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ANNOUNCEMENTS

The World Congress of Herpetology announces the

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11–19 September 1989
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This international congress will be the first of a series occurring at regular intervals at venues around the world. Such a meeting will enable all persons interested in herpetology to meet and exchange information to promote the advance of knowledge and the conservation of the world's amphibians and reptiles. The congress will consist of topical symposia, poster sessions, plenary speakers, workshops, displays, excursions, and meetings of ancillary groups. Subjects and moderators of symposia will be announced well in advance so that potential participants can volunteer. The meeting will be open to all persons. Registration will begin 1 January 1988.

For further details and mail listing, write: Dr. Ian R. Swingland, World Congress of Herpetology, Rutherford College, University of Kent, Canterbury, Kent CT2 7NX, United Kingdom.

Sponsoring organizations and individuals are welcome. For further details write: Dr. Marinus S. Hoogmoed, Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, The Netherlands.

FRONT COVER: Palaeoherpetology: Ilia of *Rana* species (A, *temporaria*; B, *arvalis*)

Official Lists and Indexes of Names and Works in Zoology

A revised and updated edition of the *Official Lists and Indexes of Names and Works in Zoology* has now been published. For the first time all the names and works on which the International Commission on Zoological Nomenclature has ruled since it was set up in 1895 are brought together in a single volume. Entries are arranged in four sections giving in alphabetical order the family-group names, generic names, specific names and titles of works which have been placed on the Official Lists or the Official Indexes. There are about 9,900 entries of which 134 are for works. In addition, there is a full systematic index and a reference list to all relevant Opinions and Directions. The volume is 366 pages, size A4, casebound.

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DIGESTION, SPECIFIC DYNAMIC ACTION, AND ECOLOGICAL ENERGETICS OF *NATRIX MAURA*

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ABSTRACT

Absorption efficiency of viperine snakes feeding on goldfish increased slightly with temperature, the rate of digestion increased greatly. Digestion was partial at 15°C and sometimes followed by regurgitation: at 10°C all prey were regurgitated. Prolonged basking in *N. maura* in the field probably serves to increase the speed of digestion. The metabolic cost of maintaining a high body temperature (T_b) during digestion is equivalent to 4 per cent of the energy of the prey.

The level and time course of raised oxygen consumption (VO_2) following feeding on fish varied with T_b, being large and short lived (2 days) at 35°C, small but long lasting (10 days) at 15°C. The total energy cost of this raised VO_2 accounted for 28 per cent of the energy in the food. VO_2 during maximal activity after feeding at 35°C was greater than that of post-absorptive snakes, indicating that the capacity for oxygen exchange does not limit the active metabolic rate of *N. maura*. There was no depression of oxygen consumption during hibernation.

Food consumption could not be satisfactorily estimated from the proportion of snakes (a) found handling prey or (b) with prey in the stomach. Data on metabolic costs, reproductive effort and growth are combined to give an energy budget for *N. maura*. The energy turnover was about a third of that predicted from studies of lizards. Snake and lizard energy budgets differ in the ratio production/assimilation; this was 0.41-0.57 in four snakes, and 0.13-0.18 in six lizards. Snakes have lower energy turnover, but allocate a greater proportion of this to reproduction and growth.

INTRODUCTION

The snake *Natrix maura* basks for long periods, the purpose of which has been suggested to be to help digestion (Hailey & Davies, 1987a). The first aim of this paper is to examine the temperature — dependence of digestion in this species. Raised VO_2 during digestion (the Specific Dynamic Action: Kleiber, 1975) is another route of energy loss during digestion. This is seldom measured, although in mammals (Kleiber, 1975) and fish (Jobling, 1981) it may account for more energy than loss in faeces. Specific dynamic action was therefore measured in *N. maura* at different temperatures.

There are several studies of food intake and growth (Dmi'el, 1967; Barnard, Hollinger & Romaine, 1979) and energetics (Gehrmann, 1975; Smith, 1976) of snakes in captivity, but little information on the ecological energetics of wild snakes (Congdon, Dunham & Tinkle, 1982). The only exceptions are food consumption estimated from metabolism and production of *Vipera* (Pomianowska-Pilipiuk, 1974), and from proportion with prey and rate of digestion of *Regina* (Godley, 1980). The final aim of this paper is to construct an ecological energy budget for *N. maura* from data on thermoregulation and metabolism, growth, reproduction, and feeding.

METHODS

FIELD OBSERVATIONS

Natrix maura were studied in the river Jalon, Spain. All snakes handled were palpated for prey in the stomach, and all snakes seen were noted, including those handling prey. Diet and foraging behaviour have been described previously (Hailey & Davies, 1986a). Sloughing state was noted for all snakes handled. Of the three stages of the sloughing cycle (pre-moult 1, skin cloudy; pre-moult 2, skin clear before sloughing; intermoult, after sloughing; respectively PM1, PM2 and IM — Taylor & Davies, 1981), only PM1 could be recognised in the field, PM2 and IM being indistinguishable.

ENERGETICS

Digestion. Absorption efficiency (AE) and time to first faeces at different temperatures were measured in 20-30g snakes fed on 2-3g goldfish, in constant temperature rooms, as described by Hailey & Davies (1986b). Snakes would not feed readily at 15°C, and not at all at 10°C, and so they were fed at 25°C and their cages were moved to other rooms. Ten snakes were used at each temperature.

Maintenance requirements. Snakes were kept at constant 25°C in 42 x 22 x 25cm cages, with a water

dish and newspaper substrate and cover, and fed whole or pieces of goldfish just sufficient to allow them to maintain weight. Each snake was given food equal to 5-10 per cent of its initial weight. It was reweighed every 2-3 days, and fed if it was below initial weight. After three weeks snakes were fasted until they were back to the initial weight. The weight of food consumed over about four weeks was converted to energy per day, using the relation 1g live goldfish = 4.0 KJ (Hailey & Davies, 1986b).

Energy contents. Sloughed skins from captive snakes were dried to constant weight at 70°C. The energy content of five skins was determined using a Parr semi-micro bomb calorimeter. Five apparently healthy snakes died in captivity as a result of accidents, and these were used for determination of the lean body energy content. Fat bodies were removed, the snakes were dried at 70°C, powered, pelleted and used for bomb calorimetry.

VO$_2$ DURING HIBERNATION

A group of 10-25g snakes were imported in October, and maintained for three weeks in a 10L: 14D photoperiod with 5h per day heating from a 250W reflector lamp and background temperature of 15°C. Those in poor condition were fed on goldfish. Standard metabolic rate (SMR, resting in daytime in a darkened chamber) was measured at 10°C and 15°C in constant pressure respirometers, as described by Hailey & Davies (1986c), with snakes fasted for at least 7 days and rested overnight at the test temperature. These were the control pre-hibernation or 'Autumn' conditions.

Two groups of ten snakes each were then placed in a 15°C constant temperature room. One group were in a cage filled with dry straw (with a jar of water for humidity) covered with a dark cloth, to stimulate hibernation (OL: 24D photoperiod group). The other group were in a transparent cage with newspaper substrate and a water dish, to stimulate positive acclimation, i.e. raised VO$_2$ to compensate for low T_b rather than lowered VO$_2$ during dormancy. This was the 12L: 12D photoperiod group. The OL: 24D experiment was repeated with 15 snakes at 10°C. All rates were corrected to STP.

SPECIFIC DYNAMIC ACTION

The increase in VO$_2$ after feeding was measured in constant pressure respirometers (15°C) or in an oxygen analyser (25°C and 35°C), as described by Hailey & Davies (1986c). Six 25-35g snakes acclimated to constant 25°C were each fed a single 3.5g goldfish and placed in a darkened respiration chamber at the appropriate temperature. Resting VO$_2$ was measured four hours later. Thereafter VO$_2$ was measured at intervals of 24 (25°C and 35°C) or 48 (15°C) hours. These measurements were made in the morning, then the snakes were placed in cages at the experimental temperature and allowed to drink. They were replaced in the respiration chambers in the evening to be rested for the next days measurements.

In a separate experiment, the effect of SDA on VO$_2$ during maximal activity was measured, to see if SDA would decrease performance. VO$_2$ during maximum activity four hours after feeding at 35°C (the temperature at which aerobic scope is maximal) was measured with the oxygen analyser, as described by Hailey & Davies (1986c).

RESULTS

FIELD OBSERVATIONS

In both the hot season (the months JJAS) and at other times (the months MAMO), large snakes were more likely to have prey in the stomach on capture than were small snakes (Table 1a, G tests of the seasons separately, P>0.05; combined data P<0.05). Prey of large snakes are absolutely larger, and take longer to digest, than those of small snakes, even though of the same relative size (Hailey & Davies, 1986a,b). They therefore remain in the stomach longer, and larger snakes are more likely to be found with food in the stomach. Female *N. maura* did not have reduced food consumption in June (Table 1b), the month when follicles reach maximum size (Hailey & Davies, 1987b).

Few snakes were seen in PM1 (0.8 per cent of 2368 captures, excluding juveniles <4g), suggesting that they are inactive and secretive in this state. Other snakes have been found to have lower selected T_b during PM1 (by about 10°C: Kitchell, 1969), related to

a)	<4g		4-15g		15-40g		>40g	
JJAS	2.3	(44)	5.0	(704)	6.5	(506)	7.5	(199)
MAMO	5.7	(53)	4.2	(409)	6.5	(354)	8.7	(196)
Total	4.1	(97)	4.7	(1113)	6.5	(860)	8.1	(395)

b)	Mature females		Others		P
June	11.0	(75)	6.0	(268)	>0.1
Rest of year	5.3	(302)	6.3	(1820)	>0.5
P	>0.1		>0.9		

TABLE 1: The percentage of *N. maura* which had prey in the stomach on capture. a) Variation with snake weight and season (the warm months JJAS vs the cool months MAMO). b) The effect of gravidity: mature females vs other snakes, during and outside the reproductive period, with P from G tests. Number of snakes in brackets.

secretive behaviour. Only five shed skins were found during this study, in an area containing thousands of snakes (Hailey & Davies, 1987c), also suggesting that sloughing occurs in inaccessible places. Juvenile *N. maura* were usually inactive when found anyway, and 11 per cent (of 97) were in pre-moult 1.

ENERGETICS

Digestion. Absorption efficiency ((C-F)/C, where C is consumption and F is faeces) of energy varied less with temperature than did the time to first faeces (Table 2). Two out of ten snakes regurgitated fish half way through gastric digestion at 15°C, and at 10°C all fish were regurgitated within a few hours.

Maintenance in capavity. The food consumption necessary to maintain weight in small cages at 25°C was described by:

Log Food (KJ.day^{-1}) = 0.72 Log Weight -1.25

based on 15 males and 10 females, r = 0.97 (Fig.1). The cost of standard metabolism of constant 25°C acclimated *N. maura* is also shown in Fig. 1, from Hailey & Davies (1986d), using the conversion 1ml O_2 = 20J:

Log SMR (KJ.day^{-1}) = 0.75 Log Weight -1.35

Thus maintenance requirements in capitivity were very little greater than those due to standard metabolism alone: 1.23 and 1.10 times SMR for 2g and 100g snakes, respectively.

Fig. 1 Food consumption for maintaining weight in small cages at 25°C o males ● females. Solid line is regression fit, dashed line is the energy equivalent of SMR (equations in text).

°C	Absorption Efficiency	Time to first faeces
10	0	Regurgitated
15	85 (4.4)*	4.0 (3.0-5.0)
20	90 (2.8)	2.5 (2.0-3.5)
25	92 (1.5)	1.3 (0.8-1.5)
30	95 (1.1)	1.0 (0.7-1.2)
35	95 (1.1)	0.8 (0.5-1.0)

* n = 8, excluding two snakes which regurgitated half-digested fish. The mean absorption efficiency including these values becomes 78 per cent.

TABLE 2: Digestion of goldfish by *N. maura* at different temperatures. The absorption efficiency of energy (%, with SD) and time to first faeces (days, with range) are shown; ten snake used at each temperature.

Energy contents. The energy content of the lean body was 19.2 KJ.g dry weight^{-1} (SD = 0.74). Dry weight accounted for 24.7 per cent (SD = 0.34) of live weight, giving 4.74 KJ.g live W^{-1}. Sloughed skins had an energy content of 24.2 KJ.g dry W^{-1} (SD = 0.4). The weight of dry skin S was related to live weight (in the range 6-105g) by:

Log S = 0.905 log W -1.96   (r = 0.99, n = 14)

The energy content of sloughed skin (KJ) was therefore related to live weight by:

Energy in skin = 0.264 W$^{0.905}$

HIBERNATION

Oxygen consumption during hibernation at 10°C and 15°C was not lower than that of snakes in autumn conditions, or in similar conditions in spring (Table 3). These values have been weight-corrected using the exponent 0.75 which has been found for *N. maura* at several temperatures and acclimation conditions (Hailey & Davies, 1986c). No reduction in VO_2 during hibernation has also been found in the warm temperate *Natrix piscator* (Thapliyal & Sharan, 1980).

Photoperiod:	12L : 12D	OL : 24D
15°C		
Autumn	47 (14,10)	34 (23,10)
2 weeks	40 (21,10)	39 (25,10)
4 weeks	45 (13,10)	45 (12,10)
Spring*	37 (14,15)	—
10°C		
Autumn	—	15 (18,15)
2 weeks	—	22 (25,15)
4 weeks	—	23 (21,15)
Spring*	19 (18,15)	—

*Spring results are from Hailey & Davies (1986c)

TABLE 3: Weight-corrected oxygen consumption during hibernation. All entries are $\mu l.g^{-0.75}.h^{-1}$ (with coefficient of variation = SD $\bar{x}$, number of snakes).

SPECIFIC DYNAMIC ACTION

VO_2 in standard conditions was elevated for several days after feeding (Fig. 2). The total volume of oxygen consumed above SMR (the area under the curves in Fig. 2) is shown in Table 4.

