from other hard water areas in Britain (Cooke and Ferguson, 1975; Cooke and Frazer, 1976; Beebee, 1981; and Cooke and Scorgie, 1983). *T. cristatus* was certainly present up until at least the 1940s, but the fact that there was only one record for this large, attractive newt, and its absence from the remaining 'wild' pools, suggests that it too was uncommon. Its absence from four of the remaining ponds may be due to the large numbers of *Gasterosteus aculeatus* present in them, as these fish are known to be important predators of newt larvae (Cooke and Frazer, 1976; Beebee, 1981).

Judging by their wide distribution in the area, and their present relative abundance in the countryside to the south (personnel observations), the remaining three species would all seem to have been relatively common.

The present situation is that both *T. cristatus* and *T. helveticus* could not be found in the study area, while there have been extensive declines of *T. vulgaris*, *R. temporaria*, and *B. bufo* in the wild. Cooke and Scorgie (1983) quote the period from the 1940s to the 1960s as being the time of major declines of all amphibian species in Britain. This was probably the case in Sunderland, but even in the 1980s the trend is continuing relentlessly.

Garden ponds have generally been hailed as an important new habitat for amphibians, but what effect have they had in Sunderland? Our initial impression that garden ponds in this area were rather uncommon was confirmed. The figure of 6.2 per cent is much lower than the 16.5 per cent obtained by Beebee (1979) in

Brighton, and even if the numbers of all those people intending to build a pond in the future is added to our total, the overall percentage would still only be 10.2 per cent. That this figure would be achieved seems unlikely due to the tendency of old ponds to be infilled, especially when houses are exchanged, and parents with young children move in.

The reasons for this difference between northern and southern England are probably complex. They may relate to the more affluent nature of the area studied by Beebee, or even to differences in the size of gardens. Whatever the reason, there is some cause for optimism. The fact that younger estates were almost as likely to have garden ponds in equal numbers to older estates may indicate a recent increase in the numbers of ponds being built, although it is more likely to be due to the increased chances of older ponds being infilled. The tendency of neighbours to be persuaded to build ponds after seeing them in other gardens indicates that the idea may yet become more fashionable. Increased media attention to wildlife gardening may also have a beneficial effect.

Not only were garden ponds less common in Sunderland, but they were also less likely to be used by amphibians than in Brighton (where 53 per cent were used, compared to only 40 per cent in the north east). Mathias (1974), Beebee (1979), and Cooke and Scorgie (1983), all stated that in garden ponds. *R. temporaria* has been the most successful at colonisation, followed by *T. vulgaris* and then *B. bufo*, with the other two newts being very scarce. This was exactly as we found in Sunderland, although the ratios of species records were slightly different. Comparing ratios of *R. temporaria*: *T. vulgaris*; *B. bufo*, Mathias and Beebee found the following ratios respectively, 4.87:1.15:1,

and 3.5:1.48:1. Our ratio of species records in garden ponds was 12:5:1. In other words *B. bufo* was much less common compared to the other two species than in Leicester and Brighton. Whilst it is likely that both *T. helveticus* and *T. cristatus* were present in the study area at too low a density to be able to colonise the first garden ponds, this was clearly not the case with *B. bufo*, and two attempts have been made to colonise pools in area 3, presumably from stock derived from pools B or C. Both of these have been only marginally successful, with breeding only by the odd pair of toads, but not on a consistent annual basis. *T. vulgaris* and *R. temporaria* have been more successful in this respect. Beebee (1979) thought that *B. bufo* preferred older, larger pools, and these characteristics are certainly lacking from many of the garden pools in Sunderland. This cannot be the full explanation, since there seemed to have been more introductions of *R. temporaria* and *T. vulgaris* to garden ponds than of *B. bufo* (although unsuccessful attempts may not have been reported). The one case of deliberate introduction of this latter species had in fact been successful, with a viable colony established for 10 years. The difference between the numbers of introductions may be due to the relative ease of finding adult *T. vulgaris* or *R. temporaria* spawn, rather than *B. bufo* spawn, which is laid in strings that are harder to handle, and are laid in deeper water (Cooke, 1975). However the fact that four (of the known 16) introductions of *Rana temporaria*, and three (of the known eight) *T. vulgaris* introductions were of stock derived from garden colonies lends further weight to the hypothesis that *B. bufo* is markedly less well adapted to colonising garden ponds in this area.

The low percentage of ponds with amphibians was probably due to the very low densities of ponds in the area, limiting the chances of natural colonisation occurring. This would explain why so many fish-free pools had no breeding populations of amphibians. It is also well known that the presence of fish can prevent survival of amphibian larvae through to metamorphosis (Cooke, 1975; Cooke and Frazer, 1976; Beebee, 1981; and De Fonseca and Jocque, 1982), although Beebee noted that *R. temporaria* tadpole mortality in ponds with fish was not always catastrophic, especially when large quantities of spawn, or very few fish were present.

In Sunderland we came to the following conclusions regarding the effect of fish. One fish keeper reported that he kept koi carp (*Cyprinus sp.*), and that these did not eat the tadpoles. In this case the pond certainly had a viable colony of *R. temporaria*. The other ponds with fish all contained either goldfish (*Carassius auratus*), golden orfe (*Leuciscus idus*) or tench (*Tinca tinca*), and these were all reported to eat tadpoles, and amphibians were less likely to be found in these ponds. When amphibians were present in fish ponds we found that it was important that there were refuges where tadpoles could develop safely. These were provided either by dense patches of aquatic plants, or by the presence of fish-free ponds in adjacent gardens producing a regular output of metamorphosing amphibians. If *R. temporaria* populations become large enough, and there are few fish in a pond there is unlikely to be total mortality due to predation (as described by Beebee)

especially since the fish may eliminate other tadpole predators such as newts or invertebrates.

In conclusion, therefore, although garden ponds in this region are still rather uncommon they have been of benefit to *R. temporaria* and *T. vulgaris* at a time when all the native amphibians are experiencing population declines in the wild. These habitats are most useful when there is a string of ponds in adjacent gardens as this reduces the risk of total predation by fish, or of all the ponds being filled in by new owners. The fact that so many colonies have been established by deliberate introduction is promising, as it indicates that conservation in the garden is becoming fashionable. Attempts to reintroduce *T. cristatus* back into garden ponds in this area (under license from the N.C.C., and into suitable ponds) would be a welcome step, as the species is probably too scarce to be able to colonise the ponds in the town naturally. Finally it would seem to be important to contact land owners with ponds to ensure that the few remaining wild populations are conserved if possible. The present survey of the county by Durham County Conservation Trust should be a help in this respect.

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HEMATOCRIT AND BLOOD VOLUME IN THE COMMON AFRICAN TOAD (*BUFO REGULARIS*)

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ABSTRACT

The volume of blood in the common African toad (*Bufo regularis*) was determined by the use of radioactively labelled red blood cells (RBC-Cr⁵¹). Blood volume obtained = 6.24 ± 0.17 . Values are expressed as per cent of body weight. Females have higher hematocrit than males ($P < 0.02$).

INTRODUCTION

A variety of methods have been utilised to quantitate the blood volume in amphibians. The plasma-hematocrit method by the dilution techniques was employed by Conklin (1930) using Evansblue dye (T-1824). Aortic puncture was used by Rouf (1969). Radioactive Chromium (Cr⁵¹) has been used by Suero, Siret, Callejas and Carmena (1980). Results reported deal mainly with frogs (see Table 2).

The present study was undertaken to measure the hematocrit and the blood volume in the common African toad (*Bufo regularis*) through the use of the radioactively labelled red blood cells (RBC-Cr⁵¹).

MATERIAL AND METHODS

Donor animals were bled by heart puncture with heparinized syringe under chloroform anesthesia. Blood volumes were essentially determined according to the method prescribed by Suero *et al* (1980). Blood was mixed in a proportion of 0.1 ml of blood to 0.3 μ Ci of Cr⁵¹. Each toad was injected with 0.1 ml of isotopic blood by heart puncture. One sample was taken from the heart at 20 minutes from the injection. Standards were prepared in isotonic saline and injected with an aliquot of the isotopic blood. DADE nuclear Scintillation counter was used to count radioactive sample. Total blood volume was obtained from the following formula:

$$TBV = \frac{SV \times WSC}{SRC}$$

Where:

TBV = Total blood volume; SV = Volume of the sample; WSC = Whole standard counts per min per ml; SRC = Radioactive counts per min per ml of the sample.

After the count was made, blood was centrifuged for 20 min at 1500 rpm and plasma and red cells volumes were measured.

Hematocrit values were determined on heart blood in capillary heparinized hematocrit tubes. The hematocrit tubes was centrifuged with BHG, Heka centrifuge (Nr. 24843) at room temperature for 5 min. at 11000 rpm, and the percentage of the packed cell volume were read on a Hawksley hematocrit reader.

In the text a significant difference is taken to mean the indicated level of probability by the t-test.

RESULTS AND DISCUSSION

Body weight, hematocrit and blood volume are shown in Table 1.

The present data show that the difference in the hematocrit value between males and females of *B. regularis* was statistically significant ($P < 0.02$) with the females having higher hematocrit than males. In this regard our results agreed with Kaplan (1954) who found statistically significant sex differences in the hematocrit of *Rana pipiens*. Although Rouf (1969) stressed the impossibility of determining any sexual influences of the highly variable blood parameters of *R. pipiens*, Harris (1972), in the same frog, reported that males always have higher hematocrit than females. This discrepancy may be attributed largely to the changes in the hematocrit of amphibians during the bleeding process due to the entry of lymph into the blood stream (Schermer, 1954).

In *B. regularis* the mean blood volume was 6.24 per cent of body weight with extremes of 5.6 per cent and 6.74 per cent. The plasma volume was found to be significantly higher than the red cell volume ($P < 0.001$). Although actual results may differ, expressed in various forms, a wide range of values from one species to another and in the same species using different techniques is found, with high differences on the plasma volume (Conklin, 1930; Prosser and Weinstein, 1950; Klarris, 1972 and Suero *et al*, 1980). In works done in various vertebrates by Thorson (1959, 1961), Conte, Wagner and Harris (1963) and Suero *et al* (1980), it was shown that large plasma volume might be regarded as a primitive characteristic.

Sex	Body weight g	No. of speci- mens	Hematocrit %	Blood volume. ml per 100 g body weight		
				TBV	PV	RCV
Male	28.88±1.62	10	25.70±4.37	6.45±0.29	5.10±0.34	1.35±0.27
Female	31.45±7.56	9	27.40±2.83	6.04±0.41	4.66±0.18	1.38±0.24

TABLE 1: *Mean body weight, hematocrit and blood volume of *Bufo regularis*

* Values are the mean ± SE.

Sp.	No. individuals		Volume (ml/100g body weight			Method	Reference
			TBV	PV	RCV		
<i>Rana pipiens</i>	14	—	8.74	6.03	2.21	Vital red	Conklin (1930)
<i>Rana pipiens</i>	10	139	8.70	7.00	1.20	Evans blue dye (T. 1824)	Prosser and Weinstein (1950)
<i>Rana pipiens</i>	14	24.65	7.46	5.62	1.84	Atomic puncture	Rouf (1969)
<i>Rana catesbeiana</i>	2	15.5	9.45	8.00	1.45	Evans blue dye (T. 1824)	Prosser and Weinstein (1950)
<i>Rana catesbeiana</i>	15	40.4	3.35	2.00	1.35	Cr ⁵¹	Sureo <i>et al</i> (1980)
<i>Hyla septentrionalis</i>	17	22.4	7.50	5.80	1.70	Cr ⁵¹	Sureo <i>et al</i> (1980)
<i>Bufo regularis</i>	19	26.55	6.24	4.88	1.36	Cr ⁵¹	Present work

TABLE 2: Hematocrit, total blood volume, plasma volume and red cell volume in different amphibians from the literature

Based on the data obtained and from published results (Table 2) and the phylogeny of amphibia we might conclude that the common African toad (*B. regularis*) possesses a more efficient circulatory

system than Hylaidae and Ranaidae in that it requires a smaller volume of transport fluid per unit mass of animal in order to carry out its essential metabolic functions.

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DIET AND FORAGING BEHAVIOUR OF *NATRIX MAURA*

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ABSTRACT

There was an ontogenetic change in the diet of the water snake *Natrix maura*, from earthworms and tadpoles in juvenile snakes to fish in adults. This was related to the absolute sizes of these prey types and to the scaling of encounter rates with snake size. Within each prey type relative prey weight RPW was independent of snake size, except for fish taken from drying pools (RPW inversely related to snake size). Overall, RPW increased with snake size (prey taken during normal foraging) or was independent of snake size (including fish from drying pools). Snakes handled fish too large for them to ingest. Multiple captures were common from drying pools, the fish being smaller than when a single fish was taken.

Foraging behaviour of wild *N. maura* could be described as exploratory activity and cruising (finding slow-moving or trapped prey during slow movement); sentinel predation (an extreme sit-and-wait strategy for catching fish); active pursuit and undirected 'fishing' (less commonly observed). Sentinel *N. maura* took up different positions in the water according to their size. Breathing took up 20 per cent of their time; those at the surface spent shorter intervals foraging and breathing than those with deeper perches. Strike rate was once per 7.4 minutes, capture success was low, 2 out of 124 strikes, neither ingested. The relationship between the different types of foraging used by *N. maura* and other naticine snakes, and their stimulus control, are discussed.

INTRODUCTION

The feeding ecology of naticine snakes is well studied, especially the role of chemoreception in the detection (e.g. Arnold, 1981; Burghardt, 1975; Dix, 1968; Dunbar, 1979; Mushinsky and Lotz, 1980) and location (Kubie and Halpern, 1979) of prey. Czaplicki and Porter (1974), Porter and Czaplicki (1977) and Drummond (1979) investigated the stimuli controlling foraging in small laboratory pools in *Nerodia*, and Drummond (1983) described this behaviour in wild *Thamnophis*. There are few studies of feeding behaviour in wild snakes, due to the difficulty of following them (Reinert, Cundall and Bushar, 1984 studied foraging in rattlesnakes with the aid of radio tracking). This paper describes the foraging behaviour and diet of wild viperine water snakes, *Natrix maura*.

METHODS

N. maura were studied in the river Jalon, Spain, from April 1981 to August 1983. During this period the river was a series of pools up to 2m deep, linked by a small stream which dried up in summer. Snakes were captured by hand, forced to regurgitate any food, and weighed with a Pesola scale. Unless stated otherwise, the expression 'with food' includes snakes handling or forced to regurgitate prey. Prey was measured or weighed, using the length — weight regression from Hailey and Davies (1986) to estimate weights of partly

digested fish. At night a powerful torch was used to find snakes, which were held in cloth bags until the following day. For data analysis snakes were grouped into four size classes: tiny (T; <4g), small (S; 4-15g), medium (M; 15-40g) and large (L; >40g). Snakes seen but not captured were assigned to one of these classes by visual estimation. The location and behaviour of each snake were noted, and some undisturbed foraging snakes were observed with 8x binoculars.

RESULTS

DESCRIPTION OF FORAGING BEHAVIOUR

Sentinel Foraging (SF)

This was the most commonly observed foraging behaviour of larger *N. maura*, but was not seen in tiny snakes. The snake was stationary in the water, on the bottom or in debris or vegetation, and made strikes at passing fish with the front part of its body which was held in a concertina position. Most strikes involved an extension of about 20 per cent of the snake's body, though occasionally the whole body was extended; in this case the snake usually then left its perch.

Location. Fig. 1a shows the positions of S, M and L SF snakes in the water during the day and at night. G tests (Sokal and Rohlf, 1981) are used to assess significance of these data, pooling classes where necessary to give >5 observations per cell. Snake size and water depth

were significantly associated during the day ($P < 0.05$) and at night ($P < 0.001$); smaller SF snakes frequented shallower water. This may be related to the ease of reaching the surface to breathe and/or to the

occurrence of different sizes of fish in different depths of water. Small fish were often seen at the margins of pools in shallow water, large fish favoured deeper water.