VO_2 during maximal activity four hours after feeding at 35°C was significantly greater (t test, P<0.01) than the active metabolic rate (AMR) of 25°C

acclimated post-absorptive snakes (from Hailey & Davies, 1986d). When the SDA had been subtracted, however, maximal VO_2 after feeding was less ($P < 0.01$) than AMR. VO_2 in $ml.g^{-0.75}.h^{-1}$ (with SD, n) were:

After feeding	2.22	(0.23,	6)
Minus SDA	1.31	(0.28,	6)
AMR	1.73	(0.31,	15)
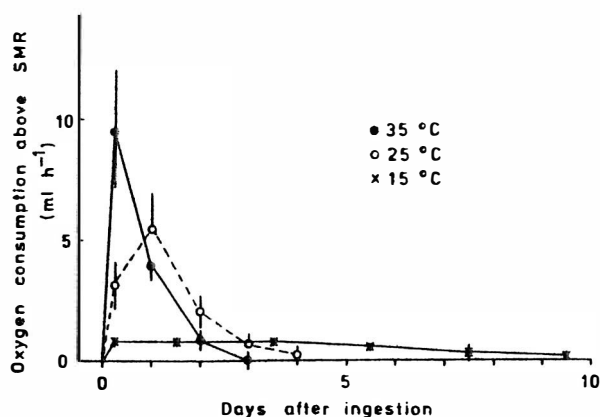
Fig. 2   Time course of increased oxygen consumption after feeding at three temperatures. Mean ±1 S.D.

DISCUSSION

DIGESTION AND THE COST OF BASKING

Temperature affects the rate of digestion (time to first faeces) more than absorption efficiency in *N. maura*, and at low temperatures digestion is incomplete and the food is regurgitated. A similar pattern has been found in other snakes: Skoczylas (1970); Goodman (1971); Greenwald & Kanter (1979); Naulleau (1981); Stevenson, Peterson & Tsuji (1985).

Together with the thermophilic behaviour of snakes after feeding (e.g. Regal, 1966; Lysenko & Gillis, 1980), this suggests that basking is often to speed digestion in these animals. Basking *N. maura* are more likely to have prey in the stomach or void faeces on capture than other individuals (Hailey & Davies, 1987a).

In this case, the metabolic cost of high T_b during basking may be deducted from the energy content of the food (analagous to the energy lost from the SDA). It is assumed that a basking snake raises its T_b from 18°C to 28°C. The former is the mean daytime water temperature during the months March to June, when basking is most common (Hailey & Davies, 1987a: the latter is the mean T_b of basking *N. maura* (Hailey & Davies, 1986d). SMR at 18°C and 28°C is about 0.056 and $0.158ml.g^{-0.75}.h^{-1}$ (Hailey & Davies, 1986c), so basking costs $0.10ml.g^{-0.75}.h^{-1}$, $= 11 J.h^{-1}$ for a 10g snake. The rate of gastric digestion is 14 per cent of body weight per day for a snake of this size at 25°C (Hailey & Davies, 1986b). Digestion was 1.3 times faster at 30°C than at 25°C (judged by the time to first faeces), by interpolation 1.2 times faster at 28°C than at 25°C. In one hour at 28°C a 10g snake would thus digest 0.07g of fish, with an energy content of 280J. The 11 J increased SMR is 3.9 per cent of the gross energy of the food. Thus the cost of basking is rather small, especially when compared to the energy lost during absorption (Table 2) and from the SDA (Table 4).

SPECIFIC DYNAMIC ACTION

Previous studies of the SDA in reptiles have measured the factorial SDA, i.e. VO_2 after feeding divided by SMR. Here, this has been calculated using the maximum observed VO_2 after feeding (4h, 1 day

| °C | Cost of SDA | | (% Total) | SMR $(ml.g^{-0.75}.h^{-1})$ | Extra VO_2 $(ml.g^{-0.75}.h^{-1})$ | Factorial SDA |
	$(ml0_2)$	(KJ)				
15	120	2.4	17	0.037	0.062	2.7
25	230	4.6	33	0.13	0.42	4.2
35	230	4.6	33	0.31	0.73`	3.4

TABLE 4: Total oxygen cost of SDA, and factorial SDA, of *N. maura* fed 3.5g (14 KJ) goldfish at three temperatures. The cost of the SDA is also shown in terms of energy (KJ) and as a proportion of the total energy content of the prey. Factorial SDA is the peak VO_2 after feeding as a multiple of SMR. SMR from Hailey & Davies (1986c), corrected to 1g.

Genus	Food	SDA	Source
Uta	mealworm	1.3	Roberts, 1968
Anolis	meat	1.4	Coulson & Hernandez, 1980
Caiman	rodents	1.6	Gatten, 1980
Alligator	fish	2.3* (1.7-3.0)	Coulson & Hernandez, 1979
Alligator	meat	3.0	Coulson & Hernandez, 1980
Natrix	fish	3.4	this study
Python	rodents	5.0* (3-7)	Benedict, 1932

*Median value, with range

TABLE 5: Published values of factorial SDA in reptiles; ranked in increasing order.

and 1.5 days after ingestion at 35, 25 and 15°C, respectively), and SMR of constant 25°C acclimated *N. maura* from Hailey & Davies (1986d) (Table 4). Mean factorial SDA was 3.4 times.

Values from other carnivorous reptiles are ranked in Table 5. Differences between the main taxa are thereby shown: snakes have the highest factorial SDA, crocodilians intermediate and lizards lowest, seemingly independent of diet. This probably reflects differences in the level of SMR in these groups (Coulson & Hernandez, 1980). For a given level of extra VO_2, factorial SDA will be greater in an animal with a low SMR; for example, SMR of snakes is about half that of lizards of similar size (Bennett & Dawson, 1976).

Ecologically, the most interesting aspect of the SDA is the proportion of food energy lost in this way. Most studies of ecological energetics interpret either energy absorbed (C-F) or assimilated (C-FU) as utilizable energy. This energy must be channelled to respiration or production, both regarded as useful. However, the energy of SDA is unusable to an ectotherm, and is lost; in an endotherm the heat generated is useful, saving other energy from being used for this purpose. Even an 18kg Python has T_b raised by less than 2°C after feeding (Marcellini & Peters, 1982), though this species conserves heat by tight coiling after feeding. The raised T_b is not accompanied by muscle spasms, which cause heat production in brooding pythons (Hutchison, Dowling & Vinegar, 1966). This thermal advantage would be negligible for a small reptile.

On average 28 per cent of the total energy of food was lost as SDA in *N. maura* (Table 4). This high value may be attributed to the chemical composition of the goldfish, which had a low energy content (4.0 KJ.g live weight⁻¹) suggestive of low fat content, and were probably mostly protein. Mammals lose 30 per cent of the energy of protein as SDA, compared to only 4 per cent for fat (Kleiber, 1975). Energy lost as SDA has not previously been measured in reptiles, but may be estimated from the time course of VO_2 in Fig. 1 of Coulson & Hernandez (1980). *Anolis* and *Alligator* were fed 5 per cent of their body weight of lean meat which, assuming an energy content of 5 KJ.g⁻¹, gives an energy loss of about 18 per cent and 26 per cent of the energy of the food. Losses as SDA in *Alligator* are thus similar to those found for *N. maura* here. Jobling (1981) reviews data for nine species of fish, which lost on average 13 per cent (range 9.5-19 per cent) of food energy as SDA.

There were two interesting effects of SDA on maximum VO_2 during activity. Firstly, the total VO_2 during activity after feeding was greater than the AMR of a post-absorptive snake at 35°C, the temperature at which AMR is maximal. Thus AMR in *N. maura* is not limited by the capacity for oxygen exchange in the lungs, or by oxygen transport by the blood, but rather by the capacity for work of the muscles or the rate of oxygen supply within the muscles.

Secondly, the VO_2 available for work during maximal activity (after the SDA was subtracted) was lower than AMR. This suggests that the oxygen exchange capacity of *N. maura* is fully used after feeding, as oxygen exchange is the only system common to VO_2 arising from SDA and from activity. If oxygen exchange were not limiting. VO_2 after feeding would be expected to be the sum of SDA and AMR. Thus the reduced capacity for movement found in recently-fed garter snakes (Garland & Arnold, 1983) may reflect a physiological limitation as well as the physical cost of carrying a weight.

FOOD CONSUMPTION

Two estimates may be made of food consumption; from snakes handling prey when sighted, and from snakes with prey in the stomach on capture, details of which are given by Hailey (1984).

Handling prey. Food intake during foraging may be estimated from the proportion of foraging snakes (taken as all those in water) which were handling prey, together with the rate of food intake during ingestion. Overall, 1 per cent of foraging snakes were handling prey, independent of snake size (Hailey & Davies, 1986a), If wild *N. maura* were foraging for 12 hours a day they would ingest 36 per cent of body weight per day, more than the maximum rate of food processing (Hailey & Davies, 1986b). Foraging must therefore account for less than 12 hours per day, or snakes handling prey are more conspicuous.

Prey in the stomach. Food intake may be estimated from the proportion of snakes which had prey in the stomach (Table 1), together with the rate of gastric digestion (Godley, 1980). The estimate for 4-15g *N. maura* is 0.66 per cent of body weight per day, or 14 $KJ.g^{-0.75}.year^{-1}$ for an active season of 245 days. After losses in digestion only 6 $KJ.g^{-0.75}.year^{-1}$ would be available to the snake, only half of the annual maintenance cost. This suggests that snakes digesting prey are more difficult to locate; secretive basking in cover may be correlated to their reduced capacity for activity.

ENERGY BUDGET COMPONENTS

The components of an energy budget for a female *N. maura* at different ages can now be estimated (Fig. 3).

Respiration: maintenance

Annual maintenance costs based on water temperatures and SMR are 10 $KJ.g^{-0.75}.year^{-1}$ in *N. maura* (Hailey, 1984), 15 per cent of which occurs during the hibernation period (33 per cent of the year). Maintenance during daily inactivity and hibernation will be equivalent to that of snakes in water at the same time, as water and refuge temperatures were similar, and there was no reduction of metabolism below SMR during hibernation.

Respiration: activity

Additional metabolic expenditure from raising T_b above water temperature is treated as a loss from the energy in food during digestion (above). VO_2 during activity has been estimated as about 2.5 x SMR in lizards, (references in Hailey, Rose & Pulford, 1987), i.e. the extra cost of activity is 1.5 x SMR. The cost of movement is low in snakes, about half of that of a lizard of equivalent size (Chodrow & Taylor, 1973). Together with the low energy use in captivity,

this suggests that the cost of activity will be low in *N. maura*, and a value of 1.0 x SMR is used to simulate the extra cost of activity. Activity is assumed to occur for 12 hours per day, evenly spread between day and night, and would thus cost $4.2 \, KJ.g^{-0.75}.year^{-1}$.

Production: sloughing

The cost of sloughing may be estimated from the proportion of snakes observed in pre-moult 1. This stage lasts one week in a thermoregulatory regime (Brown, 1956; pers. obs.), suggesting that juvenile *N. maura* sloughed every nine weeks, about four times per year. This is $2.0 \, KJ.year^{-1}$ for a 2g snake, or $1.2 \, KJ.g^{-0.75}.year^{-1}$. In the absence of other data, this value is used for snakes of all sizes. The cost of a skin is nearly directly proportional to snake weight in *N. maura*, but adults may shed less frequently. Adult natricine snakes slough every 20-50 days in a thermoregulatory regime in captivity with a good supply (Brown, 1956; Semlitsch, 1979), but this may be reduced with natural food levels.

Production: growth and reproduction

Age-specific energy use in growth and reproduction is estimated from the relation between age and snout-vent length SVL (Hailey & Davies, 1987c), and the equations for SVL-weight and SVL-fecundity (viable follicles only) of Hailey & Davies (1987b) (Table 6). Production of growth (P_g) is the increase of weight between years in relation to the median weight over that interval, with the tissue energy content of $4.74 \, KJ.g$ live weight^{-1}. Production of reproduction (P_r) uses the value one egg = 24 KJ (Hailey & Davies, 1987b). P_g and P_r have been weight-corrected with an exponent of 0.75.
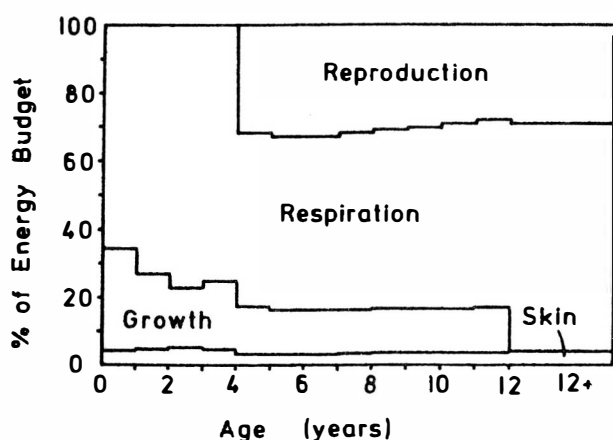

Fig. 3 Proportional allocation of energy in female *N. maura* of different ages. Respiration totals $14.2 \, KJ.g^{-0.75}.year^{-1}$, of which 10% is for hibernation, 60% for maintenance, and 30% for activity.

SIZE OF SNAKE ENERGY BUDGETS

The size of the total energy budget of female *N. maura* increases from about $20 \, KJ.g^{-0.75}.year^{-1}$ before maturity and after growth ends, to about $28 \, KJ.g^{-0.75}.year^{-1}$ when both reproduction and growth occur (Table 6). If on average energy used is $24 \, KJ.g^{-0.75}.year^{-1}$, and food intake occurs over 67 per cent of the year, then utilizable energy intake in *N. maura* is about $0.10 \, KJ.g^{-0.75}.day^{-1}$. This may be

compared with a multi-species estimate for lizards from Turner, Medica & Kowalewski (1976):

Utilizable energy intake = $0.32 \, KJ.g^{-0.81}.day^{-1}$

Thus utilizable energy intake of a 1g *N. maura* is only 31 per cent of that of a 1g lizard, falling slightly to 27 per cent and 24 per cent for 10g and 100g animals, respectively. This is readily accounted for by the low standard metabolic rates, low body temperatures, and (assumed) low factorial scope for routine activity in this reptile. Similar conclusions are reached by considering field metabolic rates, for which Nagy (1982) has summarised the data on iguanid lizards as:

Field metabolic rate = $0.22 \, KJ.g^{-0.80}.day^{-1}$

Natrix maura of different ages use 50-77 per cent (mean 59 per cent) of the total energy budget in metabolism (Fig. 3), so the field metabolic rate is about $0.06 \, KJ.g^{-0.75}.day^{-1}$. This is 27, 24 and 22 per cent of that of lizards, for 1, 10 and 100g animals, respectively.

Only two studies present sufficient information to calculate the energy utilization of other snakes. Data on growth, reproduction and metabolism from Pomianowska-Pilipiuk (1974) allow an estimate of the energy budget of an 86g female *Vipera berus* at $1310 \, KJ.year^{-1}$, equivalent to $46 \, KJ.g^{-0.75}.year^{-1}$. Godley (1980) estimated digestible food intake of 7.3g *Regina alleni* to be $19.6 \, KJ.g^{-1}.year^{-1}$ (mean of spring, autumn and winter values), equivalent to $32 \, KJ.g^{-0.75}.year^{-1}$. These values are more similar to *N. maura* than to lizards.

Information on energy budget components in the wild is available only for *Vipera* (Pomianowska-Pilipiuk, 1974). Data are also available for *Elaphe guttata* and *Heterodon platyrhionos* in captivity at constant 25°C; these have been adjusted for the difference between budgets based on assimilated food intake and on production and SMR (Smith, 1976), which is assumed to be due to metabolism during activity. The percentages due to different components were:

	Natrix	*Vipera*	*Elaphe*	*Heterodon*
Skin	4	10	2	7
Reproduction	31	19	55	34
Growth	13	21		
Respiration	52	50	42	59

The production/assimilation ratios for these four snakes were therefore 0.48, 0.50, 0.57 and 0.41. These values are three times greater than those reported for lizards:

Sceloporus (3 spp)	0.13-0.17	Congdon et al, 1982
Urosaurus ornatus	0.14	Congdon et al, 1982
Uta stansburiana	0.18	Turner et al, 1976
Chalcides bedriagai	0.15	Hailey, Rose & Pulford, 1987

Thus there seems to be a clear difference between the ecological energetics of snakes and lizards. Lizards have higher metabolic rates (Bennett & Dawson, 1976) and energy turnover, but allocate a smaller proportion of this turnover to production. The ecological energetics of widely-foraging snakes which maintain high body temperatures (e.g. *Coluber*) would be of interest, to show whether this difference merely reflects the lifestyles of the snakes studied so far.

Age, x (years)	SVL (cm)	W (g)	Fecundity (viable eggs)	Energy (KJ.g$^{-0.75}$.year^{-1}) P_g	P_r	Total
0	13	1.8	0	6.5	0	21.9
1	20	5.4	0	4.3	0	19.7
2	25	9.5	0	3.2	0	18.6
3	29	14	0	3.8	0	19.2
4	33	21	0	3.8	8.9	28.1
5	37	30	4.2	3.7	9.2	28.3
6	41	41	5.6	3.6	9.1	28.1
7	45	55	6.8	3.6	8.8	27.8
8	49	72	8.2	3.5	8.4	27.3
9	53	92	9.6	3.4	8.1	26.9
10	57	116	11.0	3.4	7.7	26.5
11	61	144	12.4	3.5	7.3	26.1
12	65	177	13.6	0	6.8	22.2
13-20	65	177	13.6	0	6.8	22.2

TABLE 6: Age — specific size, fecundity and energy budget of female *N. maura* from Jalon.

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No. 1   Note added in proof: weight-correction of SDA

The oxygen consumption of active snakes minus SDA on page 162 was calculated by subtracting net mean SDA ($9.5ml.h^{-1}$) from each value of VO_2, then converting to $ml.g^{-0.75}.h^{-1}$. This was used because SDA was not obviously related to body weight. An alternative is to subtract weight-corrected mean SDA ($0.73ml.g^{-0.75}.h^{-1}$) from each value. This gives a mean of 1.49 (S.D. = 0.26), which is not significantly different from AMR (P about 0.1). A study of the weight-dependence of SDA is needed to compare the validity of these methods.

No. 2   Corrections to Hailey & Davies (1986a.b)

Page	Col.	Para.	Line	Should read
55	1	2	13	SF (P>0.05)
55	1	3	6	7.4 minutes
59	1	1	21	a 2g 16cm snake
59	1		last	(Fig. 9)
75	1	Table 2(b)		(P>0.05)

TADPOLE DISTRIBUTION IN RELATION TO VEGETAL HETEROGENEITY IN TEMPORARY PONDS

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ABSTRACT

The distribution in ponds of five species of anuran larvae has been studied in relation to the aquatic vegetation. According to the vegetal species composition, ponds have been classified in five zones. The innermost zone in which little or no vegetation grows was poorly frequented by tadpoles, which were mainly distributed throughout the other more vegetated zones. Some preferences for a specific zone have been found for several species.

INTRODUCTION

Anurans commonly breed in temporary ponds and their larvae are considered to be adapted to the exploitation of the high productivity of this type of habitat (Wassersug 1975). Another adaptation observed is the flexibility of the breeding period of anurans in order to allocate the larval period when the ponds present adequate conditions for larval development (Díaz Paniagua 1985b, in press). Likewise, the larval stage also presents a flexibility according to the duration and the size individuals may reach, depending on the habitat conditions. Thus, tadpoles present a wide variability of sizes at metamorphosis although upper and lower limits are maintained inherent to each species (Wilbur & Collins 1973).

In this study I have studied the distribution of tadpoles in ponds in relation to the vegetation. This problem has been frequently studied for other aquatic animals, such as invertebrates and fishes (e.g. Rosine 1955, Dvorak & Best 1982, Corre *et al* 1982, Werner *et al* 1983, Keast 1984, Gregg & Rose 1985). For tadpoles, however, most of the studies concerning their distribution in ponds mainly consider physical or chemical charateristics (Noland & Ultsch 1981, Odendaal & Bull 1980, 1983, Odendaal *et al* 1982). Recently, Löschenkohl (1985), when studying niche dimensions of tadpoles, has analyzed the influence of vegetation, pointing out that vegetation may produce a shift in the microhabitat of some larval species.

METHODS

During the anuran breeding season 1984-85, tadpole populations were sampled in 16 temporary ponds in the Biological Reserve of Doñana, a locality in south west Spain. Climate characteristics during the study period has been described in previous papers (see Díaz-Paniagua 1985b). Samples were taken monthly by sweeping with a fine meshed-net at different times of day, but always in daylight. They were located at different places along a transect from shore to the centre by each pond. Each sample consisted in sweeping three times each about 1.5m long. The larvae captured were identified, measured (body length without tail) and then released. Information was also recorded about depth and composition of the vegetal species with relative references to their abundance in each sample place.

The temporary ponds were all of freshwater and on sandy soil (detailed description in Díaz Paniagua 1983). Regarding the distribution of vegetation, five different zones were distinguished according to increasing depth. 1) Grass zone: These areas were mainly characterized by the presence of most of the species growing in the surrounding meadows. The most abundant ones were *Cynodon dactylon, Panicum repens* and *Chaetopogon fasciculatus.* 2) *Illecebrum verticilatum* or *Hypericum elodes* area: This area was characterized by the presence of one or both of these plants, presenting a peculiar thick appearance on the surface. 3) Emergent plant zone: *Eleocharis multicaulis,* very abundant in certain ponds was the most common species in this area, followed by *Eleocharis pallustris, Juncus heterophyllus, Holoschoenus vulgaris* and *Juncus spp.* 4) Submergent plants zone: A dense cover of *Myriophyllum alterniflorum, Ranunculus baudotti, Elatine alsinastrum, Callitriche spp., Potamogeton trichioides,* and/or *Zannichellia peltata* chacterized this area. 5) Innermost zone: where scarce or no vegetation was found (Fig. 1).
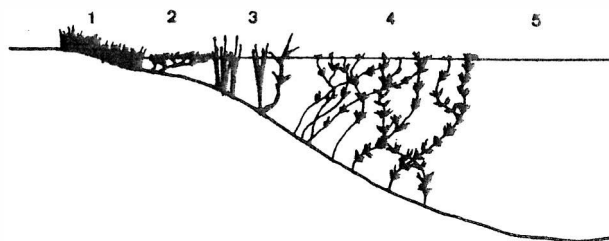

Fig. 1 Scheme of a typical temporary pond with the vegetation zones considered in this study.

Not all the zones referred to were present in all the ponds sampled. Number 1 was commonly followed by number 3, or, sometimes, in small zones, by zone 4.

The innermost zone was found only in the largest and deepest ponds, not occurring in the small and shallow ones.

These five zones were not fully defined in the ponds, where overlaps were wide and common. Therefore, a relative approximation was made according to the most abundant plant species to assign the sample places to one of the areas.

Data are presented as monthly histograms of each species, except for *Rana perezi* which occupied the ponds later than the others, thus only its total distribution is presented. Comparisons among them have been made by means of X^2-test and different degrees of freedom resulted because of the scarcity or absence of tadpoles in some vegetation zones, compelling a grouping of the data.
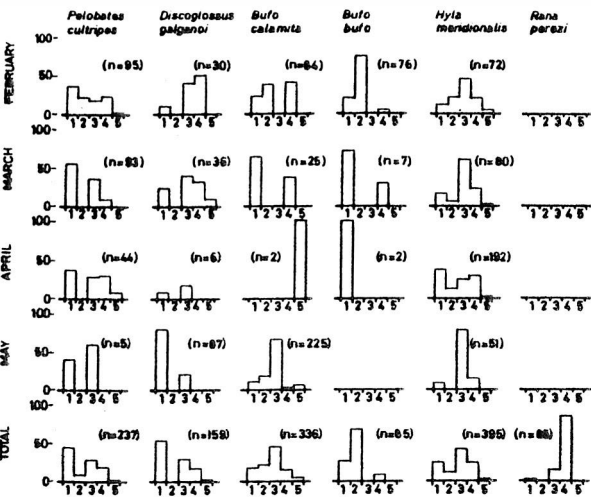

Fig. 2 Monthly distributions of each tadpole species in the five vegetation zones considered.

RESULTS

The distribution of tadpoles of the five species according to the five vegetation zones in ponds is represented in Fig. 2. The main result common to all the species was the scarce or nonutilization of the innermost zone. Very low occurrences of *Pelobates cultripes, Discoglossus galganoi* (after Capula *et al*, 1985), *Bufo calamita* and *Hyla meridionalis* tadpoles have been observed there and none in the cases of *Bufo bufo* and *Rana perezi*. On the other hand, most of anuran larvae were distributed throughout the other vegetation zones, where their typical vegetation gave characteristic heterogeneity.

Considering each species individually, there did not seem to be a particular preference for the use of one of the four zones, as suggested by the differences between the distributions during each month considered (Fig. 2). However, in certain cases there was a major utilization of a specific zone. This was the case with *Hyla meridionalis* tadpoles, which were mainly associated with emergent plants, and *Bufo bufo* tadpoles appearing mostly in the first two zones. *Bufo calamita* and *Discoglossus galganoi* appeared in very different zones, having a large variation during the whole larval period. For *Pelobates cultripes*, a similar utilization of the different zones was observed, with a slight preference for the shore zones in the earliest months.

Rana perezi tadpoles showed a clear preference for the use of the submergent plants where approximately 80 per cent of the larval population was found.

Significant differences were found in comparing the total distributions of the species, except for the pair *Pelobates cultripes-Discoglossus galganoi* (Table 1), in which a main use of the first zone occurred.

	D. galganoi	B. calamita	B. bufo	H. meridionalis	R. perezi
P. cultripes	3.51 (d.f. = 3)	65.42** (d.f. = 4)	25.39** (d.f. = 4)	30.66** (d.f. = 2)	85.67**
D. galganoi		80.47** (d.f. = 3)	34.33** (d.f. = 2)	47.65** (d.f. = 3)	113.70** (d.f. = 2)
B. calamita			8.18* (d.f. = 2)	29.20** (d.f. = 4)	141.60** (d.f. = 2)
B. bufo				13.69** (d.f. = 2)	103.79** (d.f. = 2)
H. meridionalis					90.71** (d.f. = 2)

*: p<0.05
**: p<0.001

TABLE 1: X^2-test comparisons among the total distributions of the species throughout the vegetation zones (d.f. = degrees of freedom).

DISCUSSION

It is evident from the results that tadpoles mainly inhabited the vegetated zones of ponds while rarely visiting the innermost zones. The main difference between these two types of microhabitats concern the spatial heterogeneity provided by aquatic plants. Living in this more heterogeneous zone may provide some advantages to anuran larvae. The effect of predation has been considered an important factor regulating larval amphibian populations (Morin 1983) and it must be reduced in these zones because of the greater probability of escaping from predators (see e.g. Crowder & Cooper 1982, Werner *et al*, 1983). On the other hand, the phytophagous diet of these larval species (Diaz-Paniagua 1985) also suggest that in these zones they may largely find their optimal food.

I have not considered the influence of larval size in the distribution according to the zones in ponds, but it is probably important. There must be different requirements among tadpoles of different sizes, although in this case all the species showed a great use of all the vegetation zones.

ACKNOWLEDGEMENTS

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A STUDY OF GUT FUNCTION IN YOUNG LOGGERHEAD SEA TURTLES, *CARETTA CARETTA* L. AT VARIOUS TEMPERATURES

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ABSTRACT

The effects of temperature within the range 20°C to 30°C, on rate of passage of material through the gut were studied in juvenile captive loggerhead turtles (*Caretta caretta*). Total gut clearance time (TGCT) decreased with increasing temperature ($Q_{10} = 1.6$). The difference in value of TGCT was greater between 20°C and 25°C, where it fell by 33 hours, than between 25°C and 30°C, where it decreased by 6 hours. At 25°C and 30°C the satiation ration amounted to 3.73 per cent body weight; at 20°C the value was only 0.92 per cent. It was calculated that appetite would return to satiation level at a faster rate at 20°C than at 25°C or 30°C.

Food was retained in the oesophagus of juvenile loggerhead turtles for up to one hour after feeding.