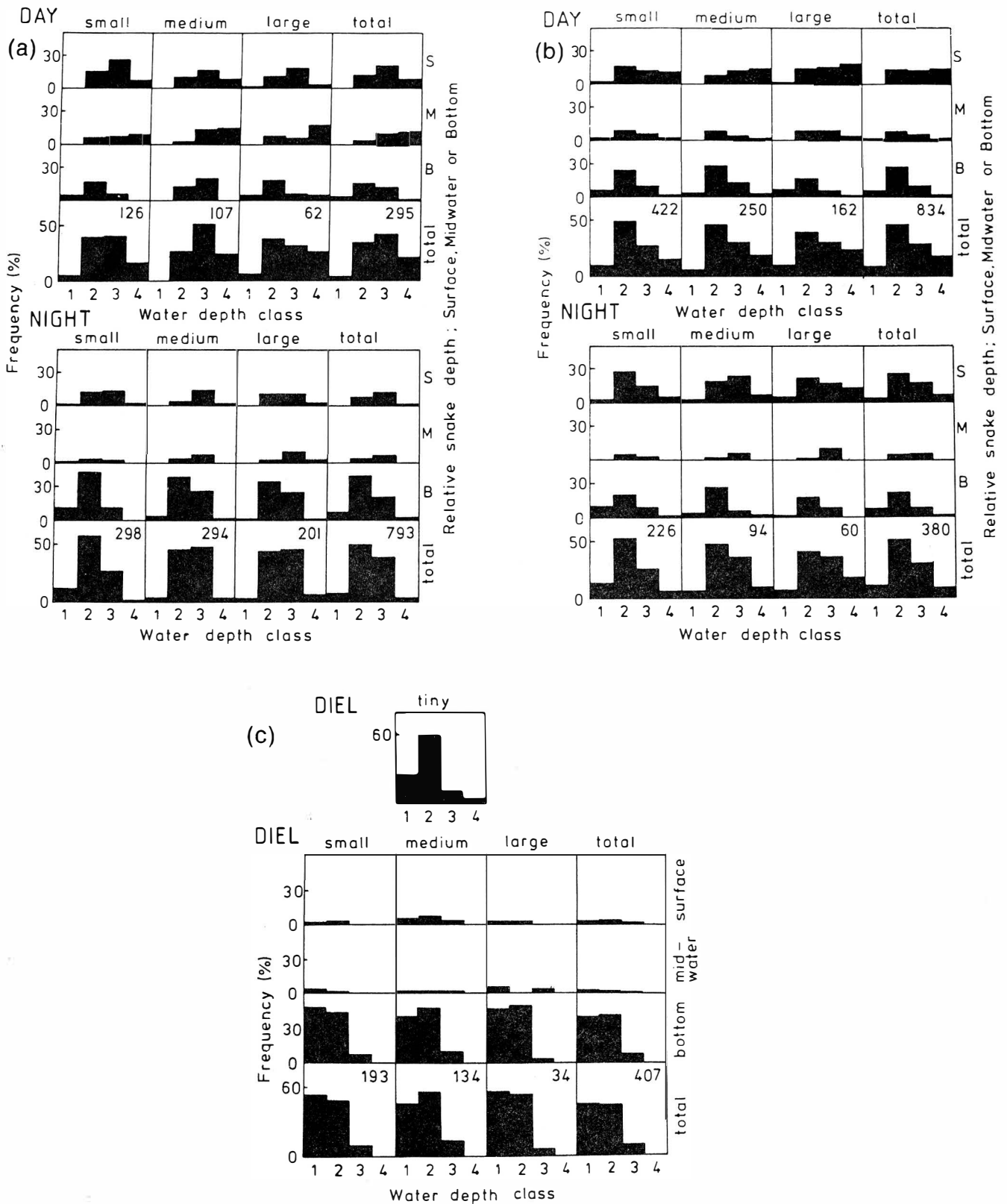


Fig. 1. Positions in the water of (a) sentinel, (b) active and (c) cruising *n. maura* of different sizes, day and night. Water depth classes are 1 = 0-5cm, 2 = 5-15cm, 3 = 15-50cm, 4 = >50cm.

All sizes of SF snakes were seen more often in shallow water at night than in the day; this association between day/night and water depth is significant ($P < 0.05$) for all size classes. Snakes were common in exposed shallow water at night, in situations where they would have been very vulnerable to predation in the day. Water depth and relative snake depth were associated in all sizes of SF snakes during the day; in deeper water snakes were often found in midwater or at the surface, in shallow water they were relatively more frequent on the bottom (Fig. 1a; $P < 0.001$ for S, M and L combined). This may be related to the distribution of fish or to the need for movement to the surface to breathe. Snakes were seen relatively more frequently on the bottom at night than during the day (Fig. 1a; $P < 0.001$ for S, M and L combined). This may be related to the difficulty of seeing fish at night; they would be much more visible when viewed from below, seen in silhouette against the sky.

These distributions may be compared with those of snakes active in the water (Fig. 1b). During the day there was no association between snake size and water depth ($0.5 > P > 0.1$), and there was a significant association between activity type (activity and SF) and water depth for all size classes ($P < 0.001$ for each class). This suggests that most activity during the daytime was not the breathing excursions of SF snakes, but was a different behaviour, probably exploration. In contrast, at night snake size and water depth were associated in active snakes ($P < 0.05$) and the water depth distribution of S and M snakes did not differ significantly between activity and SF ($P < 0.05$). This suggests that much of the activity observed at night was the breathing excursions or small positional changes of SF snakes. If SF snakes at night spent 20 per cent of their time in breathing excursions (as during the day, below), this would account for over half of the snakes seen active at night. Water depth was associated with activity type in L snakes ($P < 0.05$), these being relatively more abundant in deep water when active than when sentinel foraging.

Capture Success. Snakes achieved a low rate of food intake while SF. 48 SF S and M snakes were watched carefully for a total of 921 minutes, excluding breathing, in the day at water temperatures between 25°C and 29°C during July and August 1983. They made 124 strikes at fish (one per 74 minutes), of which only two made contact. One fish was obviously too large to be ingested and leapt from the water, dragging the snake from its perch and escaping immediately. The other was also large (~50% of the snake's weight); it was taken to some floating reeds but escaped after two minutes.

Breathing. SF snakes periodically had to interrupt foraging to breathe, accounting for 175 minutes additional to the 921 minutes actually foraging (19 per cent of the total time). Those near the surface could breathe without leaving their perches, and spent significantly shorter intervals foraging and breathing than those with deeper perches which had to leave them to breathe (Fig. 2). Surface SF snakes used 20 per cent of their time for breathing, deep SF snakes used 17 per cent for breathing and moving to the surface

and back. Most SF snakes were found already foraging; those not noticeably scared away remained for 5-65 (\bar{x} 22.8) minutes before moving away.

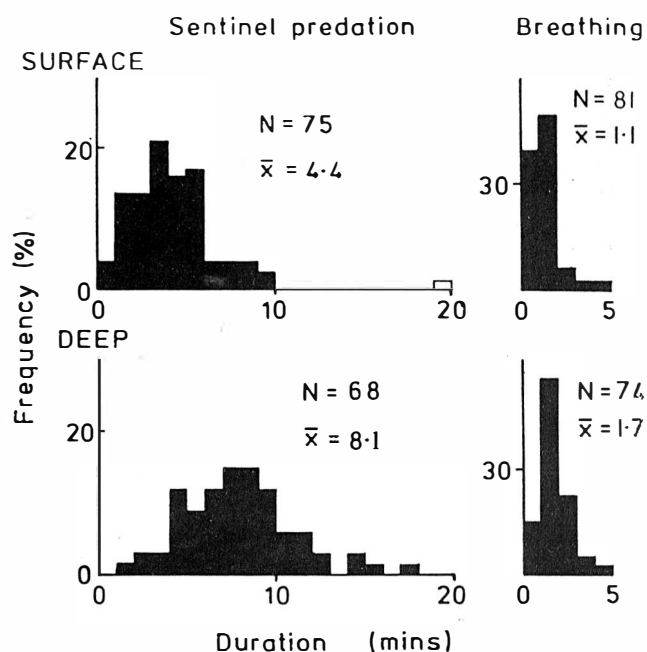


Fig. 2. Duration of periods of SF and breathing. Upper histograms refer to snakes near the surface, lower are for snakes in midwater or on the bottom. These differ significantly in both breathing and foraging intervals (G tests, $P < 0.01$ and $P < 0.001$, respectively).

Sensory control. Four snakes were seen to change from exploratory activity in water to SF after locating fish schools. They crept stealthily towards the fish, and occasional tongue flicks were seen during approach. Two other snakes moving on floating reeds saw fish below them and started SF. During daytime SF the snakes aimed strikes at fish mostly by sight. Contact stimuli were also used; SF snakes also struck at objects which touched them, including non-prey such as beetles and other snakes. At night SF snakes would approach a light, tongue flicking; they could be induced to strike if brushed lightly with fingers.

In laboratory pools (Hailey and Davies, 1986) snakes responded to introduction of fish, or other disturbance, by tongue flicking. Strikes were mostly aimed by sight, but also by contact. Snakes would strike at each other if they made contact when foraging; this was never seen in the absence of fish.

Fishing

This rare but characteristic foraging behaviour was seen five times; three at night and two in the early morning. The snakes swam round in an exaggerated manner, following a figure 8 course, with their jaws open. Fish were present nearby, but the snakes were not pursuing particular individuals or groups.

Cruising foraging (CF)

Tiny snakes did not have any special foraging behaviour, but were found moving about slowly in damp areas and shallow water, and seem to fit Regal's (1978) 'cruising forager' category. Larger snakes were also commonly found moving about slowly, but those which found fish normally reverted to SF, creeping nearer and then waiting for the fish to approach. The exception was where fish were confined in shallow drying pools. Snakes approached these pools flicking their tongues rapidly, and probably detected them by chemoreception; the fishy smell was obvious even to the human nose.

Once in the water snakes moved around after fish, lunging at them and swimming rapidly after them as far as the extent of the water allowed. Following fish about is described as CF; swimming after them is termed 'pursuit'. CF normally took place in shallow pools (Fig. 1c), but was also seen in some larger pools which became anoxic with fish gasping at the surface. Strikes were aimed as in SF, by sight and contact. CF also involved taking dead fish, earthworms and tadpoles, though such foraging was not clearly distinct from feeding during exploratory activity. Worms and tadpoles were the sole prey available to snakes in a polluted part of the river (Hailey, 1984) and no SF was seen there.

Feeding success in drying pools was much greater than that in other pools; 3.19 per cent of 439 snakes from drying pools were handling ingestible prey, compared to 0.66 per cent of 2720 snakes from other pools (G test $P < 0.001$). There was no significant difference between the feeding success of small, medium and large snakes (Table 1); overall 1 per cent of snakes in water (i.e. potentially foraging) were handling useful prey. The act of handling prey had

little effect on the susceptibility of snakes to capture by man. 64 per cent of 45 snakes handling prey were captured, compared to 53 per cent of 4863 snakes not handling prey ($\chi^2 = 1.73$, $P > 0.1$).

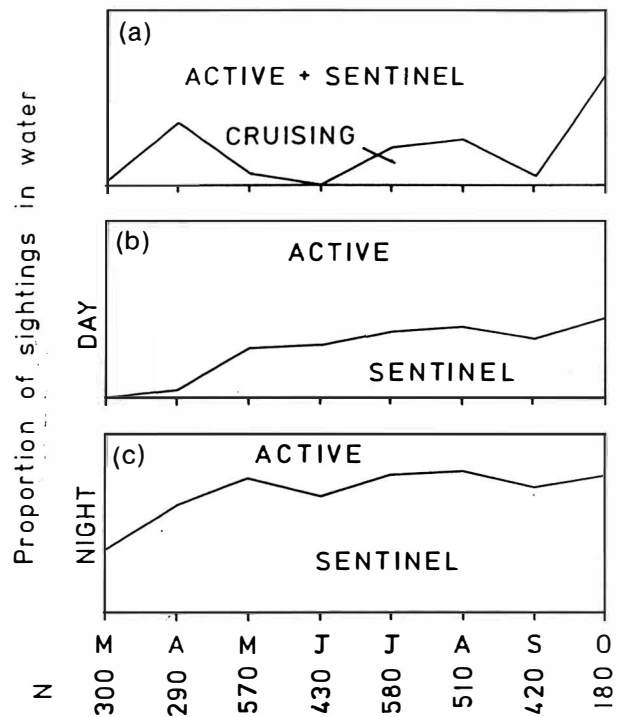


Fig. 3. Variation of activity type of snakes in water with season. (a) shows the number of cruising snakes relative to others in water, (b) and (c) show the relative numbers of active and sentinel snakes, day and night. N shown is for the total sample in the water.

	% with prey (n)			P
	Small	Medium	Large	
Drying pools	1.3 (235)	4.3 (163)	9.8 (41)	>0.1
Other pools	0.71 (1266)	0.57 (880)	0.70 (574)	>0.9
Total	0.80 (1501)	1.15 (1043)	1.14 (615)	0.5

TABLE 1: Proportion of snakes in water (potentially foraging) which were handling ingestible prey. P is for G test comparing the three sizes of snakes.

Prey type	n (n)	measured)	RPW (%) mean (range)	intensity* mean (range)
Earthworms	37	(16)	5.7 (0.5-28)	1.32 (1-3)
<i>R. ridibunda</i> tadpole	9	(6)	7.2 (2.1-13)	1.28 (1-2)
<i>R. ridibunda</i> frog	11	(6)	37 (18-54)	1 (1)
Fish (CF, regurgitated)	129	(95)	9.2 (1.1-55)	1.52 (1-6)
Fish (CF, handled)	15	(10)	33 (6.3-75)	
Fish (SF, regurgitated)	39	(26)	13 (1.0-51)	1.07 (1-2)
Fish (SF, handled)	24	(9)	44 (10-104)	

TABLE 2: Relative prey weight (RPW) of different prey types

* intensity = no of prey in snakes with that prey type.

In addition one leach and two *B. bufo* tadpoles were regurgitated, and five dead fish were seen being handled.

Direction of ingestion	RPW (%)			
	0-5	5-10*	10-15*	>15*
	number of fish			
Head first	35	26	20	24
Tail first	12	2	2	0

TABLE 3: RPW and direction of ingestion of roach

* Combined for G test. $P < 0.005$.

Fig. 3 shows the daily and seasonal pattern of foraging activity. As noted by Hailey, Davies and Pulford (1982), SF is most common at night, activity during the daytime. The seasonal distribution of CF reflects the opportunities for this type of foraging.

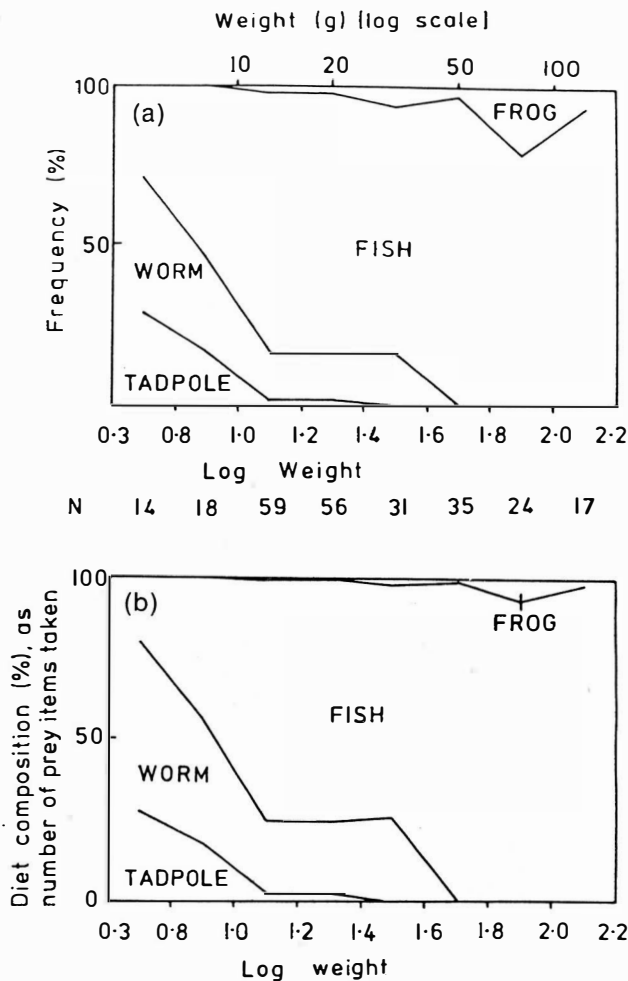


Fig. 4. Variation of diet with snake size. (a) Frequency of prey items, proportional to their energetic contribution, (b) Divided by the mean weight of each prey type, proportional to the number of prey items taken.

DIET

Taxonomic composition

Tiny snakes were found with earthworms and tadpoles (*Rana ridibunda*, the only amphibian in the river Jalon apart from *Bufo bufo*), larger snakes with fish (roach *Rutilus rutilus*, the only fish in the river Jalon) and some frogs (Fig. 4a). The importance of frogs in the diet is overestimated, as seven of the 11 found were discovered by following the characteristic calls they made while being eaten, and were thus much more obvious than the other prey types. Table 2 shows the relative sizes of the different prey types. 87 per cent of all fish were ingested head-first; large fish were more likely to be ingested head first than small fish (Table 3).

Size composition

Within each prey type relative prey weight (RPW = prey weight/snake weight, as a percentage) was independent of snake size (Fig. 5), except for fish captured while cruising in shallow pools, for which RPW was inversely related to snake size (Fig. 5b). There are two possibilities here, either selection of fish by snakes, or a change in the size frequency distribution of fish when pools dried. Large fish died first in the later stages of drying of a pool, so that larger snakes then had to take fish of low RPW. When all types of prey (excluding fish from drying pools) are pooled, RPW increased with snake size (Fig. 6). When these fish are considered as well, there was no significant effect of snake size on RPW (Fig. 6 legend).

Two snakes were found dead with fish lodged in the throat (Fig. 7a), RPW 66 and 69 per cent. About 60 per cent RPW is the largest safe size for roach ingestion (Hailey and Davies, 1986); four snakes were captured handling fish of RPW >60 per cent (Figs. 5c, 7b), and five others were seen with fish clearly well over this size, but were not captured. Eight of these observations were made in daylight, one at night. Oversize fish are not merely suboptimal, they are valueless at best, and at worst involve the snake in direct (choking) or indirect (predation) risks of death. It is therefore interesting that 9/36 fish seen being handled were oversized (though the relative frequency of such large fish will be exaggerated if snakes handle them for a long time before giving up). This has been investigated by Hailey and Davies (1986).

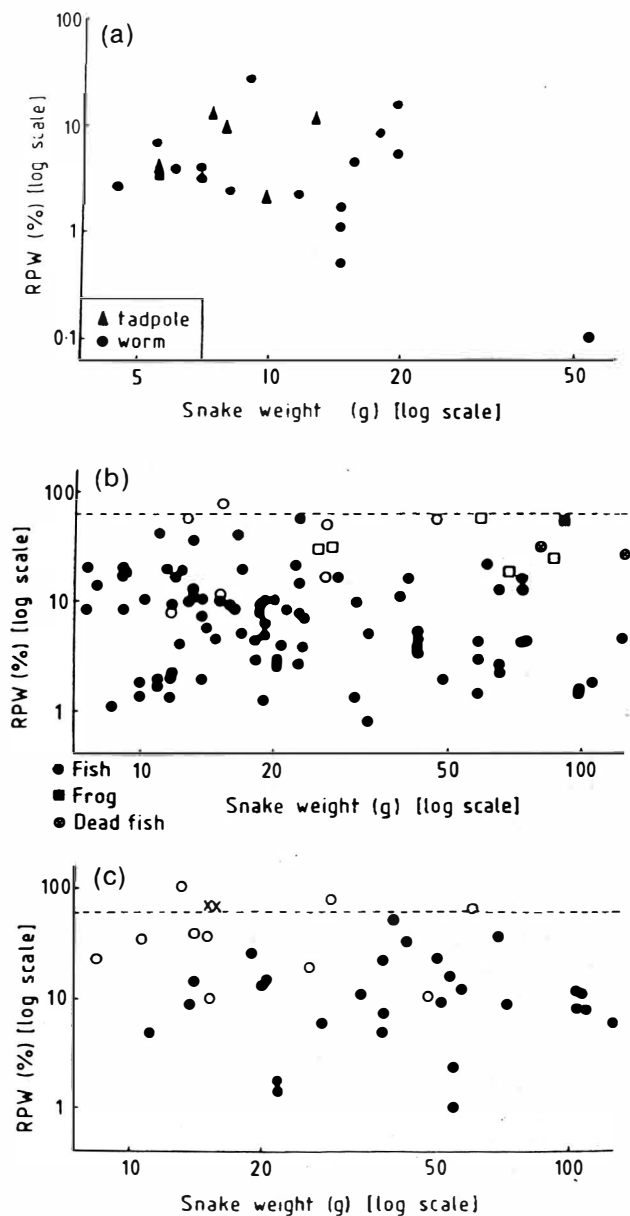


Fig. 5. Variation of relative prey weight with snake size for (a) worms and tadpoles, (b) fish from drying pools, and frogs, (c) fish from other pools. Solid symbols = regurgitated, open = handled. Dashed line shows RPW = 60 per cent. Crosses in (c) are snakes found choked on fish. Slopes of regressions of log RPW on log W do not differ significantly from 0 (t tests) except for regurgitated fish in (b), for which the equation is $\log \text{RPW} (\%) = -0.22 \log W + 1.1$ (t test $P < 0.05$).

Multiple captures

Snakes not found near drying pools had one or two prey items (Table 2). Those from drying pools had up to six fish (Fig. 8a). Such multiple captures gave RPW up to 45 per cent, but mostly below 30 per cent (Fig. 8b). Fish from snakes with only one fish were larger than fish from snakes with more than one fish (Fig. 8c). This suggests that if a snake catches a small fish it is more likely to stay to catch more than if it catches a large one.

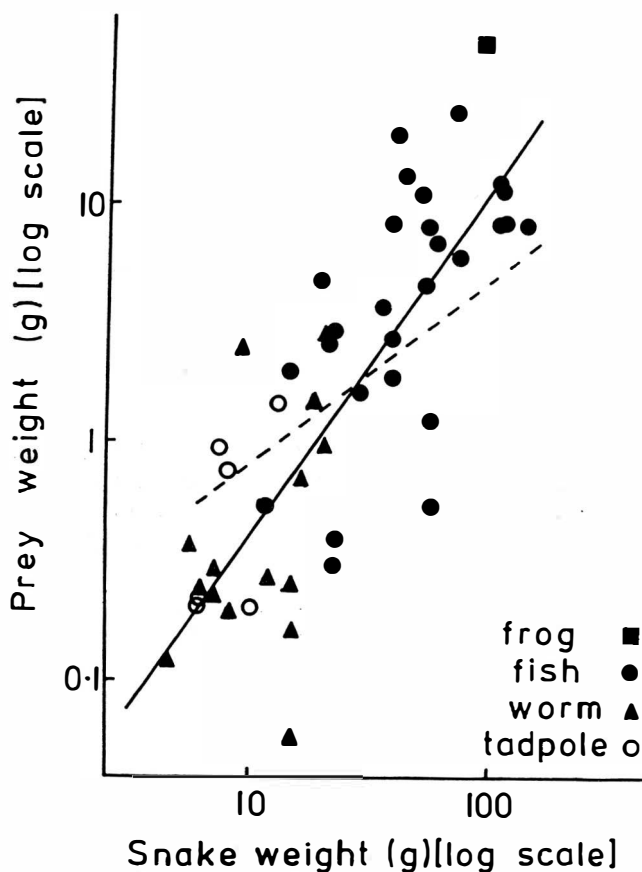


Fig. 6. Variation of prey weight with snake size, prey types combined (except fish from drying pools). The regression fit (solid line) is $\log \text{prey weight} = 1.39 \log \text{snake weight} - 1.7$ (slope differs significantly from 1, t test $P < 0.05$). The dashed line is for fish from drying pools.

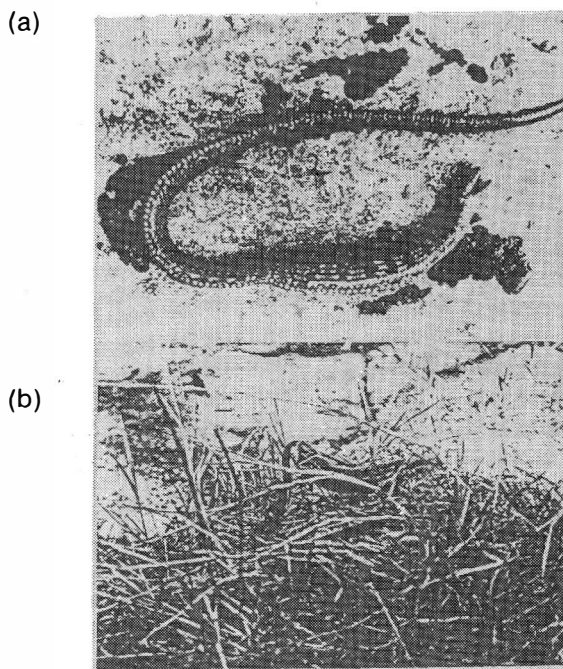


Fig. 7. (a) Snake found choked on fish, RPW = 66%. (b) Snake handling fish too large for it to ingest, RPW = 74%.

DISCUSSION

CHANGE OF DIET WITH SIZE

Changes of diet with size are known in several species of snakes (e.g. Paniagua, 1976, Saint Girons, 1980, Godley, 1981, Mushinsky, Hebrard and Vodopich, 1982). Two factors can explain this pattern in *N. maura*.

1. Very small fish were rarely seen, and were active in midwater (though often at the edge where it was shallow), and thus more difficult to catch than worms and tadpoles. T snakes foraging for worms and tadpoles in shallow puddles and on land would then be less likely to encounter fish by chance, reinforcing the diet change. The fish taken by T snakes were from drying pools, in which all sizes of snakes were found.

2. Earthworms do not grow very large, and are relatively small prey for larger snakes, which would thus have to catch more of them. As an estimate of this effect, encounter rate will be α to speed, and thus to length, whereas energy requirements will be α to metabolic rate, and thus to weight^{0.75} (Hailey and Davies, submitted). A 100g, 80cm snake would thus encounter 5x as many worms as a 29g 16cm snake, but would require 20x the energy.

Frogs were more commonly taken by the largest snakes, a pattern found in *Nerodia erythrogaster* and *N. fasciata* by Mushinsky et al (1982).

DIET COMPOSITION: ENERGY AND NUMBERS

Diet composition may be considered in terms of both the number of individuals eaten and the energetic contribution of different prey types. Where the time which a prey item remains detectable (either seen being handled or found in the stomach) is proportional to its size (Hailey and Davies, 1986) diet composition by frequency of occurrence will be equivalent to composition in terms of the energy composition. To show the diet composition by numbers, frequency of occurrence has to be adjusted by dividing by the relative size of the prey (Fig. 4b). Worms and tadpoles are more, and frogs less, important in terms of numbers compared to energy.

THE PATTERN OF FORAGING

Several aspects and types of foraging behaviour have been described in this paper and in other works on foraging in natricine snakes. This section attempts to integrate them to show the overall pattern of foraging in *N. maura* and other natricines.

Exploratory cruising

Many snakes were seen moving about in water and on land between pools, apparently exploring. This is taken as the starting point of foraging activity, and is termed exploratory cruising. Cruising is here used in the sense of Regal (1978) as a foraging method of slow movement, rather than the restricted sense of Drummond (1979). Different types of foraging behaviour may follow exploratory cruising to suit the prey situation encountered (Fig. 8).

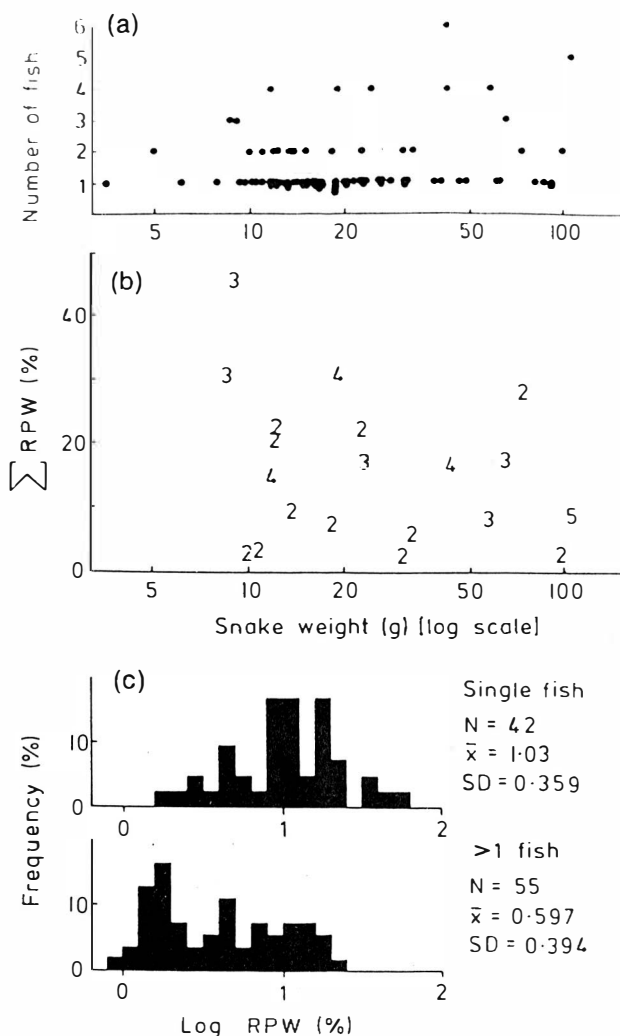


Fig. 8. Multiple fish captures from drying pools. Variation of (a) number of fish per snake with fish, (b) RPW for snakes with >1 fish (number of fish shown), with snake size, (c) Distribution of RPW of fish from snakes with 1 and with >1 fish. The means are significantly different (t test $P < 0.001$).

Slow moving terrestrial prey

Worms are discovered while cruising in moist areas; they were present in soil and under rocks near the river. Chemoreception is used to locate them and other slow moving or cryptic prey. There have been many studies showing the use of aerial chemoreception in the detection of prey, and in the discrimination between different types of prey (Arnold, 1977, 1981, Burghardt, 1968, 1970, 1971, 1975, Czaplicki, 1975, Dix, 1968, Dunbar, 1979, Fuchs and Burghardt, 1971, Gove and Burghardt, 1975, Mushinsky and Lotz, 1980). A differential tongue-flicking response to several prey types was found in T and S *N. maura* (Hailey et al, 1982); worm and tadpole surface extracts produced the greatest response. Sight is not necessary when orienting to ingest prey (Drummond, 1979), but chemoreception is (Halpern and Frumin, 1979).

Active terrestrial prey

Mobile or distant prey on land are detected (refs above) and located (trailing — Kubie and Halpern, 1979) by chemoreception. Once found, the pursuit of active prey is visual (Naulleau, 1964). This activity was not found in *N. maura* in the present study, but may occur in other areas where amphibians are common prey (Arnold and Burton, 1978). Naulleau (1964) describes this behaviour both in *N. maura*, and in *N. natrix* in which it is the usual foraging behaviour (Hailey, 1984). Prey movement may be important in eliciting attack (Brown, 1958, Drummond, 1979).

High density aquatic prey

Exploring snakes may find pools containing trapped fish. These are identified as such by chemoreception. Drummond (1979) found that *Nerodia sipedon* entered small laboratory pools with 'fishy' water but ignored those with clean water, and noted that in the field these snakes by-pass shallow pools without fish but enter those with fish.

Czaplicki and Porter (1974), Porter and Czaplicki (1977) and Drummond (1979) found that sight was important to *Nerodia* catching fish in small pools. *N. maura* crawl after fish schools, striking at fish as they pass close. This is termed cruising, and is similar to exploratory cruising. Contact may initiate striking; this is presumably important at night. After a missed strike the snake may pursue a fish or school. This was only seen where fish movement was restricted by shallow water; in open water fish can outswim snakes (Brown, 1958). Vision is important in pursuit because snakes may swim rapidly and directly after fish for several metres. Drummond (1983) and Drummond and Burghardt (1983) describe the activities of *Thamnophis* engaged in this type of foraging.

Undirected attacks

This category (Drummond, 1979) includes strikes made in the vicinity of prey rather than at one individual or small group. Fishing (Evans, 1942) was observed to be initiated by an unsuccessful strike — fish still in the vicinity are presumably located by contact. In pools with many fish *N. maura* was sometimes seen to make a lunging open-mouthed sweep through the water when in the midst of a fish school. This was interpreted as a strike at the school rather than at a particular fish. There is probably a continuum between this type of strike and fishing.

Diurnal open-mouthed searching has been described in *Nerodia* by Drummond (1979) and Mushinsky and Hebrard (1977). The latter describe the snakes swimming slowly, open-mouthed, in circles in shallow pools shovelling prey with the lower jaw and using the body to trap groups of prey. This appears to be a development of fishing ('combing' — Stoner, 1941) for the purpose of capturing small fish and tadpoles. It was not seen in *N. maura*.

Low density fish

Most pools in the study area contained fish at low density. Exploring snakes probably discover fish by sight and move closer following visual cues. Sentinel foraging (Davies *et al.* 1980, Hailey *et al.* 1982) is then

initiated. This is an extreme sit-and-wait (SW) strategy; the snake strikes from its perch rather than leaving it to rush the prey, the alternative tactic. While this distinction is not important for time and energy budgeting, it may be so for activity physiology. A sentinel predator need have no capacity for rapid locomotion (e.g. boid snakes, chameleons) whereas a rush SW predator would (e.g. *Agama* — Loumbourdis and Hailey, submitted). *N. maura* has retained its capacity for short term activity (which is similar to that of the widely foraging *N. natrix* — Hailey, 1984), probably for other foraging activities and for escape. Strikes are initiated as a result of visual and tactile cues. At night SF snakes on the bottom would be able to see fish silhouetted against the sky as they swam overhead.

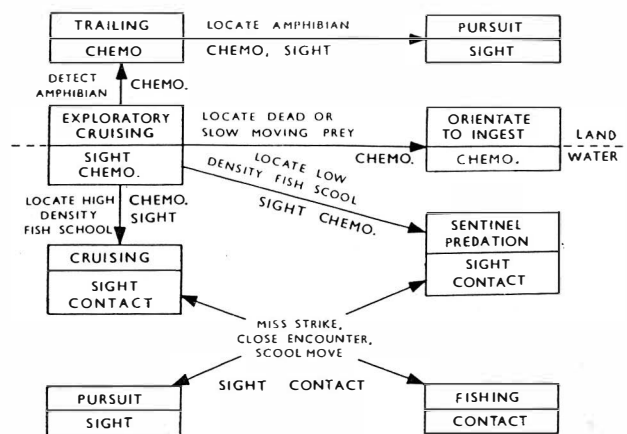


Fig. 9. Diagram of relationships between the different types of foraging behaviour in *N. maura* and other natricine snakes. Boxes are types of foraging and the senses used. Arrows show the course of activity resulting from encounters with different prey, and the senses used.

ACKNOWLEDGEMENTS

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PREY — SIZE AND PARASITE RELATIONSHIPS IN THE COMMON TOAD *BUFO BUFO*

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ABSTRACT

The gut contents of 188 Common Toads from a range of sizes were examined and 1898 prey items from 22 prey groups recorded. The use of combined gut contents (stomach and hind gut) is discussed in relation to the greater numbers of prey found in the stomach and the differences in the proportions of prey in the different parts of the gut; hind gut contents having a larger proportion of hard bodied prey. Acari, adult Coleoptera, Formicidae and Collembola were found to be the most abundant prey groups, although differences were recorded with toad size. A positive linear relationship between prey and toad size was found. A nematode gut parasite (*Cosmocerca ornata*) was recorded and the degree of infection and the percentage incidence were found to increase with toad size.