INTRODUCTION

Little is known of the behaviour and feeding activity of young marine turtles after entering the sea. It is thought that their passive migration is influenced by currents and oceanic gyre systems, (Witham 1980). Hatchlings have been found associated with sargassum rafts where they presumably feed on the associated fauna of the raft community (Carr and Meylan 1980). Juvenile loggerheads, like the hawksbill *Eretmochelys imbricata,* are thought to be omnivorous. Sargassum was found to be the most prevalent item in the stomachs of loggerhead hatchlings washed onto the Florida coast by Hurricane David in 1979, (Carr and Meylan 1980). This contrasts with the known carnivorous nature of adult *Caretta.* The rates of digestion in young green turtles were studied by Hadjichristophorou and Grove (1983) and Davenport and Oxford (1983). Davenport and Oxford also found that young *C. mydas* probably possesses a cellulose degrading gut microflora, although this was already known for adults of the species, (Bjorndal 1979).

In this study we compared the gut action of young *Caretta caretta* with that of green turtles of similar age, and studied the effect of temperature on the rate of digestion in captive loggerheads fed a high protein artificial diet.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Six juvenile loggerhead turtles were obtained from the Department of Fisheries, Cyprus. The turtles were kept in a recirculating sea water system under constant illumination. During maintenance the temperature of the water was kept at 25°C ±1 and the salinity held at 33-34 °/oo. The turtles were fed every 24 hours on an artificial diet of Omega trout pellets (OTF) at a ration of 1.5 per cent body weight per day.

The artificial diet (OTF) was used throughout these experiments. Three temperatures were chosen; 20°C, 25°C and 30°C. For each set of experiments the temperature in the recirculating system was altered and the animals allowed to acclimatize for a 4 to 5 day period. No studies of physiological acclimation appear to have been carried out on sea turtles, so the chosen acclimatization period was selected rather arbitrarily. However, sudden seawater temperature changes of similar magnitude are very common in the Mediterranean which is generally rather shallow and subject to brief storms alternating with periods of strong sunlight.

CHROMIC OXIDE MEALS

Labelled pellets were prepared by grinding OTF into a fine powder and adding chromic oxide (2 per cent by weight). The resultant green mixture was made into a paste by adding water, extruded through a hypodermic syringe, dried and cut into pellets.

Prior to chromic oxide meals the turtles were starved for 27 hours, then fed a 1.5 per cent body weight ration of the labelled pellets. The 3 hour extra deprivation beyond the normal feeding interval ensured that total consumption occurred. Normal feeding procedure was maintained before and after feeding the labelled meal.

To determine the time of production of labelled faeces accurately, the turtles were taken out of the recirculating system 1 to 2 days after consuming the chromic oxide meal and placed in holding tanks containing sea water kept at the experimental temperature. A system of slats mounted 2 cm above the bottom of the tanks ensured that any faeces produced were not broken up or consumed by the turtles. The experimental process was repeated ten times at each temperature, and average values for the following parameter calculated:

Total Gut Clearance Time (TGCT): the time taken for food to pass completely through the digestive

system estimated as the time elapsed between feeding and the appearance of the last green faeces. The relationship $TGCT = a'W^{b'}.e^{c'T}$, (where W is the weight of the animals, T is the temperature in degrees Celsuis and a', b' and c' are constants) was calculated separately for each turtle by multilinear regression since individual turtles differ in their rate of digestion. These separately calculated values were then averaged.

BARIUM SULPHATE MEALS

To study the progress of food along the gut, the turtles were fed a 1.5 per cent body weight ration of a barium sulphate labelled meal at a concentration of one part $BaSO_4$ to four parts OTF by weight. The labelled pellets were prepared in the same fashion as those containing chromic oxide. Before feeding, the turtles were starved for 27 hours and the normal feeding procedure was maintained before and after the meal. X-radiography was performed just after feeding and at various time intervals subsequently.

SATIATION MEALS

The turtles were deprived of food for the length of time corresponding to the calculated 'gastric emptying time ' GET (the time interval between appearance and disappearance of chromic oxide labelled faeces); stomach fullness is considered to be one of the main controls of appetite. They were then fed a satiation ration. To do this, 50g of pellets was weighed out and the pellets offered to each turtle until they had refused five pellets in five minutes. The amount eaten was calculated by deduction of the weight of the uneaten food from the original 50g.

The relationship:
satiation amount (g) $= a''W^{b''}.e^{c''T}$, (where W is the weight of the animals, T is the temperature in degrees Celsuis and a'', b'' and c'' are constants), was calculated for all the animals.

RATE OF APPETITE RETURN

After the satiation meal described above, each turtle (studied in pairs) was given a second satiation meal at intervals of 6, 12, 18, 24, 30 and 36 hours after the start of the first satiation meal. To express the return of appetite the Von Bertalanffy equation was fitted to the data for each temperature. The Von Bertalanffy equation assumes that data rise towards some theoretical maximum and the closer their value gets to the maximum the slower the rate of change. The equation is as follows:

$$Wt = W(1-exp(-K(t-t_0)))$$

Where Wt is the % body weight meal ingested after time t,

and W is the theoretical maximum % body weight meal.

K is a constant at each temperature.

An algorithm capable of finding an unconstrained minimum of a sum of squares (through the NAG subroutine E04FDF) was used to fit the Von Bertalanffy equation to the data. By this method estimates of W, K and t_0 were obtained for each temperature.

RESULTS

TOTAL GUT CLEARANCE TIME

Initially it was hoped that gastric emptying time (GET) could be measured. The method of labelling food with chromic oxide to estimate GET assumes that after the food has left the stomach its rate of passage through the rest of the gut occurs at a constant rate. It also assumes that the food enters the stomach immediately after eating. The time of feeding affected faecal deposition; turtles defaecated most material just after feeding. This finding suggests that passage of food through the latter part of the gut does not occur at a constant rate so GET cannot be measured accurately.

At 20°C the turtles has to be fed several times each day to ensure the complete ingestion of the 1.5 per cent body weight meal. Therefore, given the observed association of feeding and defaecation, it is not surprising that TGCT values at this temperature tend to be rather variable.

Fig. 1 shows the presence of food in the oesophagus for at least one hour after a meal. Food retention indicates that the oesophagus acts as a temporary food store or crop. This was observed in animals at 10 months (weighing approximately 500g) and 20 months (weighing approximately 2500g) of age. Whether this novel finding also applies to adult loggerheads is unknown.

Fig. 1 1 hour after feeding; food in the oesophagus.

The data (Table 1) for TGCT and body weight were found to be normally distributed in each case, and ANOVA showed that for each quantity the populations from 20°C, 25°C and 30°C differ significantly because of the growth of the animals (P<0.001). TGCT was found to decrease with increasing temperature. The increase from 20°C to 25°C had a greater effect on TGCT than the increase from 25°C to 30°C. From 20°C to 25°C the value for TGCT fell by approximately 33 hours and from 25°C to 30°C it fell by a further 6 hours.

The calculated equation for TGCT was found to be:

$$TGCT = 420W^{-0.0025}.e^{-0.049T} \text{ hours}$$

In this equation weight (W) had no effect on TGCT ($W^{-0.0025}$). The effect of temperature (T) on TGCT was pronounced. ($Q_{10} = 1.6$)).

	Temperature °C			
	20°C	25°C	30°C	L.S.D. (T5%)*
TGCT	155.8	122.0	95.3	7.358
Body Wt	1409.9	560.5	965.2	144.88

* Least significant difference

TABLE 1: Mean total gut clearance times (n = 10) and body weights at 20°C, 25°C and 30°C.

SATIATION AMOUNT

From the observed values (Tables 2, 3 and 4) there was no difference between satiation amount at 25°C and 30°C. The mean value at these temperatures was 3.73 per cent body weight, but at 20°C there was a marked drop in satiation ration (mean = 0.92 per cent body weight). Significant linear relationships of log transformed body weight on log transformed satiation amount were found by regression (Fig. 2) for 20°C (P<0.05, $R^2 = 0.35$) and at 30°C (P<0.001, $R^2 = 0.70$). At 25°C satiation amount did not vary with body wt.

This showed that body weight had a more pronounced effect on satiation amount at 20°C and 30°C than at 25°C where there was little relationship between the terms.
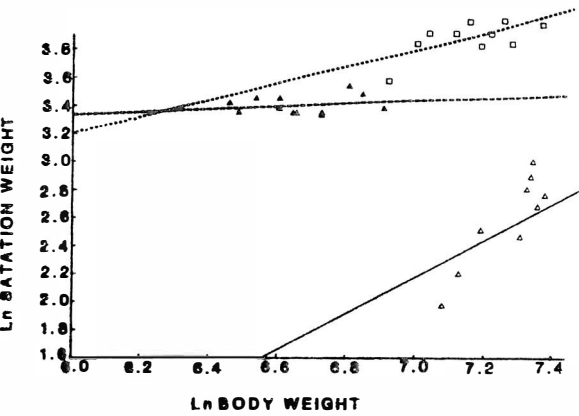

Fig. 2   In Satiation weight plotted against In body weight.

□ ; In Satiation weight at 30°C.
▲ ; In Satiation weight at 25°C.
Δ ; In Satiation weight at 20°C.

The calculated equation for satiation amount was found to be:

$$\text{Satiation amount (g)} = 0.696W^{0.0567}.e^{0.131T}$$

In this equation temperature increase was found to have a small effect ($Q_{10} = 0.27$) on satiation amount.

RETURN OF APPETITE

There are two main factors which are thought to control appetite; stomach fullness and the previous feeding pattern experienced (amount and frequency of feeding). After the first satiation meal the stomach was assumed to be full although the previous maintenance ration would have affected this value. The time of feeding will also affect the ration consumed; turtles fed at night took less than those fed during the day and ate most when fed close to their regular feeding time (9.00-

Turtle Number	Body Weight (gms)	Satiation Meal (1) 73 (hrs)* (gms)	Satiation Meal as % B.W.	Deprivation Time (hrs)	Satiation Meal (2) (gms)	Satiation Meal as % B.Wt	Satiation Meal (2) as a percentage of Sat Meal (1)
3	1183	7.2	0.6	6	4.4	0.4	61.1
4	1821	112.0	0.6	6	8.4	0.5	7.5
5	1512	16.6	1.1	12	9.9	0.6	59.6
2	1482	11.7	0.8	12	7.5	0.5	64.1
5	1535	20.1	1.3	18	29.1	1.9	144.7
4	1867	17.3	0.9	18	25.4	1.4	146.8
3	1242	9.0	0.7	24	16.9	1.34	187.7
2	1527	18.1	1.2	24	33.8	2.2	186.7
3	1558	14.6	0.9	30	20.6	1.3	141.1
5	1592	15.9	1.0	30	27.0	1.7	169.8
4	1946	17.0	0.9	36	31.4	1.6	184.7
2	1324	12.8	1.0	36	24.5	1.8	191.4

* = 'Gastric Emptying Time' (see text).

TABLE 2: Satiation and Appetite return at 20°C.

Turtle Number	Body Weight (gms)	Satiation Meal (1) 42 (hrs)* (gms)	Satiation Meal as % B.W.	Deprivation Time (hrs)	Satiation Meal (2) (gms)	Satiation Meal as % B.Wt	Satiation Meal (2) as a percentage of Sat Meal (1)
1	688	31.2	4.5	6	9.5	1.4	30.6
2	637	30.1	4.7	6	7.5	1.2	25.0
4	832	28.6	3.4	12	15.3	1.8	54.6
5	736	31.3	4.2	12	16.1	2.2	51.9
1	736	29.5	4.0	18	21.9	3.0	75.5
4	908	34.3	3.8	18	16.5	1.8	48.5
2	654	28.3	3.3	24	18.7	2.9	66.8
5	774	28.2	3.6	24	20.0	2.6	71.4
1	936	32.6	3.3	30	24.8	2.6	78.1
3	766	28.3	3.7	30	25.1	3.3	89.3
2	832	27.5	3.3	36	28.2	3.4	100.0
5	995	29.4	3.0	36	35.1	3.5	120.7

* = 'Gastric Emptying Time' (see text).

TABLE 3: Satiation and Appetite return at 25°C.

Turtle Number	Body Weight (gms)	Satiation Meal (1) 36 (hrs)* (gms)	Satiation Meal as % B.W.	Deprivation Time (hrs)	Satiation Meal (2) (gms)	Satiation Meal as % B.Wt	Satiation Meal (2) as a percentage of Sat Meal (1)
1	1276	54.5	4.3	6	26.8	2.1	49.2
2	1134	50.0	4.5	6	16.2	1.4	32.4
3	1012	35.6	3.5	12	11.0	1.1	30.9
4	1444	46.6	3.2	12	17.3	1.2	37.3
5	1285	45.8	3.6	18	30.6	2.4	66.31
6	2250	67.0	3.0	18	44.0	2.0	65.7
1	1409	59.5	4.2	24	40.9	3.3	78.3
3	1097	46.4	4.2	24	40.5	3.7	87.3
2	1225	50.1	4.1	30	49.3	4.0	98.4
5	1359	50.1	3.7	30	48.0	3.5	95.8
4	1579	53.5	3.4	36	54.2	3.4	101.3
6	2327	70.0	3.0	36	74.3	3.2	106.1

* = 'Gastric Emptying Time' (see text).

TABLE 4: Satiation and Appetite return at 30°C.

10.00 hrs). At 20°C the rate at which pellets were taken was so slow in some cases that an accurate determination of feeding cessation was impossible.