INTRODUCTION

Common Toads (*Bufo bufo*) are mainly nocturnal, opportunistic feeders, although they will feed during the day. A wide variety of prey have been noted (Smith, 1954; Frazer, 1983) and although a number of workers (including Cott, 1940; Lescure, 1964; Mazure, 1966; Mathias, 1971) have investigated the food of the Common Toad, all have concentrated on adults. The present study examines the differences between the prey of toads of different sizes, especially juveniles and sub-adults.

METHODS

The animals were captured during an investigation into the surface active Coleoptera of two areas in Cheshire (Wheater, 1984). The sites used were an area of *Phragmites* adjacent to Tabley Mere at Tabley Hall estate (grid reference SJ 727769) and a marshy site at Abbots Moss Hall (grid reference SJ 593681). More detailed descriptions of the sites have already been presented (Wheater, 1985).

At each site the animals were caught in 15 large (13.5cm deep and 9cm diameter) plastic pitfall traps laid in grids 5m by 3m. These contained 5 per cent formalin solution and remained in situ for a year, being examined at fortnightly intervals. Toads were, therefore, trapped accidentally and this paper is an attempt to examine prey differences in animals fortuitously caught. In this study 188 toads of a range of sizes were used. They were sorted into four size groups, based on snout to vent length (size I, less than 20mm; size II, between 20 and 30mm; size III, between 30 and 40mm; size IV, greater than 40mm). Few large individuals were captured, the largest being three gravid females in excess of 60mm in length. This was probably due to the size of the traps, larger animals being able either to avoid or escape from the traps. All the specimens are lodged in the Manchester Museum (catalogue numbers C975-C1001, C1014 and C1016).

The toads were dissected and the entire gut removed. This was then slit longitudinally and the contents removed. The gut contents were examined and the prey identified as far as possible. The features used in identification varied between the groups and are indicated in Table 1. These were based on the system used by Tatner (1983). Prey items were quantified, mainly on the numbers of heads or jaws present.

Prey	Structures
Isopoda	scutes, heads
Acari	usually the whole animal
Opiliones	heads, legs
Araneae	heads, palps
Myriapoda	rings, heads
Collembola	usually the whole animal
Orthoptera	heads
Hemiptera	heads
Coleoptera (adults)	heads, jaws, elytra
Coleoptera (larvae)	heads, integument, legs
Lepidoptera (larvae)	jaws, integument, prolegs
Diptera (adults)	heads, wings
Diptera (larvae)	integument
Formicidae	heads, jaws
Mollusca	shells

TABLE 1: Structures used in the identification of prey

The stomach contents were examined separately from those of the intestine and rectum.

The prey species were divided into groups based on size. This was achieved by ranking each prey type during gut content sorting. Whilst it is accepted that most taxa could overlap the size groupings, in practice this was not the case. The following scheme was used.

- Group 1 — very small
Acari, Collembola, Pseudoscorpiones.
- Group 2 — small
Formicidae, Aphididae, Diptera (adults),
Ichneumonidae, Diptera (larvae).
- Group 3 — medium
Other Hemiptera, Orthoptera, Araneae,
Opiliones, Dermaptera, Coleoptera
(larvae), Coleoptera (adults), Staphylinidae.
- Group 4 — large
Carabidae, Neuroptera, Mollusca,
Lepidoptera (larvae), Isopoda, Myriapoda.

RESULTS

It can be seen from Table 2 that the most numerous prey are the Acari, Collembola, adult Coleoptera and Formicidae. Many more prey items were found in the stomach than in the hind gut and there was a significant difference between the proportions of species from the two areas of the gut; this shows a greater proportion of hard bodied animals in the hind gut than in the stomach, with a corresponding decrease in soft bodied animals. A number of workers have used the combined gut contents as a measure of the prey type; however, in view of these results, it appears that this would bias the prey spectrum towards those animals having hard exoskeletons and therefore recognisable fragments in the hind gut. In further analysis in this study stomach contents alone were used.

The array of prey species was found to differ between toad size groups (Table 3) and the differences were statistically significant ($X^2_{6,3} = 557.4$, $p < 0.0001$). Spearman's rank correlation coefficients, between

prey numbers and toad size, were calculated. Of the 22 prey groups recognised, six were more numerous in large toads (Isopoda, Opiliones, Araneae, Myriapoda, Carabidae and Mollusca) and two were more numerous in smaller toads (Acari and Collembola). It seems that it is larger prey types that are more numerous in larger toads, whereas the smaller prey are favoured by small toads.

This impression is confirmed when the prey are aggregated into size categories (Table 4). The different sizes of toads clearly take prey of significantly different sizes ($X^2_9 = 347.95$, $p < 0.0001$).

The pitfall traps were primarily intended to catch invertebrates, and the numbers so caught were compared, using Chi-squared tests, with those found in the toads' guts. In all size groups of toads, there was a highly significant difference ($p < 0.0001$) between the contents of pitfall traps and the guts of different sized toads (Fig. 1). This is also the case with total prey capture and may be due to aspects of toad foraging behaviour. It is possible that the Araneae are under represented in the toads' guts because of their diurnal, ground-running habit, toads tending to be nocturnal hunters. Collembola are also under-represented in the prey and may be too small or too fast for toads to catch. The mechanism of pitfall trapping may also have an effect. Adult Diptera are possibly attracted to formalin (Wheater, 1984) and if so will be found in greater numbers in the pitfall traps. Other prey (Acari, adult Coleoptera, Formicidae and Diptera larvae) were found to be more numerous in toad gut contents than in pitfall traps. It may be that these groups are selected by the toads.

In Group 1 the most abundant prey were Acari (45.8 per cent), Collembola (16.09 per cent) and Formicidae (10.68 per cent).

Prey items	Stomach contents		Hind gut contents	
	No. of items	per cent of items	No. of items	per cent of items
Acari	590	31.1	218	51.9
Other Chelicerata	173	9.1	2	0.5
Collembola	236	12.4	5	1.2
Coleoptera (adults)	281	14.8	99	23.6
Coleoptera (larvae)	33	1.7	1	0.2
Diptera (adults)	66	3.5	5	1.2
Diptera (larvae)	79	4.2	4	1.0
Formicidae	271	14.3	78	18.6
Other Insecta	61	3.2	4	1.0
Mollusca	21	1.1	1	0.2
Other	87	4.6	3	0.7
Total	1898		420	
Difference between stomach and hind gut	$\chi^2 = 182.22$ 10		$p < 0.00001$	

TABLE 2. Comparison of stomach and hind gut contents

In Group 2 a similar situation was found: Acari (24.67 per cent), Formicidae (19.08 per cent) and Collembola (11.3 per cent). Total adult Coleoptera were also found in high numbers (17.13 per cent).

In Group 3, Staphylinidae (14.97 per cent), Acari (14.4 per cent), Formicidae (14.43 per cent) and Araneae (11.23 per cent) were found in greatest

numbers. There was also an increase in total adult Coleoptera (24.06 per cent).

In Group IV there were more Myriapoda (19.82 per cent), Araneae (13.51 per cent), Carabidae (11.71 per cent) and Opiliones (11.71 per cent). Total adult Coleoptera comprised 22.52 per cent of the prey.

Prey	Toad size				Correlation	
	I	II	III	IV	rs	p
Isopoda	0	0.34	0.40	0.47	0.341	0.001
Acari	4.24	3.03	1.35	0.24	-0.369	0.001
Opiliones	0.01	0.39	0.25	0.76	0.245	0.001
Pseudoscorpiones	0.01	0	0	0	-0.075	0.304
Araneae	0.44	0.81	1.05	0.88	0.159	0.030
Myriapoda	0.06	0.19	0.40	1.29	0.324	0.001
Collembola	1.49	1.39	0.80	0.12	-0.245	0.001
Orthoptera	0.02	0.07	0.05	0.06	0.082	0.264
Dermoptera	0	0	0	0.06	0.124	0.091
Aphidoidea	0.07	0.13	0.10	0	0.010	0.894
Other Hemiptera	0.01	0.24	0	0	0.040	0.584
Carabidae	0.12	0.43	0.40	0.76	0.224	0.002
Staphylinidae	0.44	1.06	1.40	0.41	0.105	0.152
Other Coleoptera	0.27	0.61	0.41	0.29	0.052	0.478
Larval Coleoptera	0.12	0.27	0.25	0	-0.003	0.965
Larval Lepidoptera	0.01	0.01	0.10	0.18	0.139	0.059
Diptera	0.27	0.42	0.50	0.29	0.069	0.347
Larval Diptera	0.58	0.31	0.25	0.24	0.021	0.771
Neuroptera	0	0	0.05	0	0.097	0.185
Formicidae	0.99	2.34	1.35	0.24	-0.017	0.815
Ichneumonidae	0.06	0	0.10	0.12	0.049	0.508
Mollusca	0.02	0.22	0.10	0.12	0.164	0.025
Mean items/toad	9.25	12.28	9.35	6.53		
Number of toads	84	67	20	17		
Differences between toad sizes	$\chi^2 = 557.4$ 63		$p < 0.00001$			

TABLE 3: Prey in toads of different sizes. The spectrum of prey groups found in the different toad size groups was compared using a Chi-squared test. The figures in the body of the table show the mean numbers of each prey group per toad. Spearman's ranked correlation coefficients were used to identify linear relationships between toad size and prey numbers.

Prey size groups	Toad size groups							
	I		II		III		IV	
	No.	%	No.	%	No.	%	No.	%
1	482	62	296	36	43	23	6	6
2	116	21	215	26	46	25	15	14
3	101	13	213	26	64	34	42	38
4	28	4	99	12	34	18	48	43
Total	777		823		187		111	
Differences between toad size groups	$\chi^2 = 347.95, p < 0.00001$ 9							

TABLE 4: Comparison of prey sizes found in different sizes toads

	Toad size groups				Total
	I	II	III	IV	
Total toads	39	38	12	11	100
Number of infected toads	2	1	3	4	10
Percentage occurrence	5	3	25	36	10
Number of nematodes per host	2	1	5	36	44
Mean nematodes per infected host	1	1	1.67	9	4.4
Standard deviation	0	0	0.94	7.65	6.15

TABLE 5: Nematode infection: incidence and mean numbers per host for different toad sizes.

PARASITES

A non-food item was also recorded: specimens of the nematode *Cosmocerca ornata* were found in the small intestines of some of the toads. A mean of 4.4 per host and an incidence of 10 per cent was observed from the Abbots Moss site. Cox (1971) provides results from Slapton Ley in South Devon showing an incidence of 40 per cent and 3.8 parasites per host. He also records a similar incidence from Skomer. It seems, therefore, that the results from this study are relatively low. However, it can be seen (Table 5) that the incidence and numbers of parasites increase with size group, and therefore age, of the host. Although he doesn't mention the fact, it seems likely that Cox's results are based on adult animals rather than a range of ages. As has previously been mentioned, the animals caught during the current study range from juveniles to adults but include few larger individuals. The results for the largest size range (Table 5) show an incidence of 36.36 per cent and are, therefore, more in line with Cox's results. The mean number of parasites per host (9) is higher here than in the 1971 study (3.8). This may be the result of the low numbers of animals caught (11) and the high level of infestation in two of these (the standard deviation is 7.65).

Specimens collected from Tabley Hall contained no nematodes and this population may be completely free of the parasite.

DISCUSSION

Cott (1940), investigating toads from Land's End, found the most frequent prey group to be Formicidae (40 per cent of all prey items), followed by Coleoptera (15 per cent) and Isopoda (14 per cent). Lescure (1964) examined the guts of 50 common toads from various areas in France and Mazure (1966) worked on toad feeding in two areas in Poland. Both workers recorded Formicidae (Lescure, 62.9 per cent; Mazure, 36.0 per cent and 76.6 per cent) and Coleoptera (Lescure, 14.3 per cent; Mazure, 55.2 per cent and 17.9 per cent) to be the most important prey species. Mathias (1971) had similar results from Ainsdale (Formicidae, 69 per cent and Coleoptera, 12.36 per cent).

During the present study, Acari were found to be the most numerous prey (31.1 per cent) with adult Coleoptera (14.8 per cent), Formicidae (14.3 per cent)

and Collembola (12.4 per cent) next. Presumably the increased representation of Collembola and Acari is due to the smaller sizes of toads examined during this study, compared to those investigated by other workers.

Differences in the abundances of prey groups can be seen between toads of different sizes, and it appears that while toads consume animals from a number of groups, they do select their prey to a certain extent. Although large prey items may have more nutritional value than smaller ones, toads of different sizes have different preferred prey sizes. The range of prey types does not seem to vary much with toad size, however the relative proportions of each group in the diet is size dependent.

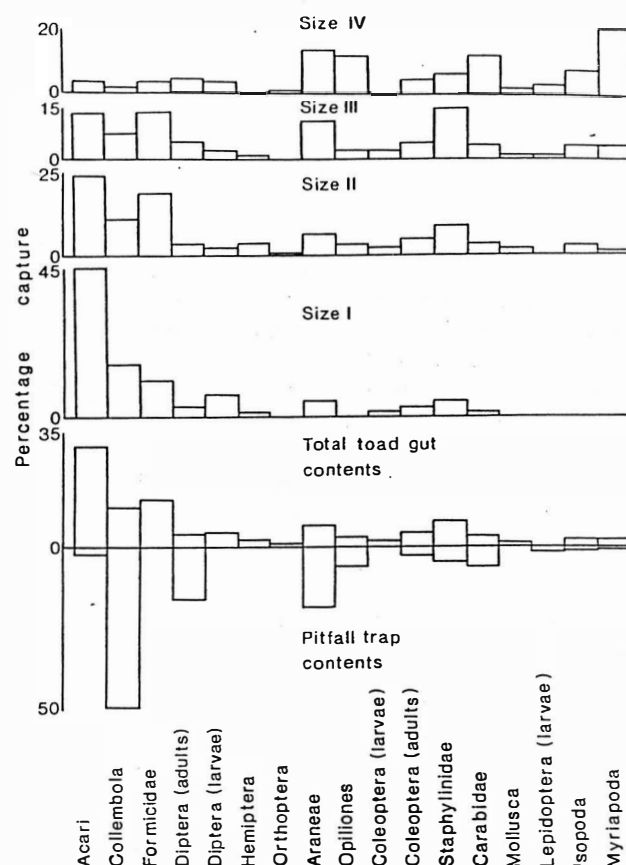


Fig. 1 Comparisons of invertebrate numbers found in the gut contents of different sized toads with those caught in pitfall traps. All are expressed as percentages of the total captures.

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MORPHOMETRY IN THE CHELID TURTLE, *PLATEMYS PLATYCEPHALA*

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ABSTRACT

A study of growth of the shell and its scutes was conducted on 121 *Platemys platycephala* (Testudines: Chelidae). Straight-line carapace length, width and height increase at approximately the same rate as the straight-line plastron length, and are highly correlated to plastron length. Similar trends were noted for increases in bridge length and the width of both the anterior and posterior plastral lobes in relation to plastron length. Unequal growth rates occur in the vertebral scutes which may be correlated with development of carapacial curvature. The femoral scute grows faster than the other six plastral scutes. Development of the middorsal groove, plastral concavity in males, and loss of the juvenile scute rugosities are also discussed.

INTRODUCTION

The relative growth of a part in relation to the entire organism, has been studied in various turtles. These studies have compared either changes in the mass or weight of the turtle with growth of the shell, or the growth of the shell scutes or other body parts in relation to increases in shell length. Cryptodiran turtles in the families Chelydridae (Lagler and Applegate, 1943; Mosimann and Bider, 1960), Kinosternidae (Mosimann, 1956, 1958; Hulse, 1976), Emydidae (Mosimann, 1958; Jolicoeur and Mosimann,

1960; Graham, 1971; Brown, 1971; Rouault and Blanc, 1978; Meek, 1982), and Testudinidae (Grubb, 1971; Bourn and Coe, 1978; Jackson, 1978, 1980; Hirth and Abdel Latif, 1981; Meek, 1982) have been previously studied. Pritchard and Trebbau (1984) summarized what little growth data have been published on South American pleurodirans, but until now no serious study has been reported. We here report the results of such a study on the neotropical chelid turtle, *Platemys platycephala*.

METHODS

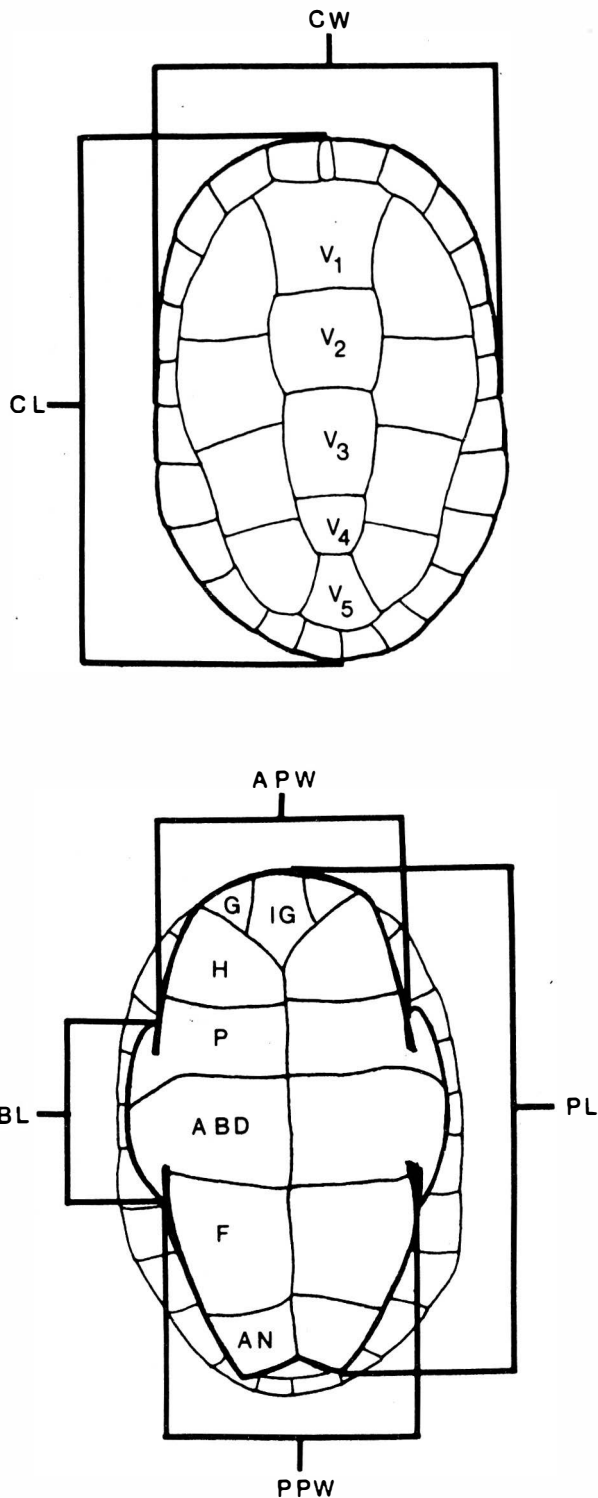


Fig. 1 Shell characteristics selected for measurement; see text for explanation of abbreviations. Carapace height (CH) is not shown, but was measured from the dorsal surface of the carapace to the ventral surface of the plastron at the level of the seam separating vertebral scutes 2 and 3. Drawings adapted from Pritchard and Trebbau (1984).

One hundred and twenty-one preserved *Platemys platycephala* were examined (Ernst, 1984). Each specimen was sexed, and straight-line measurements were taken with dial calipers (accurate to 0.1mm) of the greatest carapace length (CL), carapace width (CW), and carapace height (CH) at the level of the seam between vertebrals 2 and 3, the greatest plastron length (PL), greatest width of the anterior plastral lobe (APW), greatest width of the posterior plastral lobe (PPW), greatest bridge length (BL), greatest width and length of all five vertebral scutes, and the medial seam length (as medial length of the intergular scute) of all plastral scutes (Fig. 1). Scute and bone designations used are those of Zangerl (1969).

All data were entered into a computer, and statistical tests and procedures, including regression analysis and correlation were performed using the Minitab computer package (Ryan, *et al*, 1982). All variables were tested and found to be normally distributed. Regression equations were calculated for best-fit using the method of least squares. In all relationships plastron length (PL) was used as the independent variable due to its relatively straight growth, as a straight-line carapace measurement includes much hidden growth masked in its curvature (Ernst, 1977). Mosimann (1956) has noted that there is no independent variable in the turtle's shell, but it is assumed, for example, that the lengths of the plastral scutes are more dependent upon the length of the plastron than the converse.

Data in several morphometric studies have been first converted to logarithms (Lagler and Applegate, 1943; Graham, 1971; Meek, 1981), but not in others (Mosimann, 1956; Brown, 1971; Hulse, 1976; Rouault and Blanc, 1978). According to Bailey (1959), if the relationship is a straight line and not curved, the use of logarithms is not necessary. Regional plots of our data clearly showed their relationships to be linear, and so logarithmic conversions were not used.

RESULTS AND DISCUSSION

Fig. 2 illustrates the relationships of growth in carapace length, width and height to plastron length. Pearson's correlation coefficients (r) for the three variables show their growth to be highly correlated with lengthening of the plastron ($P < 0.001$). As expected, the carapace had the greatest relative rate of growth, as it lengthened at almost the same rate as the plastron. *Platemys platycephala* has a flattened carapace, and this is indicated by the slightly greater growth rate in width than in height. No significant difference in shell lengths occurs in *P. platycephala* (Ernst, 1984), and growth in shell proportions is almost constant, although overall growth slows with age, as it does in other turtles. The smallest juvenile examined was 46.4mm in carapace length, while the largest adult measured was 168.1mm.

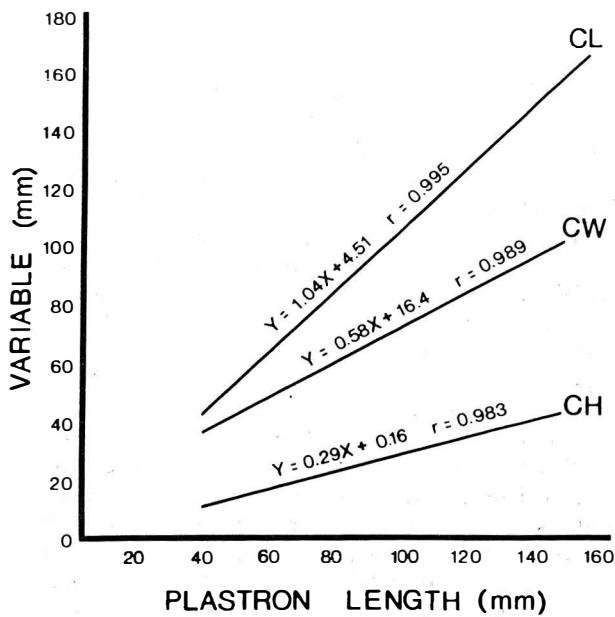


Fig. 2 Relationships of carapace length (CL), carapace width (CW), and carapace height (CH) to plastron length (PL) in *Platemyis platycephala*, N = 121.

Shells of *Platemyis platycephala* exhibit a well-developed middorsal groove in adults extending from the posterior portion of the first vertebral scute to the anterior portion of the fifth vertebral scute. However, this groove is poorly developed in hatchlings. As the carapace lengthens, increases in height are greatest in a pair of longitudinal keels that lie along the dorsal portions of the pleural scutes and lateral portions of each vertebral scute and the underlying costal bones.

The midportion of the five vertebral scutes does not increase in height at as fast a rate as do these keels, resulting in the lower middorsal groove. *Platemyis platycephala* usually lacks neural bones, and middorsal growth is achieved by increases in width of the underlying costal bones which meet at the carapacial midline.

The vertebral scutes increase in length at different rates (Table 1). All five had a greater width to length ratio in hatchlings. The first remains broader than long throughout the life of *Platemyis platycephala*, but the width to length ratio seems to increase with age. Vertebrals two to four show a steady growth in length as opposed to width; the third eventually becomes more long than it is wide (width/length < 1.00). This also occurred in the fourth vertebral of 17 (25.4 per cent) of 67 *P. platycephala* over 120mm carapace length. Vertebral five showed the most variation in proportional growth; while that of most specimens remained broader than long, 12 (17.9 per cent) of 67 turtles over 120mm had this vertebral longer than broad. As in other species of turtles, the carapace of this chelid becomes slightly depressed both anteriorly and posteriorly with age and some carapacial growth is masked in the development of this curvature. Vertebrals two to four, and especially three, cover that area of the carapace not greatly involved in this progressive curvature, and perhaps their greater increases in length versus width reflect this as opposed to those of the first and fifth vertebrals which are directly involved in the curvature. It is interesting that the third vertebral should lengthen faster than the other four, since most theories on scute growth are based on the premise that all scutes grow at equal rates and retain the hatchling proportionality throughout life (Sergeev, 1937). Obviously, this is not always true.

Carapace Length	N	Vertebrals														
		One			Two			Three			Four			Five		
		L	W	W/L	L	W	W/L	L	W	W/L	L	W	W/L	L	W	W/L
40 —	1	12.0	13.7	1.14	8.2	14.1	1.72	8.3	12.7	1.53	5.6	9.0	1.61	7.3	7.7	1.05
50 —	8	14.8	17.4	1.18	9.5	18.2	1.91	9.3	15.9	1.70	7.4	10.4	1.41	8.0	8.5	1.06
60 —	20	15.9	19.3	1.22	10.5	20.1	1.84	10.5	17.2	1.64	8.7	11.7	1.35	9.7	9.8	1.01
70 —	3	19.0	21.3	1.15	13.4	20.0	1.49	12.4	17.5	1.41	10.3	13.6	1.32	11.5	12.1	1.05
80 —	8	19.8	25.0	1.25	15.4	23.4	1.99	15.1	19.9	1.32	13.8	14.6	1.05	13.5	16.3	1.20
90 —	8	22.3	26.9	1.22	16.6	22.7	1.37	16.6	20.2	1.22	12.5	14.9	1.19	14.7	17.3	1.17
100 —	2	23.6	30.7	1.31	17.9	25.6	1.43	18.3	21.4	1.17	14.2	15.8	1.11	14.2	16.4	1.15
110 —	4	24.4	31.0	1.27	19.5	25.5	1.31	22.1	22.5	1.02	17.4	17.3	0.99	20.0	24.3	1.21
120 —	15	27.1	33.7	1.24	22.5	27.2	1.21	24.5	24.4	0.99	17.5	19.1	1.09	21.1	23.3	1.10
130 —	13	28.8	35.4	1.23	23.1	27.1	1.17	28.0	24.7	0.88	17.4	20.1	1.15	23.2	24.4	1.05
140 —	19	30.2	38.2	1.26	25.3	27.8	1.10	29.7	25.3	0.85	21.2	21.1	0.99	30.1	27.2	0.90
150 —	13	30.6	40.2	1.31	29.9	30.6	1.10	30.6	27.1	0.88	21.3	21.9	1.02	28.8	30.2	1.05
160 —	7	33.8	43.9	1.30	29.8	30.2	1.01	29.2	28.5	0.98	23.4	23.8	1.02	33.1	34.0	1.03

TABLE 1: Proportional changes of vertebral scutes in *Platemyis platycephala*; all measurements in mm.

Upon emerging from the egg, the carapacial scutes of *P. platycephala* are covered with small rounded rugosities. These start to disappear (possibly due to abrasion) at about 100mm carapace length, but may still be present in 120mm individuals (2/12 = 16.7 per cent).

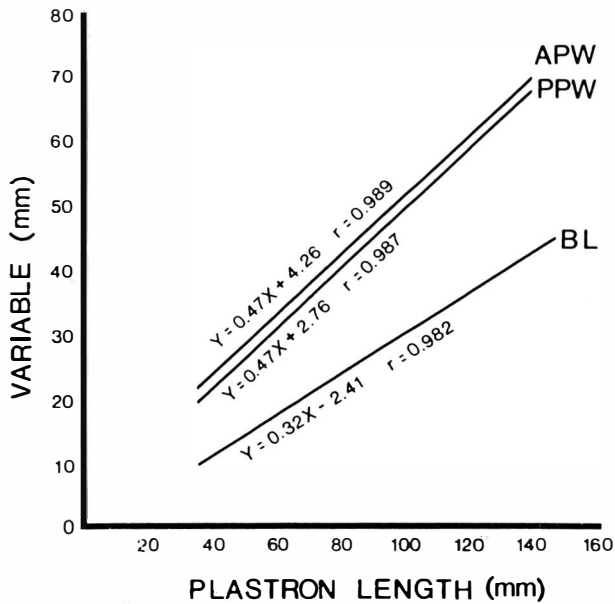


Fig. 3 Relationships of the width of the anterior plastral lobe (APW), width of the posterior plastral lobe (PPW), and bridge length (BL) to plastron length (PL) in *Platemyis platycephala*, N = 121.

Fig. 3 illustrates the relationships of growth in length of the bridge, and growth in width of the anterior and posterior plastral lobes in comparison to plastron length. Growth in these three variables was highly correlated ($p < 0.001$) with plastron length, and all three grew at approximately the same rate as did the

Variable	Plastron
IGL	$Y = 0.14X + 6.34$ $r = 0.89$
GL	$Y = 0.10X + 2.98$ $r = 0.93$
HL	$Y = 0.11X - 0.57$ $r = 0.88$
PECT	$Y = 0.11X - 0.29$ $r = 0.89$
ABD	$Y = 0.21X - 1.46$ $r = 0.97$
FEM	$Y = 0.22X - 3.07$ $r = 0.98$
ANL	$Y = 0.12X + 2.05$ $r = 0.92$

TABLE 2: Relationship between plastron length and plastral scutes in *Platemyis platycephala*. IGL = intergular length; GL = gular length; HL = humeral length; PECT = pectoral length; ABD = abdominal length; FEM = femoral length; ANL = anal length. Correlation coefficients are all significant ($p < 0.0001$).

plastron. This is especially true of the increases in width of the two plastral lobes, which had almost identical growth rates. In juvenile *P. platycephala*, the posterior plastral lobe is usually slightly narrower than the anterior lobe, and this relationship remains nearly constant with plastron growth. As in some other species of turtles, the anterior plastral lobe becomes slightly recurved with age in *P. platycephala*. This upturning is first noticeable in both sexes at about 115mm plastron length. Pritchard and Trebbau (1984) reported that male *P. platycephala* also have a slight but consistent difference in the shape of the posterior projections of the anal scutes, which curve dorsal in adult females.

Plastron Length	N	Mean Length						
		IGL	GL	HL	PECT	ABD	FEM	ANL
30 —	1	8.1	4.8	4.7	3.9	7.6	6.6	3.4
40 —	5	12.3	6.8	4.7	4.7	9.5	8.0	6.9
50 —	18	13.7	8.1	5.4	5.8	10.4	9.5	8.0
60 —	8	15.8	9.4	5.9	6.6	11.8	10.7	9.4
70 —	8	18.1	10.3	6.9	7.8	15.2	13.3	11.4
80 —	8	19.5	11.6	8.9	8.9	16.4	15.8	13.1
90 —	3	20.5	11.6	9.8	8.9	17.9	17.8	14.2
100 —	2	23.4	13.9	10.3	11.3	21.5	22.5	13.2
110 —	12	23.2	14.4	11.0	12.1	21.6	21.8	16.7
120 —	12	24.4	15.0	12.7	14.3	23.5	24.3	16.9
130 —	27	26.5	15.2	14.1	14.7	27.1	27.6	18.2
140 —	14	28.1	17.1	15.1	14.2	30.4	29.7	19.0
150 —	3	28.4	16.8	15.2	15.7	33.6	30.4	22.2

TABLE 3: Changes in length of plastral scutes in *Platemyis platycephala*; all measurements in mm.

Adult male *P. platycephala* have concave plastrons, but adult females retain the flat juvenile plastron. The male concavity is first noticeable at about 114mm plastron length, and this probably indicates that male maturation occurs at a plastron length of 110-120mm.

Tables 2-3 show the changes in length of the seven plastral scutes with increasing plastron length. All increased at a relatively steady rate in comparison with plastron growth, but the femoral scute grew at a faster rate than the other six. This can best be seen by comparing its length in any size class with those of the abdominal and intergular scutes. In the smaller juvenile size classes, both the abdominal and intergular were longer than the femoral, but the femoral became longer than the abdominal in the 100-109mm size class, and it finally passed the intergular in the 130-139mm size class. Perhaps this relative lengthening of the femoral has some reproductive significance.

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SELECTION OF PREY FROM GROUPS: WATER SNAKES AND FISH

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ABSTRACT

This paper investigates the selection, ingestion and digestion of different sized goldfish by viperine water snakes *Natrix maura*. A previous study had suggested that sentinel foraging *N. maura* preferentially select medium sized fish to give the maximum rate of energy intake during ingestion. It was however found that snakes preferentially struck at the largest fish available in the range 1-20 per cent relative prey weight, even though these fish gave no advantage in ease of capture or rate of energy intake during ingestion or digestion. The advantage of this selection is shown to result from the schooling behaviour of fish and the low rates of capture during sentinel foraging. It was confirmed that snakes capture and attempt to ingest fish too large for them. A large fish provides an energy supply large in relation to the snake's requirements (covering about 60 days maintenance) compared to the small cost of handling before rejection. It would thus be better to handle all fish unless much too large, rather than rejecting those closer to the maximum and possibly making a mistake.

INTRODUCTION

Prey in groups may be difficult to catch for several reasons (Bertrum, 1978). Their vigilance and ability to defend themselves or confuse the predator may be greater, and if only one of them can be captured at a time then the rest can escape while this is being handled. This paper discusses how viperine water snakes, *Natrix maura*, can maximise their energy intake while catching fish from groups. The snakes were studied during sentinel sit-and-wait foraging, their usual method of catching fish: the repertoire of feeding behaviour used by this species is described by Hailey and Davies (1986). In the area where the snakes were collected there was only one species of fish (roach, *Rutilus rutilus*), avoiding the complication of choice between prey species (Voris, 1972; Voris, Voris and Liat, 1978).