The data (Tables 2, 3 and 4) was expressed in the form of the Von Bertalanffy equation for the return of appetite. The calculated equations for each temperature are as follows:

30°C; $Wt = 7.18(1-exp(-0.0177(t+5.42)))$
25°C; $Wt = 4.34(1-exp(-0.0326(t+5.65)))$
20°C; $Wt = 1.86(1-exp(-0.0894(t-3.79)))$

The calculated values for the total squares of the absolute and relative errors of the fitted function showed that the reliability of the estimates of W, K and t_0 was greatest at both 20°C and 25°C where more of the curve was expressed by the sample points (Fig. 3). The curves in Fig. 3 were extended beyond the area of the data to illustrate which part of the curve at each temperature the points expressed. At 30°C the observed values lay in the exponential phase of the curve and consequently the estimate of W is questionable. The greatest theoretical body weight meal size (W) was at 30°C with a value of 7.2 per cent body weight. At 25°C it was 4.3 per cent and the lowest value was at 20°C where it was 1.9 per cent. These values all exceeded the observed values for the first satiation meals, which were as follows: 30°C mean satiation amount = 3.73%; 25°C, 3.73%; 20°C, 0.92%. The greatest differences between first satiation meal size and theoretical maximum were at 20°C and 30°C where the maxima were approximately twice the size of the first satiation meal. The rate of achieving the theoretical maximum was greatest at 20°C, (K = 0.0894). At 25°C and 30°C the values for K were 0.0326 and 0.0177 respectively.
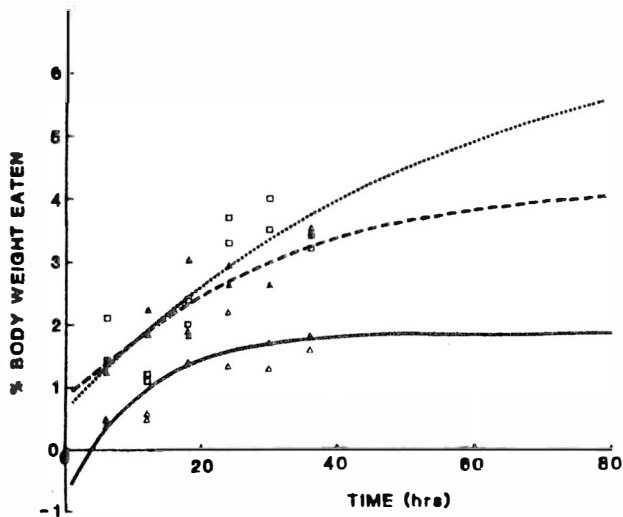
Fig. 3   % body weight eaten (g) after the first satiation meal.

□ ; % Satiation weight at 30°C.
▲ ; % Satiation weight at 25°C.
Δ ; % Satiation weight at 20°C.

DISCUSSION

The results of this study demonstrate that temperature has, over the range between 20°C and 30°C, a considerable effect on the rate of passage of food through the digestive system of young loggerhead turtles. The differences in satiation amount and TGCT were much greater between 20°C and 25°C than between 25°C and 30°C. The results at the two higher temperatures were identical for satiation (3.73 per cent of the body weight), and there was only a 6 hour difference between clearance times. In contrast, between 20°C and 25°C there was a 33 hour difference in clearance time and at 20°C, the satiation ration was only 0.92 per cent of the body weight. Rather surprisingly, appetite returned to satiation level faster at 20°C than at 25°C or 30°C, but this presumably reflects the much lower satiation ration.

These data support available field and growth data. Observations indicate that, in coastal feeding areas, marine turtles largely return to feed or become active when the temperature rises in late spring to around 20°C (Carr *et al.*, 1980). Carr *et al.*, (1980) found that adult *C. caretta* hibernated in the mud of submarine canyons off Cape Canaveral in February when water temperatures averaged 11°C, but by mid March when the water temperature had risen to 19°C the turtles were resting on the bottom. Carr *et al.* (1980) also noted an influx at this time of turtles from other areas.

Hughes (1974) studied growth in hatchling logger-heads. At 14°C and 15°C turtles ate little and lost weight, while those at 17°C and 18°C ate more but grew much more slowly than turtles kept at 24°C. It appears that active feeding starts at approximately 20°C though the preferred temperature of *Caretta* is over 25°C. In this respect loggerhead turtles appear to closely resemble *Chelonia mydas*. Bjorndal (1980) found that water temperature affected digestive efficiency in the green turtle, with efficiencies becoming more variable during the winter months when the temperature approached 20°C.

The studies of gut dynamics described here were compromised to a certain extent by the unavoidably small number of turtles available, which meant that their weights had changed somewhat between experiments at different temperatures. Fänge and Grove (1979) considered the problem of using different sized animals in digestion studies. If (as in the present study) meals of constant percent body weight are fed to experimental animals, then the absolute rate of digestion of food will be faster in a larger animal (because the surface area of food bolus exposed to enzyme action is greater), but digestion will be completed sooner in a smaller animal (because the surface area-to-volume ratio of the smaller meal is greater).

It took 122±7 hours for food to pass completely through the gut of *C. caretta* but for *C. mydas* of similar size it took 176±11 hours (Hajichristophorou and Grove, 1983). These shorter evacuation times may be indicative of the more carnivorous habit of *Caretta*. Young loggerheads appeared to be far more voracious feeders than young green turtles. The satiation ration of *Caretta* at 25°C was twice the size of that of *Chelonia* and appetite return was 25 per cent quicker in loggerheads.

During passive migration the young loggerhead turtle presumably relies on an opportunistic feeding strategy. The adaptation of the oesophagus as a temporary food store allows the animal to take advantage of occasional overabundances of prey. The oesophagus possesses soft conical papillae on its luminal surface. These papillae project towards the stomach, but it is not known whether they act solely to prevent food returning to the mouth or whether they also have a glandular function. Oesophageal food storage has not been reported for other sea turtles, and is certainly not characteristic of *Chelonia mydas* in which food always reaches the stomach within 5 minutes (Davenport and Oxford, 1984).

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HABITAT DESTRUCTION AND ITS EFFECT ON A POPULATION OF SMOOTH NEWTS, *TRITURUS VULGARIS:* AN UNFORTUNATE FIELD EXPERIMENT

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ABSTRACT

Partial clearance of the terrestrial vegetation surrounding a pond in southern England resulted in a significant decrease in the size of the smooth newt (*Triturus vulgaris*) population breeding there, relative to a nearby, intact pond. This finding supports the suggestion of Beebee (1981) that the terrestrial habitat surrounding a pond is an important determinant of that pond's suitability for amphibians.

INTRODUCTION

In a survey of the status of British amphibians in which England, Scotland and Wales were divided into 12 'survey regions', populations of the smooth newt (*Triturus vulgaris* L.) were reported to have suffered declines in three regions. Over 70 per cent of the respondents in this survey blamed these declines on loss of suitable habitat due to human activity (Cooke and Scorgie, 1983).

Loss of ponds is an obvious cause for concern amongst those involved in the conservation of amphibian populations. However, loss of the terrestrial habitat surrounding extant ponds can also have detrimental effects on the amphibians which visit the ponds in order to breed and feed. The importance of such habitat was stressed by Beebee (1981), who surveyed a large number of ponds in southern England and found that those with marginal scrub habitat were more likely to support amphibian populations than

were those without (all other requirements being equal).

In 1986, the author was afforded the opportunity to study the effect of terrestrial habitat destruction on smooth newts at a local level. In 1985, as part of an investigation into the reproductive biology of this species, breeding population size was assessed at two, closely-situated ponds. In the autumn of that year, about one half of the marginal terrestrial vegetation was removed from one pond; the other pond was left intact. In 1986, the two ponds were surveyed once more, and the influence of habitat destruction on smooth newt breeding population size was determined.

METHODS

The two study sites are ponds situated on the Conniburrow housing estate in Milton Keynes, Buckinghamshire, southern England. They are approximately 0.25 miles from one another. In 1985, both

	Marigold Pond	Cleaver Pond
Ordnance survey reference	851398	851394
Surface area (sq. m.)	200	250
Maximum water depth (cm)	23	60
Pond substrate	Thick clay mud and plant litter	Thick clay mud and plant litter
Shore	1985 and 1986: stony, with some support from wooden slats	1985: muddy banks. 1986: muddy banks. with some support from slats
Amphibians present	*Triturus vulgaris, T. cristatus, Bufo bufo, Rana temporaria*	*T. vulgaris, B. bufo*
Dominant terrestrial vegetation	*Crataegus monogyna*	*C. monogyna*
Dominant aquatic vegetation	*Elodea canadensis, Lemna minor, Potamogeton pectinatus*	*E. canadensis, L. minor, P. natans*

TABLE 1: Summary of some physical and biological characteristics of the two study sites.

ponds were subjected to a detailed physical and biological survey, some of the results of which are summarised in Table 1. Marigold Pond was not subjected to removal of vegetation between the breeding seasons of 1985 and 1986, and can thus be regarded as the 'control' pond. Cleaver Pond was subjected to vegetation removal along its northern shore, and is thus the 'experimental' pond. The vegetation was cleared by local government to improve access to Cleaver Pond and render it safer when visited by children (the latter is clearly a laudible reason for the clearance).

Censuses of the smooth newts in each pond were initiated in March in both of the two years of study. Each site was visited two or three times per calendar week, from between 1930 and 1100 hr (at or around the time of dusk). At Marigold Pond, each visit consisted of slowly walking a circuit of the perimeter of the pond, scanning the shallower and less-vegetated areas by torchlight. The number of smooth newts seen in the water was recorded. At Cleaver Pond in 1985, only a small area at the western end of the pond was accessible for torching, due to the thick vegetation surrounding the pond elsewhere. During each visit, the author stood at a spot at this end of the pond, and counted the number of smooth newts which were visible during a period of 10 minute in duration. In 1986, access to Cleaver Pond was greatly improved, but the same method of census was employed as in the previous year.

In 1985, visits to the ponds were terminated in mid-June; in 1986, visits were continued until early July. For analytical purposes, the numbers of smooth newts seen at each pond from week 10 to week 19 in both years of the study are considered.

RESULTS AND DISCUSSION

The data obtained during the censuses are summarised in Table 2. For both ponds the numbers of smooth newts counted in 1986 were lower than in 1985. The decrease for Marigold (control) Pond was 29.7 per cent, compared with a decrease of 75.4 per cent for Cleaver (experimental) Pond. This difference is statistically significant (X^2 = 13.9, P<0.001). It is

possible that this difference at Cleaver Pond merely reflects a change in the behaviour of the newts; although no direct alterations were made to the aquatic habitat, destruction of the terrestrial vegetation may have had indirect effects on the aquatic habitat. Whilst this possibility cannot be dismissed entirely, torching of those parts of Cleaver Pond rendered more accessible in 1986 did not result in a high count of aquatic newts (23 in total). This suggests that the between-years difference at Cleaver Pond was not due to a gross change in the distribution of newts in the pond.

	Cumulative No. newts at:			
	Marigold Pond		Cleaver Pond	
Week	1985	1986	1985	1986
10	0	0	0	0
11	3	0	0	●
12	13	5	3	0
13	52	8	12	2
14	109	—*	22	—*
15	214	13	29	7
16	317	53	36	8
17	341	124	45	11
18	443	203	55	16
19	492	346	65	16

*No circuits made in that week.

TABLE 2: The cumulative number of smooth newts counted by torchlight at each of the study ponds in each of the two years of the study.

This result supports the hypothesis that destruction of the terrestrial habitat in the close vicinity of a pond can have a severely detrimental effect on the smooth newt population using that pond as a site for breeding and feeding. It also provides empirical verification of Beebee's (1981) conclusion that the presence of such habitat is important in determining the suitability of a pond for amphibians. The longer term consequences of habitat destruction at Cleaver Pond are unclear, but two obvious possibilities exist: first, the population of newts may fall below the 'effective population size' and

thus risk extinction, or secondly, the population may stabilise at a new, lower level. Only long term field work would provide the answer.

The benefits afforded by terrestrial vegetation along the shores of a pond are of two types. The first, direct benefits, include the utilisation of the habitat as a refuge during the winter. This was certainly the case for Cleaver Pond in the winter of 1984, when the newts (as well as common toads, *Bufo bufo*) were known to have used rabbit burrows in the vegetation as hibernaculae (Verrell, 1985). These burrows were destroyed in the autumn of 1985. The second type of benefit can be termed 'indirect', and includes protection from human interference. Aside from the dumping of domestic and garden refuse, the most common form of interference in Conniburrow is the collection of breeding amphibians by children (the 'small child effect'). It seems unlikely that this effect was more severe for Cleaver Pond than for Marigold Pond in 1986, and thus unlikely that differential interference was the major factor responsible for the sharp decline in smooth newt population size seen at the former site.

In summary, the activities of a local government provided an unfortunate opportunity to assess the importance of the terrestrial habitat surrounding a pond for the smooth newt population breeding and feeding there. Destruction of this habitat resulted in a sharp reduction in the size of the breeding population, probably due to the removal of overwintering refuges. Improved accessibility to the pond, and a con-commitant increase in the intensity of the 'small child

effect', probably exacerbated this. It is thus clear that there can be a serious conflict over the interests of those committed to amphibian conservation and those who wish to make ponds safe and accessible public amenities. In such conflicts, it seems probable that the amphibians will be dealt the worst hand.

ACKNOWLEDGEMENTS

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ENZYME (ALDOLASE) ACTIVITY IN HYPEROSMOTIC MEDIA (NaCl AND UREA) IN THE TERRESTRIAL TOAD, *BUFO VIRIDIS* AND FROG *RANA RIDIBUNDA*

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ABSTRACT

In this study we examined the adaptation of the enzyme Aldolase from frogs and toads to different temperatures and to hyperosmotic media of 400-1000mOsm/Kg of urea or NaCl. Maximum enzyme activity was found between 200-400mOsm/Kg NaCl, both in enzymes from green toads and from marsh frogs. However, above 500mOsm/Kg, the activity of enzymes from green toads was significantly higher than the activity of enzymes from marsh frogs.

The activity of aldolase from green toads decreased very slowly as the media concentration of urea increased. However, the activity of aldolase from marsh frogs decreased rapidly under the same conditions.

The maximum activity of aldolase from both frogs and toads was at 25°C. The activity of aldolase from green toads was significantly higher than the activity of aldolase from marsh frogs when measured only at high temperatures (35°C). The results of this study support the idea that the biochemical systems of terrestrial amphibia are tolerant to hyperosmotic media.