There were two specific problems to investigate. Firstly, wild *N. maura* capture and handle fish too large for them to ingest (Hailey and Davies, 1986). As snakes must swallow prey whole, these fish are not only suboptimal, they are at best useless and at worst involve risks of choking or predation. This was investigated by offering snakes fish of different sizes to find the largest they could ingest, and whether they would strike at and attempt to handle even larger fish in conditions of good visibility.

Davies, Patterson and Bennett (1980) investigated selection and ingestion of different sizes of goldfish by *N. maura*. They found that medium sized fish gave the highest rate of energy intake during ingestion, and suggested that such fish were preferentially taken from mixtures with 'suboptimal' smaller or larger fish. Their

data show, however, that the larger fish in each mixture were preferentially taken, even when they were 'suboptimal' (Fig. 6b in their paper: 17 per cent of encounters were with large fish and 83 per cent were with 'optimal' medium fish; 36 per cent of ingestions were of large fish). There are several possible explanations for this apparent paradox:

1. Medium fish are preferentially selected, but the opposite result was obtained by chance. The selection experiment was therefore repeated with much larger samples.

2. Medium fish are preferentially struck at, but larger fish are easier to catch or ingest, and so more of them were eaten. Prey selection was therefore recorded both in terms of the number eaten and the number of strikes made.

3. There is a difference between the size — energy relations of roach (to which the snakes are presumably adapted) and goldfish. Goldfish energy content is independent of size, and the rule 'choose large fish' gives a lower rate of intake when applied to them. If large roach have higher energy content (per g) than small roach, the same rule applied to roach may give the maximum rate of energy intake. The energy content of roach of different sizes was therefore measured.

4. The efficiency of digestion is related to fish size. If large fish are digested more efficiently than small fish, then the rate of intake of usable energy during ingestion may be greater from large fish, even though smaller fish give a greater rate of gross energy intake. Absorption efficiency was therefore measured for different sizes of fish.

5. Ingestion time may be an inappropriate measure of handling time. If the time needed to digest a fish is much longer than that needed to ingest it then the rate of digestion will limit food consumption. A large fish may give a greater rate of food intake per unit time if digested faster than several small fish. The speed of digestion of fish of different sizes was therefore measured.

6. The model where foraging animals choose prey on the basis of maximising the rate of energy intake per unit handling time may be inappropriate to the problem of selecting prey from groups.

METHODS

All experiments used 25°C acclimated snakes and were at 25°C unless stated otherwise. Statistical tests follow Sokal and Rohlf (1981).

PREY CHARACTERISTICS

100 roach (2-13cm) were netted, blotted dry, weighed, and the following were measured with vernier calipers: standard (excluding tail fin) length, maximum height, maximum width. They were then killed and dried separately in foil envelopes in a field oven at 50-70°C, and stored in a desiccator. Additional fish of 2-5cm were dried in groups as extra material for calorimetry. In the UK they were re-dried to constant weight at 70°C, then grouped into 1cm length classes, powdered, pelleted, and the energy content found using a Parr semi-micro bomb calorimeter, two determinations per sample. Morphometric and energy data were obtained in the same way for goldfish, which were purchased in fortnightly batches from a local supplier and remained unfed at 10-15°C until used. Fish size relative to snake size was expressed as relative prey weight, RPW (prey weight/snake weight x 100).

HANDLING AND INGESTION

Snakes were kept overnight in 42cm x 22cm x 25cm plastic cages with 0.5-1 litre water dishes, and single live goldfish were introduced the following day. Ingestion time was taken as the time from capture until the snake's jaws closed behind the fleshy part of the fish (i.e. excluding the tail fin). There was an additional, shorter, time for the fish to reach the stomach, but this was hard to measure precisely. Two groups of snakes, small (10-30g) and large (50-110g), were given a range of relative fish sizes within the limitations of fish supply (usually 1-8g). For comparison, handling times were also measured at 15°C and 35°C.

In a second series of trials 20-30g snakes in cages with 2-3 litre water dishes were offered live fish of 10-70 per cent RPW to see if they would capture, and could ingest, them. Fish were introduced singly in the morning and the cages were observed hourly throughout the day. A capture attempt was recorded if the fish was seen being handled, or was removed from the water, or showed signs of a struggle (torn fins, loose scales in the water). Fish did not leap spontaneously from these large water dishes.

DIGESTION AND ABSORPTION

The term digestion is used for gastric digestion, the term absorption for the whole digestive process to the voiding of faeces. 20-30g snakes housed singly in cages with 0.5 litre water dishes were fasted for 10 days, then fed *ad lib* until more than 10g of 1-2g or 2-3g fish, or three 6-9g fish, had been eaten. The time interval between the first fish eaten and the first production of faeces was noted (Greenwald and Kanter, 1979). Afterwards, the snakes were fasted until faeces production ended.

On several occasions during each experiment, and at the end, the faeces (excluding urates) were collected and dried at 70°C. Ten snakes were used for each fish size; their faeces were pooled, and the energy content determined from two samples with the bomb calorimeter. Absorption efficiency

$$\frac{\text{Consumption} - \text{Faeces}}{\text{Consumption}} \times 100$$

of energy was calculated for each snake in each group using the mean energy content of faeces from that group.

After some of the observations on ingestion time the snakes were checked every four hours during the day until the fish could no longer be detected by palpating the stomach gently. Ingestions were staggered (after trial and error) so that this end point of digestion would occur during the day.

SELECTION AND CAPTURE

Ten large snakes were kept in a 2m x 1m arena with a 1m x 1m x 0.35m pool. Air temperature was 15°C, with two 250 W reflector lamps provided for thermo-regulation for 12 h a day. Low intensity room lighting was provided at night (just bright enough to read newsprint). Aquarium heaters maintained the water at 22-25°C. Small branches in the water were used as perches.

20 large (5-8, \bar{x} 6g) and 40 small (2-3, \bar{x} 2.5g) live goldfish were kept in the pool, those eaten being replaced twice daily until 50 had been eaten. The fish were then removed and the snakes were fasted for a week. The same mixture of fish were then introduced and the experiment continued until a further 50 had been eaten. The number of strikes made at small and large fish was observed in this second period, mostly on the day following fish introduction, when most of the snakes were foraging. The first half of this experiment was repeated using 20 large and 20 small fish, then 20 large and 80 small fish.

The whole experiment was repeated with 10 small snakes in a 1m x 0.6m x 0.3m pool, containing 10 large (4-5, \bar{x} 4.5g) and 20 small (2-3, \bar{x} 2.5g) fish. As the starting number of fish was rather small there was the possibility that if the snakes began foraging simultaneously they could substantially alter the relative abundance of large and small fish before these could be replaced. This was avoided by feeding the snakes before the first trial so that they did not all begin foraging together.

RESULTS

PREY CHARACTERISTICS

The weight-length relationship of 2-13cm roach was $\text{weight (g)} = 0.0113 \text{ length (cm)}^{3.18} r^2 = 0.99 n = 100$.

Energy content of the tissue did not vary with roach size (Hailey, 1984, Fig. 5.10), the mean value being 5.1 KJg live weight⁻¹.

The factor limiting the size of fish which a *N. maura* could ingest is assumed to be the stretched circumference of its neck at the narrowest point, as the jaws can open wider than this (pers. obs.), and the cross-sectional shape of the body is highly plastic. The dimension of a fish limiting its ingestibility would then be its maximum circumference, estimated as the circumference of an ellipse with diameters width x height. For roach

$\text{Circumference (cm)} = 2.75 \text{ weight}^{0.314} r^2 = 0.99 n = 100$.

Small goldfish were stouter than roach:

$\text{weight} = 0.0459 \text{ length}^{2.75} r^2 = 0.97 n = 134$

and, for the same weight, had a greater maximum circumference:

$\text{circumference} = 2.82 \text{ weight}^{0.364} r^2 = 0.97 n = 68$.

Energy content of goldfish was 4.0KJg live weight⁻¹, independent of size (Hailey, 1984).

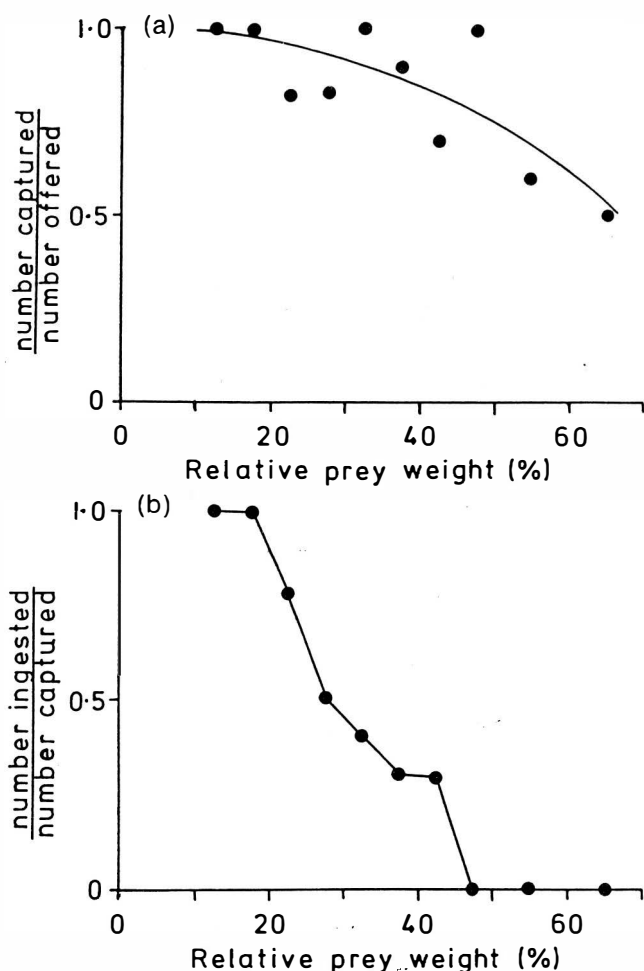


Fig. 1 Frequency of (a) capture and (b) ingestion of fish of different RPW by 20-30g snakes. Curve fitted by eye. Each point is for 10-15 fish.

HANDLING AND INGESTION

Snakes captured and attempted to ingest fish of all sizes offered (RPW 10-70 per cent), but could only ingest those of RPW less than 45 per cent (Fig. 1). Capture position (the part of the fish caught by the snake; head, middle or tail) was independent of RPW (Table 1a). Large fish were more likely to escape after capture (Table 1b) and to be ingested head-first (Table 1c, see also Loop and Bailey, 1972), but equally likely to be removed from the water for ingestion (Table 1d). Fish caught by the tail were more likely to escape after capture than those caught by the head (Table 1e), but this was not significant. Ingestion direction was associated with capture position; fish caught by the head were always ingested head-first, some of those caught by the middle or tail were ingested tail-first (Table 1f). 'Difficult' ingestions (involving fish caught by the tail which had to be turned right round, or tail-first ingestions) usually took place on land (Table 1g).

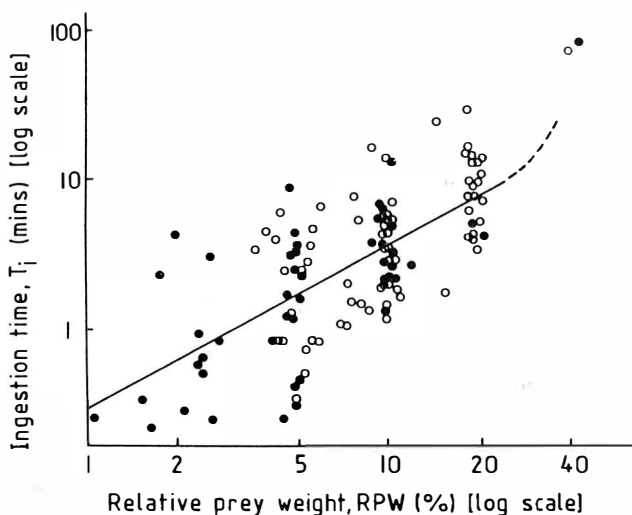


Fig. 2 Ingestion time vs RPW for small (o) and large (●) snakes. Regression slopes (excluding the two largest fish) for both groups and for the pooled data differ significantly from 0 but not from 1 (t tests). The equation for the pooled data is: $\log T_i = 1.08 \log RPW - 0.52$ ($r^2 = 0.47$).

Ingestion time was linearly related to RPW for fish of RPW 1-25 per cent, and did not differ between the two sizes of snakes (Fig. 2). Values of ingestion time are similar to those of Davies *et al* (1980) for prey of 1-10 per cent RPW. Fish of RPW above 40 per cent took much longer to ingest. Since the energy content of fish tissue was independent of size, RPW/ingestion time is a measure of the rate of energy intake during ingestion. This was highly variable and not significantly affected by RPW, although apparently greatest for fish of RPW about 5 per cent (Fig. 3). This pattern is similar to that found by Davies *et al* (1980, Fig. 5d in that paper). Some of the variability in ingestion time is attributable to capture position; fish caught in the middle or at the tail but ingested head-first had to be turned round, increasing ingestion time (Table 2a). There was, however, no effect of the direction of ingestion itself on ingestion time of small fish (Table 2b).

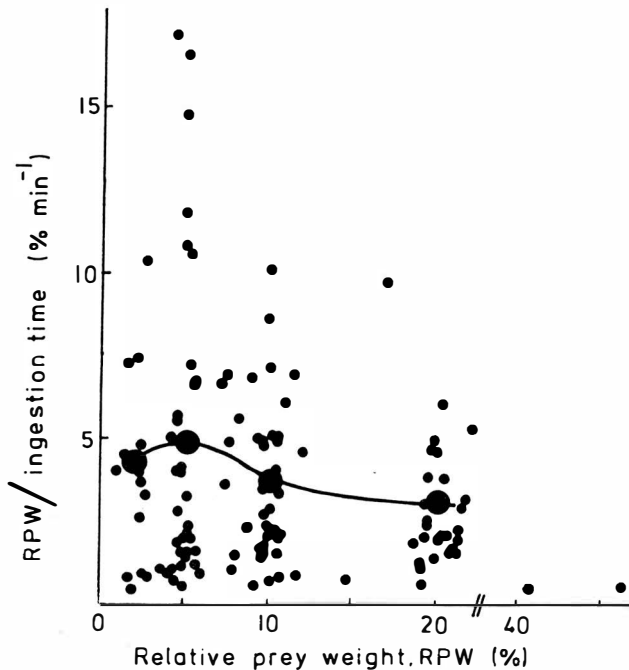


Fig. 3 The rate of energy intake during ingestion (RPW/Ti) vs RPW, data for small and large snakes combined. Large points are means for the RPW classes 1.5-3.5, 4-6, 8-12 and 18-22 per cent, curve fitted by eye. There is no significant variation of RPW/Ti between these classes (Kruskal-Wallis test $P > 0.1$).

(a) Capture position and relative prey weight.

RPW (%) (parts a-d)	1-4	4-8	8-15	15-25
Capture position	Number of captures			
Head	8	17	20	24
Middle	5	11	15	16
Tail	4	16	10	19

G test $0.9 > P > 0.5$.

(b) Fish escape after capture and relative prey weight.

	Number of captures			
Escaped	2	6	3	31
Ingested	15	38	42	28

G test $P < 0.001$.

(c) Direction of ingestion and relative prey weight.

Direction of ingestion	Number of ingestions			
Head first	10	35	40	28
Tail first	5	3	2	0

8-15 and 15-25 per cent RPW classes combined for g test, $P < 0.01$.

(d) Place of ingestion and relative prey weight.

Place of ingestion	Number of ingestions			
In water	8	15	19	10
On land	7	23	23	18

G test $0.9 > P > 0.5$.

(e) Fish escape after capture and capture position.

Capture position	Head	Middle	Tail
Small fish (RPW < 15 per cent)			
Escaped	3	2	6
Ingested	42	29	24
Large fish (RPW > 15 per cent)			
Escaped	10	9	12
Ingested	14	7	7

G tests: small fish and large fish separately, both $0.5 > P > 0.1$; combined $0.1 > P > 0.05$.

(f) Capture position and direction of ingestion (fish of RPW < 15 per cent)

Capture position	Head	Middle*	Tail*
Direction of ingestion	Number of ingestions		
Head first	42	24	19
Tail first	0	5	5

* Combined for testing, Fisher's exact test $P < 0.001$. χ^2 test for no preferred direction of ingestion of fish captured by the middle (against expected equal probability of head or tail first ingestion) $P < 0.001$.

(g) Capture position, direction and place of ingestion (fish of RPW < 15 per cent)

Capture Position	Tail, or	Head or Middle,
Direction of ingestion	Tail first	and Head first
Place of ingestion	Number of ingestions	
In water	3	39
On land	26	27

G test $P < 0.05$.

TABLE 1: Qualitative aspects of fish capture and ingestion, with tests of the null hypothesis: there is no association between row and column categories.

There was no effect of temperature on RPW/ingestion time between 15-25°C, but this was higher at 35°C (Table 2c). The capacity of *N. maura* for activity certainly increases between 15°C and 25°C (Hailey and Davies, *in press*), so there is presumably an effect of goldfish performance which cancels this out. Goldfish were noticeably less vigorous at 35°C, and often survived for only an hour or two.