INTRODUCTION

The green toad is terrestrial and lives in a wide range of habitats reaching the southern limit of its distribution in Israel, where it penetrates into the desert (Warburg, 1972). Katz (1973) succeeded in adapting green toads to 800mOsm/Kg NaCl and Degani (1985b) adapted the green toad to 800mOsm/Kg urea. Degani et al. (1984) found that after three months in the soil, blood plasma concentration reached a maximum of 1400mOsm/Kg with urea concentration at 900mM. Intracellular urea concentration in the muscle of these toads amounted to 500mM urea. The plasma osmolarity of R. ridibunda did not reach 600mOsm/Kg in any of these conditions (Katz, 1973; Degani, 1985a). B. viridis appears to show an ability to tolerate a wide variety of osmotic plasma concentrations, which help it to adapt to a wide variety of osmotic environments.

Urea accumulation in the intra — and — extracellular fluids appear to play a critical role in adaptation of amphibians to terrestrial life (Bentley, 1966; McClanahan, 1967 and 1972; Johns, 1980; 1982; Degani et al., 1981; 1984). Data presented by McClanahan (1972); and Jones (1982) suggested that the rate of urea synthesis increases in Xenopus laevis, Scaphiopus couchi, Bufo woodhousei and Hyla cadaverina, when the water potential of the environment decreases. During dehydration, the plasma, urine and intracellular body fluid osmolalities of these amphibians were elevated. This was caused not only by increased urea but also by increased concentrations of Na^+, Cl^- and K^+ (Degani and Warburg, 1984). However, there is no information on the adaptation of enzymes to such high concentrations of urea and NaCl.

The hypothesis examined in this study is whether the enzymes of terrestrial amphibia are more tolerant to high temperatures, and to urea and NaCl concentrations, than aquatic species. In the present study the activity of Aldolase was compared in the green toad (Bufo viridis) and the semi-aquatic marsh frog (Rana ridibunda).

MATERIAL AND METHODS

Green toads (B. viridis) and marsh frogs (R. ridibunda) were collected from the same locality in Northern Israel (Naharia) and were kept in the laboratory in a terrarium containing soil and small vessels of water, at a temperature of 20-23°C.

Samples of muscle were taken (200mg) from the hind-legs of green toads and marsh frogs and the fructose — 1.6 Diphosphate Aldolase activity was determined after homogenization (polytron homogenizer, model Kinematic CH-6010 Krins-LU-Switzerland) in 1ml TEM buffer phosphate pH 7.8.

The assay of activity was performed as described by Gracy et al. (1970). Aldolase activity was measured after the enzymes were acclimated for 20 minutes in different solutions of NaCl (from 100 to 1000mOsm/Kg) or urea (from 400 to 1000mOsm/Kg). Enzyme activity was also measured at different temperatures (15°C, 20°C, 25°C, 30° and 35°C) in a

solution of 300mOsm/Kg. Aldolase activity was measured by monitoring the rate of oxidation of NADH at 340nm on a Gilford Spectrophotometer at 25°C. One unit of enzyme activity is defined as 1μmole of substrate (FDP) that is cleaved in one minute at 25°C. Aldolase activity was calculated to mU by the equation: $100D = 0.0806\mu mole/ml/min. = 0.0806$ unit of activity (U).

RESULTS

The activity (%) of aldolase during acclimation to NaCl solution up to 1000mOsm/Kg is shown in Fig. 1. Maximum enzyme activity was found between 200-400mOsm/Kg NaCl, both in enzymes from green toads and from marsh frogs. However, above 500mOsm/Kg NaCl, the activity of enzyme from green toads was significantly higher than the enzyme activity of marsh frogs.
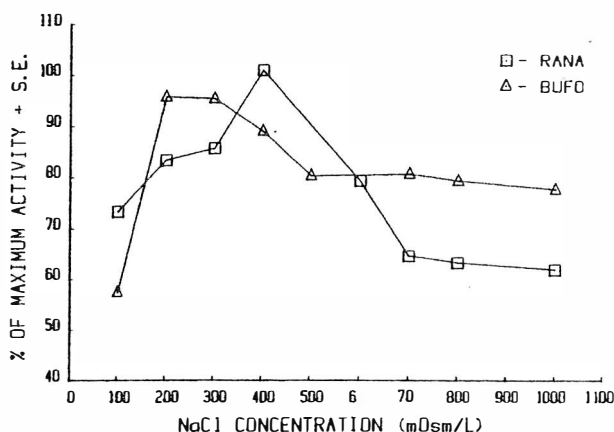

Fig. 1   Comparison between enzyme activity of Bufo viridis and Rana ridibunda in different NaCl osmotic pressures.

There were no significant differences found between the aldolase activity from green toads or marsh frogs acclimated to 400mOsm/Kg (200mOsm/Kg NaCl and 200mOsm/Kg urea) (Fig. 2). In media of osmolarity above 400mOsm/Kg increase due to additional urea caused the activity of aldolase from B. viridis to be higher than that of the enzyme from R. ridibunda. The activity of aldolase from marsh frogs decreased rapidly after acclimatisation to a high urea concentration, and the activity of aldolase from green toads decreased slowly (Fig. 2). Both enzymes from green toads and from marsh frogs decreased with a linear correlation to increasing media urea concentration (Table 1). The slope of the linear equation for green toads is smaller than the slope of the linear equation for marsh frogs.

The maximum activity of aldolase from both green toads and marsh frogs was found at 25°C (Fig. 3). There was no significant difference between the activity of aldolase from green toads and marsh frogs at temperatures of 15-30°C. However, there is a significant difference only at a temperature of 35°C (P<0.05; t-test). At this temperature the activity of aldolase from green toads was higher than the activity of aldolase from marsh frogs.
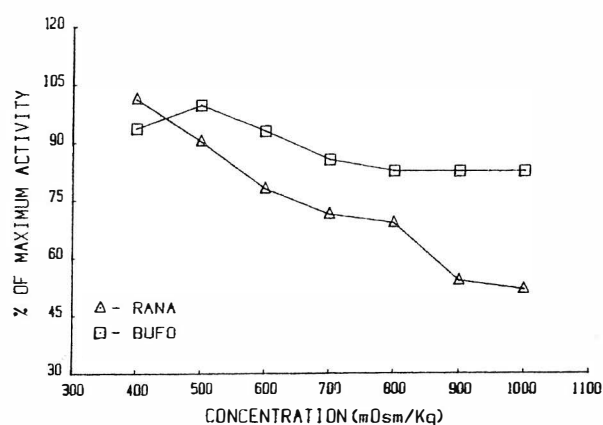
Fig. 2   Enzyme activity from *Bufo viridis* and *Rana ridibunda* in different urea solutions.
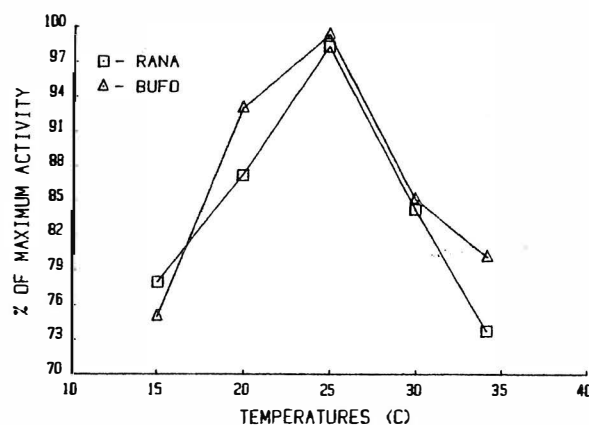

Fig. 3   Temperature effect on enzyme activity from *Bufo viridis* and *Rana ridibunda*.

Rana				Bufo			
Equation NaCl	r	N	P	Equation NaCl	r	N	P
y = –0.8099 x +1345	0.95	11	<0.001	y = –0.5430 x +1259	.87	13	<0.05
Urea				Urea			
y = –1.7109 x +2170	.91	22	<0.001	y = –0.3946 x +1523	.71	12	<0.01

TABLE 1: Enzyme activity equations of *Bufo viridis* and *Rana ridibunda* acclimated to different solutions according to the most significant correlation.

Notations:

Y = Enzyme activity (mu) and X = osmolality (mOsm/kg).

There are significant differences (P<0.05) between the slopes of both pairs *Rana : Bufo* in NaCl, *Rana : Bufo* in Urea.

DISCUSSION

The osmotic concentration recorded in the body fluid of green toads following prolonged dehydration in the soil is the highest reported so far for any terrestrial amphibian (Degani *et al.*, 1984). A similar high osmotic concentration was recorded in the terrestrial spade foot toad (*Scaphiopus couch*) (Shoemaker, 1969; McClanahan, 1972) from the Arizona desert. Both *Bufo* and *Scaphiopus* store urea in their body fluids and this allows them to raise the bodily osmatic pressure more efficiently than acquatic species (Balinsky, 1981; Degani *et al.*, 1984).

There are some physiological mechanisms described which increased the plasma osmolality by increasing the plasma Na+, Cl– and urea during dehydration or saline adaptation. For example by reducing the glomerular filtration rate of the nephrone and increasing the influx of Na+, Cl– through the nephrone, bladder and the skin (Jorgensen, 1950; Bentley, 1958; Maetz, 1968). Accumulation of urea occurs slowly and may be due to both urea retention and, possibly to increased synthesis due to a higher concentration of presursors in the urea cycle (Jones, 1980; Balinsky, 1981; Lee *et al.*, 1982).

In this study we found that aldolase activity is tolerant to a high urea concentration only in terrestrial green toads but not in semi-aquatic marsh frogs. These results might explain the results of previous studies in our laboratory. The accumulation of urea in the plasma of green toad is accompanied by an intracellular space both *in vivo* and *in vitro* (Degani *et al.*, 1984; Degani, 1985a,b). In the green toad from soil the intracellular urea is less concentrated than that in the plasma. (Degani *et al.*, 1984), The urea concentration in the plasma of the green toad was significantly higher than that in the plasma of the marsh frog, both adapted to a hyperosmotic (urea) environment (Degani, 1985a). Crab-eating frogs (*Rana cancrivora*), the only anuran that lives in sea-water had a maximal urea concentration in the plasma of 350mM (Gordan *et al.*, 1961) and this is similar to the urea concentration (265mM) found in the plasma of green toads adapted to sea-water (Katz, 1973). The muscle of the crab-eating frog is not only tolerant to urea, but actually requires it. Thesleff and Schmidt-Nielsen (1962) were unable to observe contractions unless urea was present in the medium, and they routinely added 250mOsm urea to the medium bathing the muscle.

Muscle tissue of green toads seems more tolerant to high urea concentration than the muscle of marsh frogs (Degani, 1985a). In conclusion while these previous studies show that different physiological mechanisms are tolerant to high urea concentrations,

this study shows that in terrestrial amphibians there might also be enzymes which are able to adapt activity to these conditions (Delsone and Whitford, 1973; Licht *et al.*, 1975; Degani, 1985a).

Rapid dehydration or adaptation to salinity causes an elevation of Na^+ and Cl^- in he tissues (Degani and Warburg, 1984) so that the enzymes are exposed to high Na^+ and Cl^- concentrations (Degani, 1985a). In this we found that an enzyme (aldolase) of green toads tolerates a higher concentration of Na^+ and Cl^- than does the same enzyme from marsh frogs and this is maybe a partial explanation of the greater tolerance both to dehydration and to saline environments of the toad compared to the frog.

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THE INFLUENCE OF TEMPERATURE AND ACTIVITY ON AEROBIC AND ANAEROBIC METABOLISM IN THE VIVIPAROUS LIZARD, *LACERTA VIVIPARA* (JACQUIN).

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ABSTRACT

Aerobic and anaerobic metabolic rates were determined at temperatures between 20°C and 35°C for the viviparous lizard, *Lacerta vivipara*. Both parameters were found to be maximal around the preferred body temperature (30°C) with a low thermal temperature dependence above PBT. It is noted that *L. vivipara* does not need a large rate of anaerobic support and aerobic metabolism could supply the energy needed for activity.

INTRODUCTION

The active oxygen consumption of reptiles, particularly lizards, exceeds the resting (standard) oxygen consumption rate and the aerobic scope (the difference between the resting and active oxygen consumption rates) is maximal around the preferred body temperature (PBT) with a low thermal temperature dependence above this level (Bennett and Dawson, 1976; Bennett, 1982; Al-Sadoon, 1983). Maximal aerobic scope tends to be strictly temperature dependent in reptiles with the exception of iguanid and agamid lizards that can maximise this scope at the PBT (Bennett, 1982). It is also known that reptiles employ anaerobic metabolic scope (which is derived from the difference in lactate concentration levels between active and resting lizards) as a major energy source during the initial stages of forced activity (Bennett and Licht, 1972; Al-Sadoon, 1986) and the total metabolic scope (aerobic and anaerobic) is greatest at the PBT (Bennett and Dawson, 1972; Al-Sadoon, 1986).

The present study examines the aerobic and anaerobic metabolism of the viviparous lizard, *Lacerta vivipara* (Jacquin) to determine their contributions to the metabolic scope of this species.

MATERIALS AND METHODS

Common lizards, *L. vivipara*, were collected from the New Forest, Hampshire (Southern England) and housed in large tanks in the laboratory with food and water *ad lib*. The lizards remained in good condition throughout the experimental period despite the fact that they were fasted for at least 5-6 days preceding use. They were divided into two groups, one for the aerobic measurements and the other for anaerobic measurements.