DIGESTION AND ABSORPTION

Fish size had no effect on the initial rate of absorption (time to first faeces), on the rate at which food could be processed (*ad lib* feeding rate), or the absorption efficiency (Table 3). Values of *ad lib* feeding rate and absorption efficiency are similar to those for other natricine snakes feeding on fish (Brown, 1958; Goodwin, 1971). Fish of higher RPW remained palpable in the stomach for longer (Fig. 4). The relationship is best shown by the 7-20g snakes, for which the widest range of RPW was used; it appears to be linear, passing through the origin. Data for larger snakes fall above this line, as expected since their prey are absolutely larger. Comparison of Table 3 and Fig. 4 suggests that the *ad lib* feeding rate (6 per cent day⁻¹) is lower than the rate of gastric digestion (14% day⁻¹).

(a) Effect of capture position (head first ingestion only).

Capture position		
Head	6.4	(39)
Middle	2.8	(25)
Tail	1.6	(19)

These are all significantly different ($P < 0.05$).

(b) Effect of direction of ingestion.

Capture position	Direction of ingestion	
	Head first	Tail first
Middle	2.8 (25)	3.0 (5)
Tail	1.6 (19)	1.9 (5)

There are no significant differences between head first and tail first ingestions of fish captured in the middle or by the tail ($P < 0.05$).

(c) Effect of temperature.

15°C	4.4	(36)
25°C	4.2	(83)
35°C	9.8	(15)

35°C data differ significantly from combined 15° and 25°C data ($P < 0.01$).

TABLE 2: The effect of capture position, direction of ingestion, and temperature on the rate of energy intake during ingestion for fish of RPW < 15 per cent. Values are mean RPW/ingestion time (% min⁻¹) (with n). P values are for Wilcoxon two sample tests.

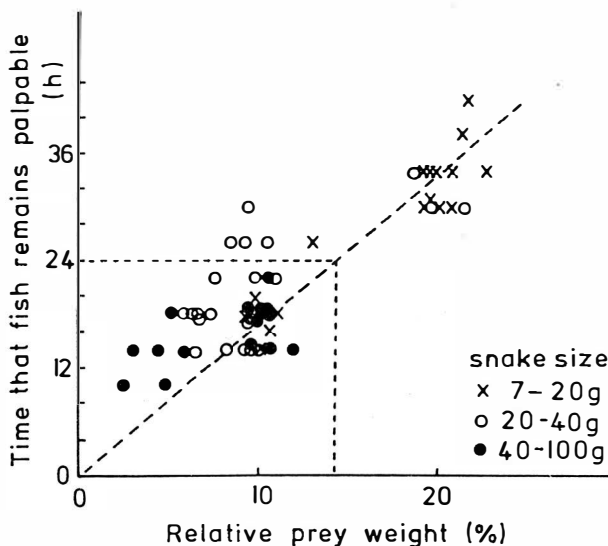


Fig. 4 The effect of RPW on the length of time that a goldfish remained detectable by palpating the snake's stomach. Dashed line fitted by eye to the 7-20g snake data. Dotted lines show estimation of the rate of gastric digestion as 14 per cent day⁻¹.

Fish Weight (g)	Absorption efficiency (%)	Time to first faeces (h)	Ad lib feeding rate (% day ⁻¹)
1-2	89.1 (3.5)	32 (16-36)	6.6 (1.5)
2-3	91.9 (1.5)	32 (20-36)	5.8 (1.2)
6-9	90.8 (0.7)	32 (16-40)	7.4 (1.3)

TABLE 3: The effect of fish size on the rate and efficiency of digestion. Each value is the mean for 10 20-30g snakes, each fed >10g of fish (with SD): time to first faeces is shown as the mode and range, in four hour intervals.

SELECTION AND CAPTURE

Both sizes of snakes struck at the larger fish about twice as often as expected from their relative abundance (Table 4). For the large snakes, capture success (CS = captures/strikes) and ingestion success (IS = ingestions/captures) were similar for the two fish sizes, and so the large fish were ingested about twice as frequently as expected from their relative abundance. For the small snakes (Table 4b) capture success of the large fish was greater but ingestion success was much lower, so that the frequency of ingestion of large fish did not differ significantly from their relative abundance.

DISCUSSION

HANDLING USELESS FISH

Hailey and Davies (1986) found wild *N. maura* apparently choked on roach of RPW 66-69 per cent, and suggested that the maximum RPW for safe ingestion of roach would be slightly below this. This is confirmed by feeding on goldfish, the largest of which to be successfully ingested had an RPW of 43 per cent. For a 20g snake this is an 8.6g goldfish, maximum circumference 6.2cm; a roach of this circumference would weigh 13.2g, i.e. 66 per cent RPW for the 20g snake. Thus both in captivity and in the wild, *N. maura* captured and attempted to ingest fish too large for them. This apparently maladaptive behaviour probably results from:

1. The large amount of energy which a large fish represents in relation to the snake's energy requirements, and thus the large disadvantage of mistakenly leaving a fish as too large which could have been ingested. Energy requirements of *N. maura* are about 65Jg^{0.75} day⁻¹ for maintenance and low activity (Hailey, 1984), 0.6kJ day⁻¹ for a 20g snake. A 12g roach (RPW 60 per cent) would yield 36kJ after losses in absorption and specific dynamic action (respectively 10 per cent and 30 per cent of the total 60kJ content of the fish — Hailey, 1984), equivalent to 60 days maintenance.

2. The difficulty of making an accurate judgement of fish size. It would thus be better to attack fish unless definitely too large; this costs only a few minutes handling before rejection.

(a) Large snakes: 80 (50-110)g.			P
Fish weight (g)	6 (5-8)	2.5 (2-3)	
RPW (%)	7.5	3	
Number present	20	40	
Number eaten	55	52	$\chi^2 P < 0.001$
Selectivity	2.1	0.47	
Number of strikes	101	93	$\chi^2 P < 0.001$
Selectivity	2.2	0.46	
Number of captures	13	13	$G 0.9 > P > 0.5$
Capture success	0.13	0.14	
Number of ingestions	9	9	$G P > 0.999$
Ingestion success	0.7	0.7	
Number present	20	20	
Number eaten	33	18	$\chi^2 P < 0.05$
Selectivity	1.8	0.54	
Number present	20	80	
Number eaten	20	36	$\chi^2 P < 0.005$
Selectivity	2.2	0.45	
(b) Small snakes: 25 (20-30)g.			P
Fish weight (g)	4.5 (4-5)	2.5 (2-3)	
RPW (%)	18	10	
Number present	10	20	
Number eaten	39	66	$\chi^2 0.5 > P > 0.1$
Selectivity	1.2	0.85	
Number of strikes	114	102	$\chi^2 P < 0.001$
Selectivity	2.2	0.45	
Number of captures	30	15	$G P < 0.05$
Capture success	0.26	0.15	
Number of ingestions	10	14	$\chi^2 P < 0.001$
Ingestion success	0.3	0.9	

TABLE 4: Selection and capture of fish from groups in large pools, with χ^2 or G tests of the null hypothesis; columns and rows are independent. Snake and fish weights shown as mean and range. The number of fish eaten exceeds the number present in the pool as fish were replaced as they were eaten. Selectivity of fish eaten (or of strikes) for large fish was calculated as:

$$\frac{\text{Number large eaten}}{\text{Number small eaten}} \times \frac{\text{Number small present}}{\text{Number large present}}$$

PREFERENCE FOR LARGE FISH

Of the six possible explanations for snakes preferring large fish listed in the introduction, the first five can now be rejected. Preference for large fish is thus not due to chance in a small sample (1), or to differences between energy content (3), efficiency of digestion (4) or rate of digestion (5) of different sizes of fish. The capture success with large goldfish was significantly greater than with small fish (Fig. 5a; G test $P < 0.01$), but ingestion success was significantly lower (Fig. 5b; G test on data pooled so that no frequency is < 5 , $P < 0.001$). When capture and

ingestion success are combined, the possibility of a strike leading to a successful ingestion is independent of RPW (Fig. 5c), and explanation 2) can be rejected. This leaves the possibility that snakes selecting fish from groups are doing so on some other basis than their energy intake per unit handling time.

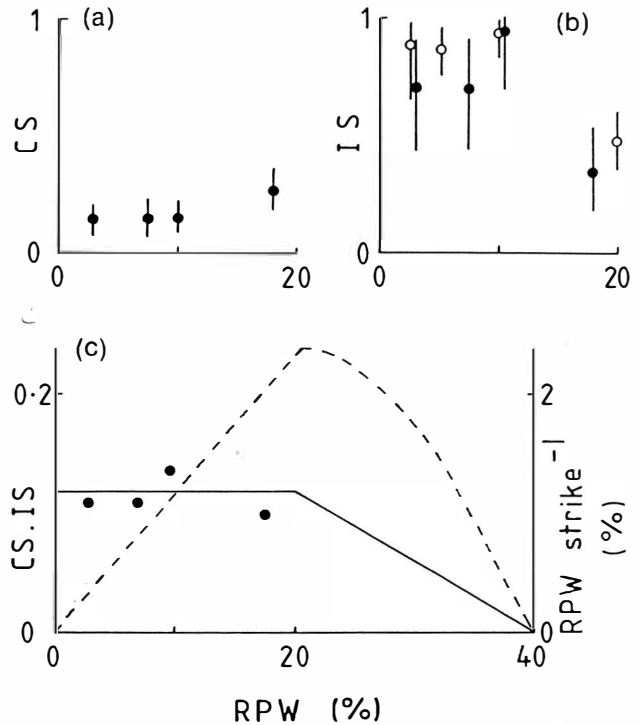


Fig. 5 (a) capture success (captures/strikes) and (b) ingestion success (ingestion/captures) for snakes feeding on goldfish of different RPW. Bars are 95 per cent CL of the proportions. Data from large pools (●, Table 4) and small dishes (○, Table 1). (c) Strike success (ingestions/strikes = CS/IS) (solid line) and the resulting energy intake per strike (dashed line).

Schooling fish such as roach and goldfish are encountered in groups from which the snake can select an individual at which to strike. The maximum energy intake *per strike* will be given by selecting from the group the fish giving the greatest value of CS.IS.RPW. The group is likely to move away or be more wary after a strike at one of its members (pers. obs.), so that only one strike may be possible on each group, or subsequent strikes may be much less successful.

Now consider instead the energy intake *during a period of foraging*. If a snake forages for a length of time T and selects fish of a given energy content (measured as RPW) and ingestion time T_i , its energy intake E will be:

$$E = (T-H).R.CS.IS.RPW \quad (1)$$

where R is the strike rate (time^{-1}) and H is the time spent handling fish:

$$H = (T-H).R.CS.((IS.T_i) + ((1-IS).T_e)) \quad (2)$$

where T_e is the handling time of fish which escape after capture.

R will be the same for all fish in a group, and so provides no basis for preferring one fish to another. The same applies to (T-H), since H is very small in

relation to T: field data in Hailey and Davies (1986) show that H is about 0.002 T. The important part of equation 1 is thus:

$$E \propto CS \cdot IS \cdot RPW$$

i.e. the maximum energy intake would be from the fish giving the maximum intake per strike. Depending on the values of CS and IS, this is likely to be achieved by selecting fairly large fish (Fig. 5c).

In the long term there will be an additional advantage of selecting large fish: insurance against reduced availability in the future. Even if there is no advantage in selecting a particular size of fish when the rate of intake during a period of foraging is considered, if the quality of foraging opportunities is unpredictable it would be better to ingest a large fish when available.

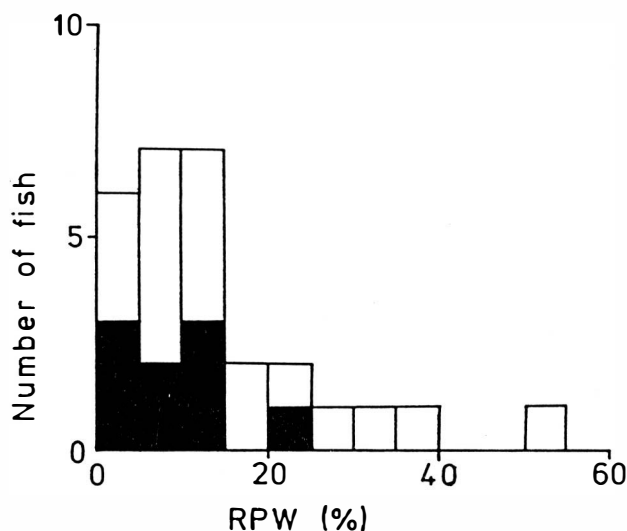


Fig. 6 Frequency distribution of RPW of regurgitated roach from wild snakes. Data for snakes >30g are shaded.

There is some evidence from prey regurgitated (Fig. 6) that fish above 20 per cent RPW were not preferentially selected in the wild. The size distribution of fish available is not known, and therefore selection cannot be shown directly. It can be inferred, however, as the distributions of RPW for small and large snakes are similar. In the absence of selection, or as a result of selection for the largest fish available, small snakes would catch fish of similar absolute size, and therefore higher RPW, to those taken by large snakes.

This sample model will be modified according to the behaviour of the local fish. If they are highly mobile, as are roach, they are likely to move away while the snake is waiting for a larger one to come nearer. It would then be better to strike at the best fish within striking distance. The potential for selection will be reduced if fish schools are made up of fish of similar size. If such schools are found in characteristic positions (e.g. water depth), the position a snake chooses will be more important than the selection of individual fish in determining the sizes of fish taken (Hailey and Davies, 1986). The mechanism of selection is not known; the snakes may use some simple rule such as strike at the fish within striking distance which appears largest. Water snakes are known to form search images for prey colour (Czaplicki and Porter, 1974; Porter and Czaplicki, 1977).

Capture success with goldfish (17 per cent of 410 strikes) was significantly higher than that with wild roach (Hailey and Davies, 1986: 1.6 per cent of 124 strikes, $\chi^2 P < 0.001$). The field observations were made in the few pools left with fish during a drought, and so snakes were common and the fish were frequently attacked. The capture success with goldfish may be a better estimate of that with unsuspecting roach in the wild, but would be compensated for by lower strike opportunity at low fish density.

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ACID TOLERANCE OF NATTERJACK TOAD (*BUFO CALAMITA*) DEVELOPMENT

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ABSTRACT

The tolerances of spawn and tadpoles of the natterjack toad to varying degrees of acidity have been investigated. The results show that:

1. Spawn and small tadpoles are more vulnerable than large tadpoles to low pH.
2. Total mortality of spawn occurs below pH 4.0 with the critical range for survival being between pH 4.0-4.5.
3. Growth rates of tadpoles are increasingly inhibited by pHs between 6.0 and 4.0 even in the presence of excess food.
4. It takes more than 24 hours for spawn to be killed by exposure to low pH (3.5).
5. Healthy spawn is less vulnerable to acid damage than spawn containing large numbers of dead eggs at the outset.

INTRODUCTION

Natterjack toads *Bufo calamita* are endangered and protected in Britain, having undergone major declines during the 20th century (Beebee, 1976;1977). Most of the losses have been from heathland sites in southern and eastern England and much conservation effort is currently orientated towards reversing this trend which has left only two very small populations on this type of habitat in the United Kingdom. One special aspect of heathland ecology relevant to amphibian fauna is the abundance of acid ponds on the podsolised sandy substrates. In extreme cases pools with pHs of less than 3.0 have been found and most usually fall between pH 3.0-5.0 with only a small proportion closer to neutrality. It is already known that natterjacks avoid acid ponds whenever possible and that larval development is impaired at low pH (Beebee and Griffin, 1977; Strijbosch, 1979). This study set out to obtain more detailed information on the effects of acid conditions on natterjack egg and larval development.

MATERIALS AND METHODS

Very small sections of natterjack spawn (generally no more than 100 eggs from the end of a string

containing 5-7,000) were taken from a maximum of four strings at one of the surviving heathland populations of the species. Batches of 10-20 eggs were allowed to develop in 2 litres of tapwater at a variety of pHs adjusted and maintained by the addition of H_2SO_4 . Control tanks at neutral pH contained equivalent amounts of added Na_2SO_4 and all were supplied with food *ad libitum* (Beebee, 1983). Development was monitored under laboratory temperature (18-25°) or environmental temperature (2-23°) regimes and tadpole growth rates together with survival of eggs and tadpoles recorded. After metamorphosis surviving toadlets were released at the site of capture.

RESULTS

Eggs, partly grown (12mm) and well grown (20mm) natterjack tadpoles were tested initially for their abilities to survive a 10 day period at a variety of pHs. Prior to the experiment, the small and large tadpoles had been reared in tapwater at pH 7.0. It can be seen from Table 1 that large tadpoles survived at pHs as low as 3.5 whereas spawn and young larvae were killed at or below pH 4.0. Evidently early stages of development were more susceptible to acid toxicity than later ones.