Aerobic measurement

Oxygen consumption rate for resting and active lizards was determined using ten lizards at 20°C, 25°C, 30°C and 35°C in a double-chamber volumetric system (Al-Sadoon and Spellerberg, 1985, a,b). Estimations of active metabolism were obtained from lizards subjected to electrical stimulation. Each individual was weighed placed into the sealed animal chamber of the volumetric system and were subjected to electrical shocks (10-14 volts) for at least five minutes via small stainless steel pin electrodes connected to a stimulator. These reached the animal through the top of the chamber and were implanted subdermally into its belly anterior to the hind limbs to stimulate rapid movement (period of stimulation). Thereafter, oxygen consumption determinations were taken every minute during the maximal activity period (a period of five minutes). Then the lizard was left to rest for another five minutes (recovery period) and oxygen consumption was recorded every minute during this postactive recovery period. The date were expressed as ml O_2/g body weight/hr and corrected to STP (see Fig. 2).
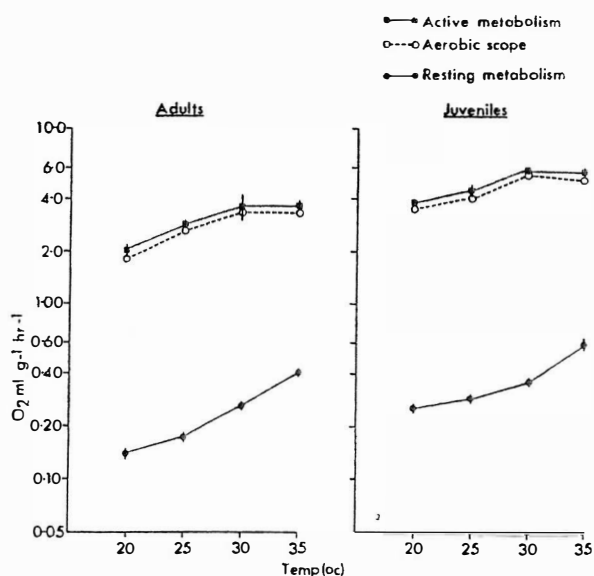

Fig. 1 Resting, active metabolism and aerobic scope of adult and juvenile *L. vivipara* determined at various temperatures. Each point represents the mean oxygen consumption of a number of lizards. Vertical lines represent ± standard errors.

Anaerobic measurement

Total lactate production at different temperatures was determined in the whole body homogenates of resting and active lizards according to the method of Bennett and Licht (1972) and the data were expressed as mg lactate/g body weight.

Statistical analyses of differences between mean values of various groups at each temperature were performed using one-way analysis of variance (ANOVA) and were considered significant at $P < 0.05$.

RESULTS

Resting and active oxygen consumption rates

Mean values of resting oxygen consumption expressed as $(ml\ O_2\ g^{-1}\ hr^{-1})$ were observed to increase with rising temperature from 20-35°C in both adult and juvenile lizards (Fig. 1). During the first 1-2 minutes of stimulation, the lizards were continuously moving around the animal chamber and the amounts of oxygen consumed during this period were considered to represent the active oxygen consumption.

This was also observed to increase with rising temperature from 20-30°C, but remained almost constant $(Q_{10} \simeq 1)$ at 30-35°C in both adult and juvenile lizards. The overall Q_{10} values of active lizards were lower than those of resting ones (Table 1) and so were the total means for active oxygen consumption during five minutes of post-activity $(P < 0.05)$ at all temperature levels tested (Fig. 2). On the other hand, the aerobic scope increased with rising temperature from 20-30°C but dropped between 30°C and 35°C in both adult and juvenile lizards (Fig. 1).

Resting and active lactate production

Mean values whole-body lactate concentration expressed as mg lactate per gram body weight at different temperatures (20-35°C) for juvenile and adult lizards are shown in Fig. 3. There was no significant difference $(P > 0.05)$ in these values between resting adult or juvenile lizards over the entire temperature range, but they increased in active ones at 20-30°C and dropped between 30-35°C (Fig. 3). The Q_{10} values for resting and active lactate concentrations are given in Table 1.
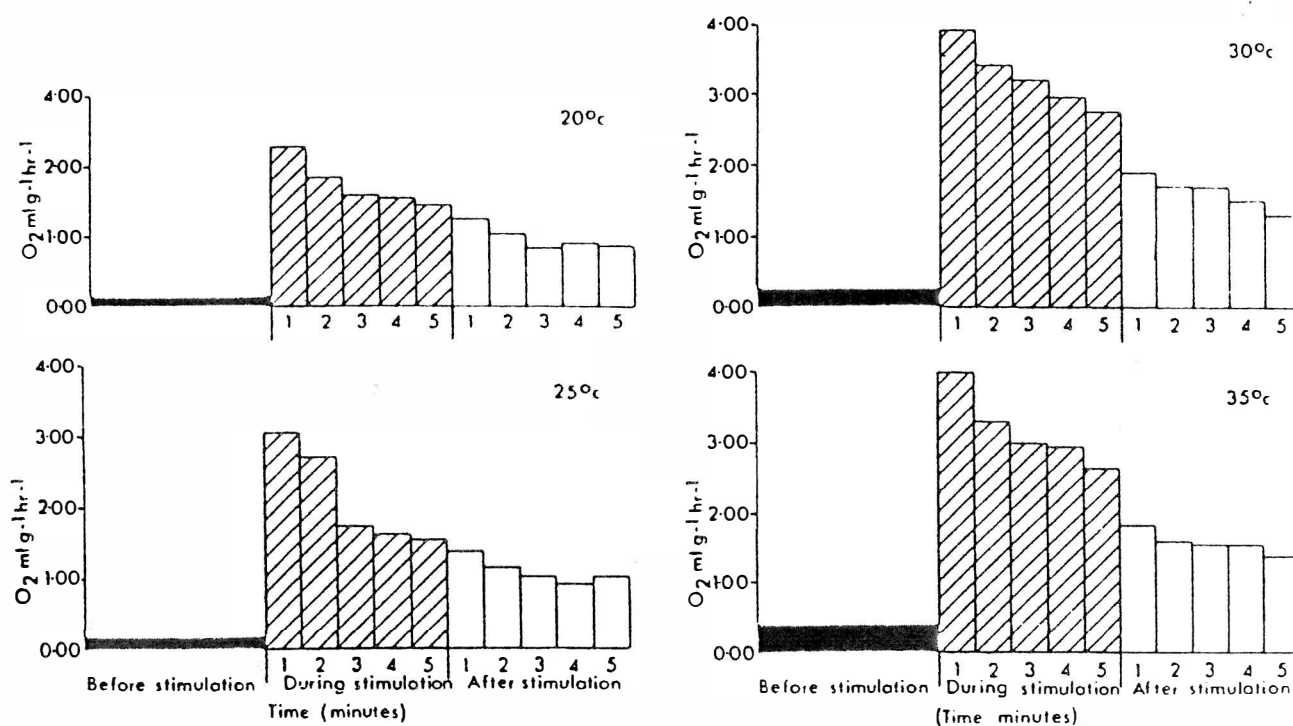

Fig. 2 Oxygen consumption rate of six male adult *L. vivipara* prior to stimulation and at one minute intervals, during 5 minute of stimulation and 5 minute of recovery. ■ resting O_2 consumption, ▨ active O_2 consumption, ▢ post active O_2 consumption.

Temperature interval (°C)	Q_{10} values for oxygen consumption						Q_{10} values for lactate production					
	Resting		Active		Aerobic scope		Resting		Active		Anaerobic scope	
	juv.	adults	juv.	adults	juv.	adults	juv.	adults	juv.	adults	juv.	adults
20-25	1.33	1.45	1.33	2.00	1.33	2.04	1.50	1.05	1.40	1.35	1.35	1.65
25-30	1.50	2.40	1.76	1.64	1.78	1.59	1.00	1.52	1.06	1.40	1.09	1.32
30-35	2.75	2.40	0.93	0.97	0.84	0.92	1.16	0.68	0.94	0.59	0.83	0.52
Overall Q_{10} (20-35)	1.78	2.03	1.30	1.47	1.26	1.44	1.20	1.03	1.12	1.04	1.07	1.04

TABLE 1: Q_{10} values for aerobic and anaerobic metabolism of resting and active lizards of *L. vivipara* at various temperatures.
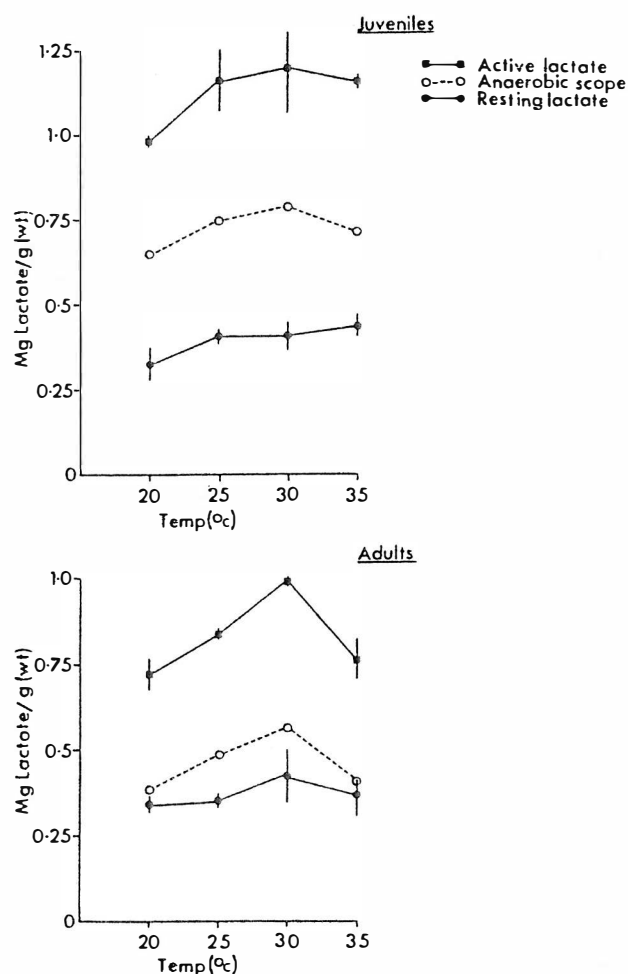
Fig. 3   Whole-body lactate concentration of resting, active (stimulated) lizards and the anaerobic scope of juvenile and adult *L. vivipara* determined at various temperatures. Each point represents the mean of several animals. Vertical lines represent ± standard errors.

The highest Q_{10} values for active juvenile lizards were between 20-25°C and between 25-30°C for active adults and the lowest were between 30-35°C for both of them. The anaerobic scope values for both increased with rising temperature from 20°C to 30°C and decreased at 35°C (Fig. 3). There was no significant difference (P>0.05) in the overall Q_{10} values between active and resting lactate production in either juvenile or adult lizards (Table 1).

DISCUSSION

The results indicate that the metabolism-temperature curves of both juvenile and adult *L. vivipara* are similar in shape but those of the resting and active juveniles are above those of the adults. This may be explained by the weight-specific metabolism which varies inversely with body weight (mean weights of the adults and juveniles were 3.8 and 1.4g respectively). Similar observations were made by Al-Sadoon (1983) for the desert skink, *Chalcides ocellatus*.

The resting oxygen consumption values of juvenile and adult *L. vivipara* are in line with values reported for lizards of comparable size (see Andrews and

Pough, 1985). However, the active oxygen consumption data obtained in the present study are the first for any lizard of the size of *L. vivipara*.

The aerobic metabolic scope for juvenile and adult *L. vivipara* was observed in the present study to increase with rising the temperature from 20°C to 30°C and the lizard appears to maximise this scope at its PBT which thereafter became independent of temperature. The maximisation of the aerobic scope at the PBT is understandable as, under natural conditions, most reptiles are known to be capable of thermoregulation. At temperatures exceeding the PBT, the aerobic scopes of several lizard species were shown to be temperature independent (Bennett and Dawson, 1972; Wilson, 1974; Bennett et al., 1975; Bennett and Gleeson, 1976; Al-Sadoon, 1986).

As in the observations of Bennett and Licht (1972) on six species of lizards of comparable size to *L. vivipara*, the present results show little variation in resting lactate production between juveniles and adults. On the other hand the anaerobic scope values of adult *L. vivipara* reported in the present study are lower than those reported for lizards of similar size. However, comparison between the anaerobic scope values of juvenile *L. vivipara* (wt $\bar{x}$ 1.2g) with those lizards of similar size show little variation (values for *Xantusia vigilis* (wt $\bar{x}$ 1.2g) were 1.19, 1.32mg lact./g (wt) at 20°C and 30°C respectively, and scope values of for *Scincella lateralis* (wt $\bar{x}$ 1.7g) were 0.94, 0.88mg lact./g (wt) at 20°C and 30°C respectively, Bennett and Licht, 1972). This variation in the anaerobic metabolism between *L. vivipara* and other lizards of similar size could be due to the method of measuring the anaerobic metabolism in these lizards. The previous anaerobic values (Bennett and Licht, 1972) were calculated as the amount of lactate produced during activity to exhaustion by stimulating the animal for a longer period of time (4-6 minutes). These values were termed the 'anaerobic capacity' whereas the present values for *L. vivipara* are taken from stimulating the animals for a shorter period of time (2 minutes). Unlike the aerobic scope, the anaerobic scope and the anaerobic capacity are less temperature dependent and are less than predicted for biological reaction rates in general. The Q_{10} ranges from 1.09 to 1.35 and from 1.32 to 1.65 above 20°C in *L. vivipara* adults and juveniles respectively (Table 1). However, the anaerobic scope has very low temperature dependence (Q_{10} less than 1) above the PBT. This temperature dependence in the anaerobic metabolism may be of great importance for these animals during activity, particularly when avoiding predators and when the lizard's temperature is below the preferred levels. Similar observations were made by Al-Sadoon (1986) on *C. ocellatus*.

The data obtained for *L. vivipara* (adults and juveniles) during the initial stages of forced activity in the present study might indicate that the animals rely mainly on the aerobic contribution of ATP (Table 2) as a major source of energy at the voluntary body temperature (20°C to 35°C) and that the ATP produced by aerobic, anaerobic and total metabolic scope for the animal increases with rising temperature till reaching maximal levels at 30°C (PBT for

Exper. Temp. (°C)	Aerobic scope ATP (μmole/g/2 min)				Anaerobic scope ATP (μmole/g/2 min)				Total metabolic scope ATP (μmole/g/2 min)	
	juv.	(%)	adults	(%)	juv.	(%)	adults	(%)	juv.	adults
20	34.80	76	18.17	74	10.83	23	6.34	26	45.63	24.51
25	40.21	76	26.00	76	12.59	24	8.17	24	52.80	34.17
30	53.75	80	32.86	78	13.15	19	9.38	22	66.89	42.24
35	49.49	80	31.03	82	12.01	19	6.80	18	61.50	37.83

TABLE 2: Aerobic and anaerobic contribution to the total metabolic scope during 2 min. of activity in juveniles and adults of *L. vivipara*.