Development Stage	pH							
	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
Eggs	0	8	10	10	8	10	10	10
12mm tadpoles	0	10	8	8	10	10	10	10
20mm tadpoles	9	10	10	10	10	10	10	10

TABLE 1: Sensitivity of spawn and tadpoles to low pH. Experiments started with 10 eggs or tadpoles per tank, and figures are numbers surviving after 20 days at laboratory temperatures.

	pH							
	3.5	4.0	4.5	5.0	5.5	6.0	7.0	4.0 ¹
Numbers hatching (laboratory temp)	0	16	19	19	20	20	20	
Growth rates (laboratory temp)	–	0 (0.00)	0.58 (0.06)	0.67 (0.18)	0.92 (0.12)	0.81 (0.03)	0.92 (0.06)	0.33 (0.12)
Numbers surviving 10 days (laboratory temp)	–	0	16	16	18	18	20	6
Numbers metamorphosing	–	0	10	14	18	18	19	0
Numbers hatching at low conductivity (laboratory temp)	0	20	20	20	20	20	20	
Numbers hatching (environmental temp)	0	2	18	16	20	20	20	
Hatch time (days) (environmental temp)	–	20	18	15	14	14	14	

TABLE 2: Effects of pH on survival and growth from spawn. Tanks initially contained 20 eggs each in 2 litres of water, and all figures except line 2 (growth rates) and line 7 (hatch times) represent numbers surviving to a particular stage. Growth rates are given as mm day⁻¹, over a 10 day period with standard deviations in parentheses. 'Low conductivity' tanks contained a 1:5 dilution of tapwater: glass distilled water, with a conductivity at 25° of 180 μ S cm⁻¹. 1 = Fate of larvae transferred from pH 7 to pH 4 after hatch.

A closer study of pH effects on spawn development is reported in Table 2. Acid-induced mortality was similar at two different water conductivities, indicating that at least over the range tested (which was similar to that seen in the wild) nutrient status of the water did not act in any cooperative way with pH to affect the viability of spawn. The temperature regime did however have some effect on survival to hatch. Spawn reared under relatively warm conditions in the laboratory showed an 80 per cent hatch rate at pH 4.0, whereas eggs outside exposed to uncontrolled environmental temperature fluctuations experienced 90 per cent mortality at pH 4.0, but 90 per cent hatch at pH 4.5. Moreover, hatch times and growth rates were directly related to pH. Eggs which did survive at pH 4.0 took 50 per cent longer to emerge from their jelly surrounds at environmental temperatures (in a rather cold spring) than those at pH 5.5 or above. Even under laboratory conditions growth rates of tadpoles at pH 4.5 were only 60 per cent of those seen at and above pH 5.5. Hatching tadpoles maintained at pH 4.0 in the laboratory failed to grow at all and eventually died; tadpoles from spawn hatched at pH 7.0 and then placed at pH 4.0 grew at only about one third the rate of siblings at pH 7.0 and also gradually died off.

The results of Table 3 show that acidification to pH 3.5 was a relatively slow killer of natterjack spawn. Exposure for up to 24 hours was tolerable without ill effects, though by 48 hours all the eggs were dead and would not recover when transferred to higher pH. Tadpoles hatching from spawn exposed to pH 3.5 for 24 hours grew and metamorphosed normally.

Another factor apparently influencing the susceptibility of natterjack spawn to low pH was its general condition at the start of the experiments. In cases of spawn strings with large numbers of dead eggs, even those apparently viable (as judged by shape and pigmentation) showed much reduced hatch rates below pH 5.0 (Table 4).

DISCUSSION

Natterjack toads are known to be susceptible to at least two kinds of chemical catastrophe in their breeding pools; high salt concentrations resulting from tidal inundations are not infrequent at some sites and the effects of this salination on spawn and tadpoles has been investigated (Mathias, 1971; Andren and Nilsen, 1979; Beebe, 1985). A second type of problem may be

Developmental Stage	Time of Exposure to pH 3.5 (hours)						
	0	0.25	1.00	4.00	24.00	48.00	72.00
Hatch	10	10	10	10	10	0	0
Metamorphosis	10	9	10	10	9	–	–

TABLE 3: Survival times of spawn at low pH. Tanks started out with 10 eggs, and these were transferred from water at pH 3.5 to neutral tanks at the times shown. Figures are the subsequent survival numbers to hatch and to metamorphosis. Experiments were at environmental temperatures.

encountered in inland sites, where heathland podsoles often underlay acidic, nutrient-poor surface waters. Oligotrophic or dystrophic conditions are unlikely to have any serious direct consequences for natterjack development (Beebee, 1983) arising from low concentrations of inorganic ions or high concentrations of organic solutes, but the high levels of acidity can be very destructive of amphibian spawn (Beebee and Griffin, 1977; Strijbosch, 1979).

The results of this study show that the critical range of acidity for natterjack toads lies between pH 4.0 and 4.5. At or below pH 4.0 there is likely to be little survival even to hatch under field conditions of fluctuating temperatures, and many *Sphagnum*-dominated pools fall within this lethal range. Between pH 4.0 and 5.0 other environmental factors, especially temperature, may be crucial modulators of survival. Less mortality is likely under consistently warm conditions though even up to pH 5.5 the extent of acidity has a significant impact on tadpole growth rates irrespective of food supply. Longer development times increase mortality indirectly through higher risks of desiccation and predation (Banks and Beebee, in preparation). In the present study, natterjack development was found to be slightly less vulnerable to acid kill than was observed by Beebee and Griffin (1977), though the overall pattern was similar. The earlier study employed spawn containing a high percentage of initially non-viable ova, and the results presented here are probably a more accurate reflection of the tolerance of normal healthy spawn.

Low pH, at least down to 3.5, killed spawn much more slowly than tidal inundation (Beebee, 1985). It would clearly be worth moving fresh spawn from an acid pond to a more suitable one. A similarity to high salt toxicity was however observed in the critical lethal range of pH, i.e. around pH 4.0. At pH 3.5, as at high salt, eggs did not develop at all; at pH 4.0, close to the lethal limit, eggs developed slowly to hatch but subsequently died. Survival to hatch but not beyond was also seen near the lethal salt limit (Beebee, 1985).

This kind of experimental information should form a basis for understanding events in the field. Natterjacks certainly avoid acid ponds in Britain when a choice is available though occasional spawnings in ponds below pH 4.0 have been seen. In such circumstances the eggs have always died. In the

Netherlands, attempts to spawn at low pH also result in very high spawn mortality but at least one site is known where a large population of natterjacks is maintained by a pond in the pH range 4.0-4.4 (Strijbosch, 1979; Hulswit and Mulder, 1984). Clearly there are situations in which *Bufo calamita* can survive at the edge of its pH tolerance despite the disadvantages of spawn and tadpole mortality which follow. It may be that the more continental climate enjoyed by the Netherlands, with warmer temperatures in the breeding pools, assists natterjack survival under these extreme pH conditions.

Some comparative information, particularly for North American species, is also available. *Bufo americanus* hatch rates drop precipitously below pH 4.6 and this species is also sensitive to low concentrations of inorganic Al (less than $50\mu\text{g litre}^{-1}$) which can act cooperatively with low pH. Other amphibians tested (*Rana sylvatica* and *Ambystoma maculatum*) were less sensitive to low pH than the bufonid (Clarke and Hall, 1985). With the natterjack there seems to be a generally good correlation between pH effects seen in the laboratory and those observed in wild populations. There is therefore little need to consider secondary effects of low pH, such as mobilisation of Al. One exception to this may be the observation that large tadpoles have been seen to die in pondwater of pH 3.5-4.0 quite rapidly (unillustrated data) whereas they are tolerant of such acidity in buffered tapwater. Perhaps in this case heavy metal effects were also manifest, but for the most part H^+ probably acts directly on natterjacks to interfere with Na^+ uptake and secretion as has been shown for a number of North American amphibia (Freda and Dunson, 1984). Hopefully a better understanding of acid threats to amphibians will lead to improved conservation management procedures.

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Spawn Batch	pH of Trial Tank		
	4.0	5.0	6.0
1 (65-70% eggs dead at start)	0	95	100
2 (65-70% eggs dead at start)	0	0	70
3	100	100	100
4	80	90	100

TABLE 4: Susceptibility of different batches of spawn to low pH. Hatch rates of 4 separate batches of spawn, each derived from 2-4 strings, were compared at 3 pHs, and figures shown are percentages of apparently viable eggs which hatched successfully. Batch 1 was that of Beebee and Griffin (1977); Batch 2 was obtained in summer 1983 with a high proportion of dead ova thought to be caused by inefficient fertilisation (Banks and Beebee, in press); Batches 3 and 4 were from strings which later experienced more than 99% hatch.

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APPARENT LACK OF TERRITORIALITY DURING THE BREEDING SEASON IN A BOREAL POPULATION OF COMMON FROGS *RANA TEMPORARIA L.*

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ABSTRACT

The movements within a population of individually marked male Common Frogs *Rana temporaria* were studied during the breeding season. No signs of territoriality were found. The population was characterised by a high degree of disorder and internal movements. Site fidelity within the pond occurred, but was rare. Some other features of the reproductive biology of the species are also described.

INTRODUCTION

Anurans show a great interspecific variation in their behaviour at the breeding site. In most species, males seem to take the most active part in the activities in the breeding ponds. The ability of the females to actively choose a mate is somewhat difficult to prove, but has been discussed by Licht (1976) and Halliday (1983).

A survey of anuran reproductive and mating strategies is given in Wells (1977). As far as the temporal pattern is concerned, there seem to be two broad categories: *prolonged* and *explosive* breeders. Among the former we find species such as the Green Frog *Rana clamitans* and the Bullfrog *Rana catesbeiana*, which maintain well-developed social structures in their breeding ponds, and where male territoriality is an important aspect of the mating strategy (Emlen

1968, Emlen 1976, Howard 1978, Martof 1953 and Wells 1978).

The typical explosive breeders, on the other hand, have a short annual breeding period of one or a few weeks (Wells 1977). There seem to be no species within the group possessing territorial breeding pond behaviour.

The Common Frog, occurring widely in the cooler parts of the Palearctic, is considered a typical explosive breeder by Wells (1977). Its reproductive biology has been studied in Britain (Savage 1961, Ashby 1969), the Netherlands (van Gelder and Hoedemakers 1971, van Gelder, Evers and Maagnus 1978), Poland (Kozłowska 1971), Finland (Koskela and Pasanen 1975) and Sweden (Ericsson and Elmerg 1979, Elmerg and Ericsson 1980). The mating behaviour of its Nearctic relative the Wood Frog *Rana sylvatica* is described by Howard (1980).

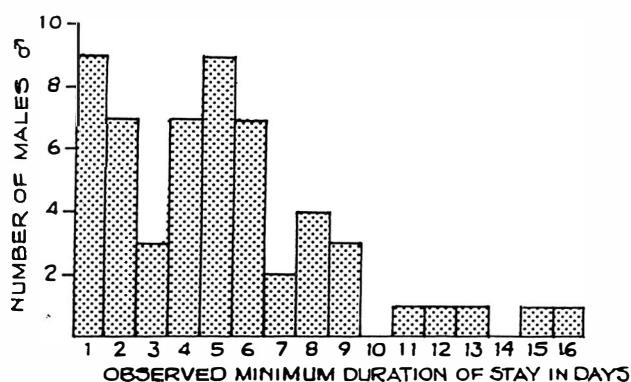


Fig. 6. Observed minimum duration of the stay in the breeding pond.

Even though this study focused on the males, all frogs were caught regardless of sex. In all, 13 females were caught, thus constituting only 14 per cent of the individuals (observed sex ratio 6.2 males to one female).

The average of R was 0.91 (SD ± 0.16) in the 22 frogs caught three times or more. The corresponding d value was 5.71 metres (SD ± 2.88). The relationships between R and d for the individual frogs are shown in Fig. 7. In theory, territorial or site tenacious frogs will show low values of both R and d .

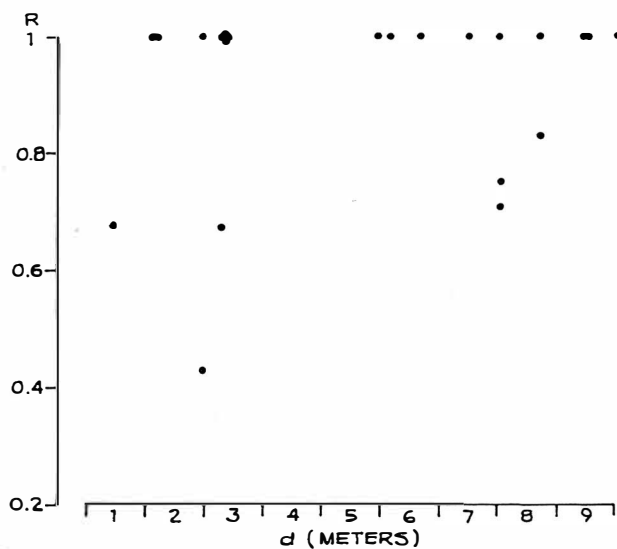


Fig. 7. Individual males plotted according to their R and d values ($n = 22$). Stationary males will hypothetically appear in the low left corner, and the mobile in the upper right.

No aggressive encounters between the males were observed. Spawning began 30th April and culminated 5-6th May.

DISCUSSION

The total catch could have been increased by adding some sampling nights. However, this would also have increased the disturbance, and was ruled out

considering the short breeding period. The following discussion concentrates on the 22 individuals caught three times or more.

The number of males caught for the first time remained at a relatively constant high level during the first part of the main calling period (Fig. 3b). This is because the migration from the wintering site (river Tvärån) to the pond takes some time to complete for the population as a whole. Obviously, the continuous movement of frogs arriving and departing over a large part of the breeding season is likely to hinder the establishment and defence of territories.

The time that each individual spends in the pond is of great importance for the possibility of establishing territories within the population. As the observed minimum average duration of the stay is only 5.1 days, it is concluded that many males spend only part of the main calling period in the pond. Consequently, it may be a poor investment of energy to establish and defend a territory under these circumstances.

The spatial distribution of the catches shows a marked concentration to certain parts of the pond. Also among the squares in which catching activities were prevented by high water levels, there was an obvious concentration of the chorus to the ones bordering the other favoured, accessible squares. This clustering of the calling males may hinder the establishment of territories. In the territorial *Rana clamitans*, a regular spacing between the calling males was noted by Martof (1953). Emlen (1968) estimated the minimum territory radius of *R. catesbeiana* to be approximately three metres. The spatial distribution and the density of the Umeå population are clearly not compatible with a territorial structure like that of either *R. clamitans* or *R. catesbeiana*. Rather, they are in good agreement with the general characteristics of explosive breeders as described by Wells (1977).

The movements of the individual frogs are harder to interpret. Out of the 22 caught three times or more, 16 were found at least once in the square where they were first caught, or in a neighbouring square. Only one of the 22 was caught in all three major calling areas of the pond (the southern, northwestern and northeastern parts — Figs. 1 and 5). Nine individuals were caught in two of the major calling areas, while the remaining 12 were caught in one only. These observations indicate that the movements within the pond are limited in most males, and that certain areas are preferred.

Of the three males caught the most times, two fit well into the pattern of limited movement described above. The third, on the other hand, was caught all seven times in a minor clump of sedge in squares 41, 51 and 61. It is worth pointing out that this male not less than seven times moved from outside the grid in the northern end of the pond to this very spot! This could hardly be termed as anything else than a remarkable site fidelity. Surprisingly enough, this male was caught twice the preceding year — in the same area as in 1980!

The R values show that most of the frogs have been caught in a good number of squares, that is, a new one on almost every occasion. In absolute terms (average of d), though, the movements seem less extensive. No comparisons can be made at this point, however, and

future studies may show whether this population of Common Frogs had a high or low degree of internal movement.

In conclusion, there is an impression of disorder, but individual movements are usually restricted to a certain part of the pond, and a few males exhibit a high degree of site fidelity. If we assume that the males establish territories smaller than the squares of the grid of this study, the expected spatial distribution of the calling males would be quite different from the one found. The small and irregular distances among the calling males and observations of their behaviour show that territoriality *sensu stricta* was not in effect in this population. Also, as no territorial pattern was established, the frogs remained mobile.

According to Wells (1977), the mate-locating behaviour among explosive breeders varies with the density of the population; at high densities males move widely or adopt a strategy of 'limited area searching', and at low densities they become more or less stationary. The population here studied seem to be dominated by 'limited area searching' males. Assuming that the density of the population studied (80-100 males in 300m²) could be termed as high, my data would support the general pattern in Wells (1977).

It should be noted, though, that there is always a risk of over-simplifying when trying to describe anuran reproductive behaviour. The great variation among the males in this study stresses this important point. Mating strategies are individual, and great caution must be taken when applying the term to populations or species.

What was then the breeding success of the males? Out of the 11 found amplexed with females, only three belonged to the category caught three times or more. The percentage of successful matings in this category was equal (14 per cent) to that of the frogs caught one or two times only. Although the sample in this study is small, there seems to be no reason to believe that males calling actively and for a long time have markedly higher breeding success than those who do not.

The observed sex ratio of 6.2 males to one female seems somewhat high compared with the 2:1 ratio of a nearby population censused during migration (Elmberg and Ericsson 1980). This discrepancy may be within the normal variation between years or populations, or random, but may also result from the fact that the males are so much easier to catch in the breeding pond than females (due to more exposed habits and longer stay). Nevertheless, the number of males greatly exceeds the number of females in the breeding pond at any given moment. If not territorial, the Common Frog must have another means of assuring that mating is not a random process.

There is a need for further studies establishing the actual mating strategy generally adopted by the Common Frog. Attention must be paid to characters such as size and sound of the males, and the effects of the latter on males as well as on females in the breeding pond (see Howard 1978). Comparisons of mating strategies in populations in different parts of the range of a species would be of wide interest to the understanding of the reproductive biology and evolution of anurans.

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