L. vivipara, see Avery, 1979) before declining at temperatures above that level. At the PBT, aerobiosis was observed in the present study to provide 78 per cent and 80 per cent of the total scope during the two minutes of forced activity for adults and juvenile *L. vivipara* respectively (Fig. 4). A similar observations on other animals indicated that aerobic scope accounted for more than 80 per cent of total ATP produced during a 3 minute of activity in the Giant toad *Bufo marinus* (Miller and Hutchison, 1980). Bennett and Licht (1973) reported that *Bufo boreas* depend on aerobic metabolism to sustain activity. The larger values of the aerobic scope in *L. vivipara* could be related, to some extent, to the behaviour of this species in the field. In its natural habitat of heathland, field edges and wooded areas, *L. vivipara* is a shuttling heliotherm that emerges in sunny mornings to spend a considerable part of the day basking, foraging and feeding (Avery, 1971). If disturbed, its reaction is to seek refuge within seconds. Hence, such type of behaviour does not need a considerable rate of anaerobic support and aerobic metabolism alone is sufficient to supply the required energy.

Moreover, small lizard species had much greater aerobic scope levels than larger ones. This difference may be related to the greater pressure from predation for smaller animals, and also the capacity of larger lizards for defence against predators. Also, other physiological functions such as oxygen transfer across the lungs, could be the reason for this variation. These considerations would also suggest that juveniles of *L. vivipara* would have much higher aerobic scope than adult lizards.
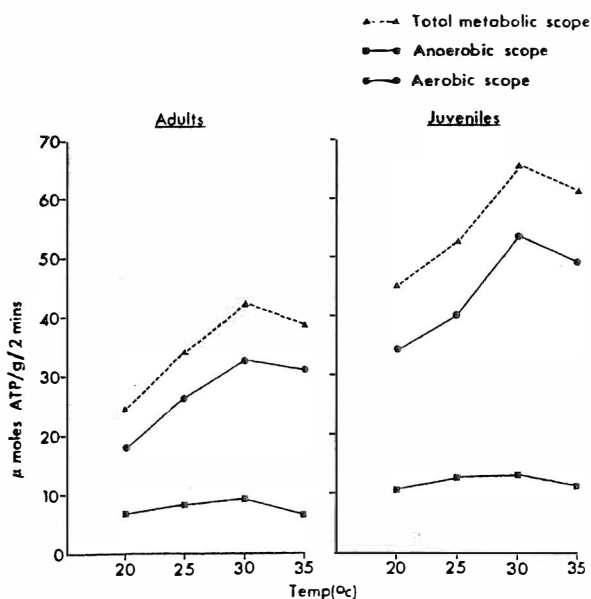
ACKNOWLEDGEMENTS

Fig. 4 Aerobic, anaerobic and total metabolic scope ATP generation during 2 minute of burst activity in *L. vivipara* (adults and juveniles). ATP was measured by the method of Bennett and Licht (1972).

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GROWTH, MOVEMENT AND POPULATION DYNAMICS OF *NATRIX MAURA* IN A DRYING RIVER

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ABSTRACT

Viperine water snakes were studied by mark-recapture in a small river in Eastern Spain from 1981 to 1983, a period of drought. Observed growth rates between captures were low and highly variable. Growth rings were counted in skull bones; narrow rings could not be found, and the observed rings were probably from periods of faster growth or normal growth before the drought. The rings predict that males and females reached maturity in their third and fifth years, respectively. The effect of drought was greater on growth than on reproduction. Movements of snakes captured several times at long intervals suggest that the home ranges of mature males and females were 170m and 250m of river, respectively, although some individuals moved 1km between years. A review of published data showed that widely foraging grass and garter snakes have greater displacements between captures than the more sedentary water snakes.

There were estimated to be 1060 and 390 adult males and females in the main study area, which was a 2km length of river which included most of the permanent unpolluted water in the river system. Annual survival of adult snakes remaining within the study area was estimated as 0.53 ± 0.16 and 0.71 ± 0.25 in males and females, respectively. A simple model of the dynamics of this population was developed from results on survival, recruitment, growth and fecundity, as a hypothesis for further study. The model suggested that: 1) There was dispersal of adult males but not adult females — this was supported by the population size structure in peripheral areas where mature females were scarce and which were probably stocked by dispersal. 2) The number of adult males and females was stable or increasing, and juvenile survival of about 0.65 year^{-1} would be necessary for total population stability.

INTRODUCTION

The dynamics of snake populations have proved difficult to study, as these animals are difficult to find or catch (especially juveniles), they have slow growth without external indicators of age, and often show long

seasonal movements. After surveying the available data (which suggested that those populations which had been studied were unable to maintain themselves), Turner (1977) concluded 'one is left with distinct reservations as to the suitability of snake populations for this sort of ecological endeavour'. After the

extensive studies of the 1950s and 1960s (Carpenter, 1952; Tinkle, 1957; Fitch, 1960, 1963, 1965, 1975; Viitanen, 1967; Prestt, 1971) the popularity of large scale marking efforts has declined. Since then, population studies have concentrated on snakes which gather at hibernacula (Parker, 1976; Gregory, 1977) where large numbers can be captured in a short time.

During a study of the physiological ecology of the viperine water snake *Natrix maura*, a large number of individuals were marked and released. This paper presents information on their growth, movements and numbers, and a model of the dynamics of the population as a hypothesis for further study. This work is continuing in cooperation with Spanish herpetologists and in parallel with further physiological studies. In this way long-term data on one snake population can accumulate as a by-product of other work; we agree with Turner that pure snake population studies are uneconomical in terms of the data obtained per unit research time.

SITE DESCRIPTION

Natrix maura were studied in the river Jalon, eastern Spain (39°N, 0°E) between August 1981 and August 1983. A map of the river bed is shown in Fig. 1; Hailey (1984) gives a more detailed map including topography, neighbouring river systems, and the estimated catchment area. The river is 40km long in total, with a catchment area above Jalon village of 135km². Most parts of the river were investigated, and the only permanent fresh water was found near the villages of Alcalali and Jalon; elsewhere the river was a dry rocky barranco. There was a treated sewage outlet and an area of polluted water below each village along the river.
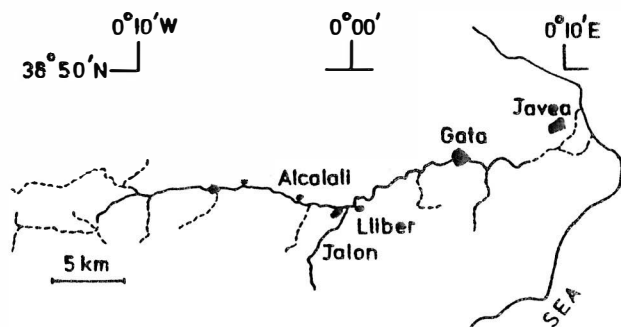

Fig. 1   The river Jalon, based on the Mapa Militaria 1961. ———— River, ———— Barranco. The only permanent clean fresh water found during the study was in the area of Alcalali and Jalon.

The study area was a 2km length of river at Jalon, from C-F in Fig. 2. A detailed map of this area (Hailey, 1984) was produced with compass and measuring line, enabling captures to be located to the nearest 10m. This area was permanently wet, but the river was reduced to a series of pools when the connecting stream dried up in summer. There was no water for several km above Alcalali or below Lliber.

The stream meandered across the river bed, which was an area 5-50m (in most places 10-20m) wide and about 3m below the level of the surrounding terraced
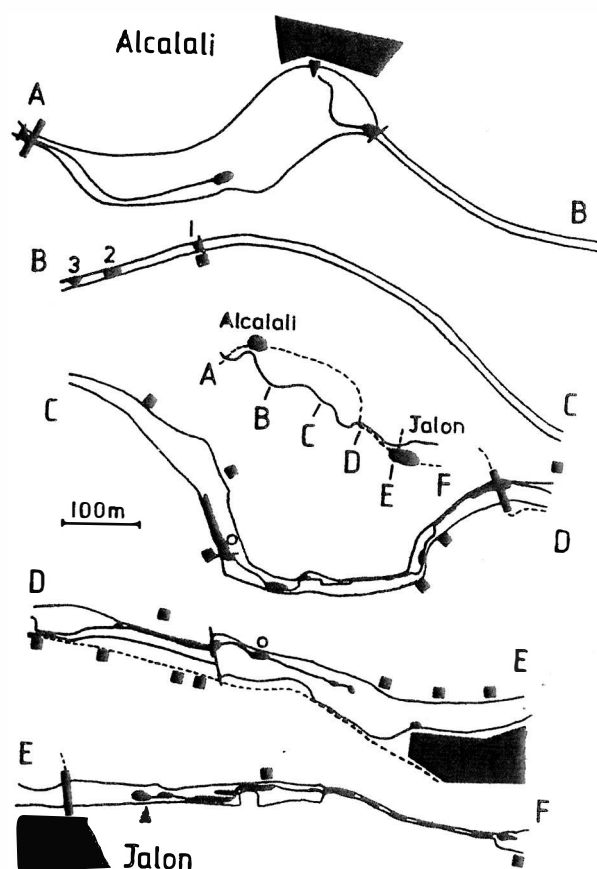

Fig. 2   The study area between Alcalali and Jalon — the edges of these villages are shown as shaded areas. The outline of the river bed is shown, together with the course of the stream and positions of pools. ■ House, ——— Road, ▲ Sewage outlet, ○ Rock pile where juveniles were common. Thin bars across the river are weirs, thick bars are bridges. The inset shows the sections of river in situ.

farmland (mostly citrus groves and vegetable plots). Some parts of the river bed were damp and muddy with *Juncus* reeds and grass, and other parts were dry and stony with oleander bushes. Most of the river bed was was flanked with dense bands of bamboo. Two herds of about 100 sheep and goats used the area in dry weather, passing up and down the river on the way to other pasture, feeding on the way.

The study took place during a period of drought, which lasted from 1979 to 1983 in Alicante and Valencia provinces. The river flowed three times during the study; water levels rose in a few hours due to the large catchment area of bare hills, and fell in a few days. The estimated area of water in the region C-F varied during the study between about 0.2 to 0.8 ha, mean 0.3 ha; flow rates measured with markers in the current were between 0 and $0.1 m^3.s^{-1}$. Area and flow increased to about 4 ha and $15 m^3.s^{-1}$ when the river flowed.

The stream bed was stony, with few water weeds apart from algal mats. There were a few large beds of bulrushes, otherwise cover was provided by the marginal bamboo and rocks and stone walls. The availability of prey has already been described (Hailey and Davies, 1986a), particularly the drying pools with trapped fish which were a feature of the drought.

METHODS

Snakes were captured by hand after searching systematically along the stream and over the river bed. At night they were located with a torch, retained overnight in cloth bags for handling, and released the next day at the place of capture. Each snake was weighed with a Pesola scale and measured against steel tape rule. All lengths are snout-vent lengths, SVL.

In most cases sex was determined from the appearance of the tail, which is long and has a swelling at the base in males. This was often unclear in small snakes and those in poor condition, and these were probed with a grass stem or a round-ended nylon bristle to determine the presence of hemipenes (Schaefer, 1934). An attempt to use plastic mesh tunnel traps failed; although snakes were captured in this way, the traps and fences were soon disturbed by sheep and moved or destroyed.

Snakes were marked by clipping the ventral scales, and they were also recognised by natural markings (Hailey and Davies, 1985). Some snakes were removed for studies of metabolism and reproduction (Hailey and Davies, 1986b, 1987a respectively). These were mostly from outside the study area; small snakes from Alcalali (Fig. 2, A-B) and adult females from pools 1-3 (Fig. 2, B-C). The heads of these snakes were analysed for growth rings.

1460 individuals were marked in the area C-F from August 1981 to August 1983, 1413 of these during the main sampling sessions. About 400 more were captured in the area B-C from June to August 1983, only one of which (an adult male) was originally marked in the area C-F; most of these snakes were marked and released, but are not included in the population analysis. Similarly, about 300 have been captured at Alcalali (A-B) at various times, but no marked snakes have been found or released there. In total the 1860 snakes marked in the area B-F were captured 2410 times, many of the recaptures being at short intervals.

GROWTH RINGS

Heads were boiled in water (sometimes in the field) for several hours to soften the flesh, then the ectopterygoid bones were removed, cleaned of muscle, and air-dried. These were cleared in glycerol for 0 to 16 hours, in proportion to the size of the bone, and examined under 40 x magnification (Bryuzgin, 1939; Petter-Rousseaux, 1953). Mandible bones were treated similarly, but proved to have less clear rings and were not used.

RESULTS

GROWTH

Observed growth

Only data from captures separated by at least 100 days of active season (allowing for a 120 day hibernation period for recaptures in different years) have been used. Errors in measurement of SVL make short term growth difficult to study in snakes which grow slowly. Observed growth rates were highly
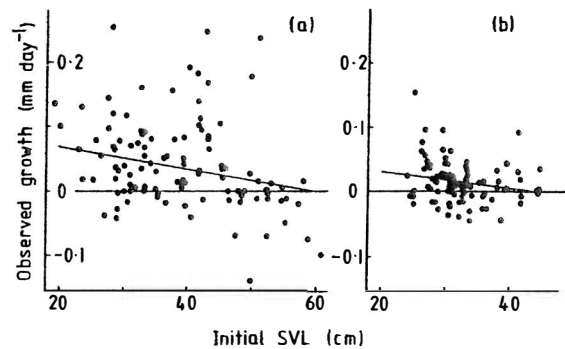

Fig. 3 Observed growth rates of *Natrix maura* between captures at intervals of >100 days. a) females, b) males. Equations (1 and 2) in the text.

variable (Fig. 3), reflecting the high variability in feeding opportunities in time and space in the drying river (Hailey and Davies, 1986a). Only about 5 per cent of this variability could be explained by the size of the snake, although the regressions of growth rate (mm SVL. day^{-1}) on initial SVL (cm) were significant, and are used as summaries of size-specific growth:

Females: Growth rate = 0.104 - 0.00172 SVL   (1)
$$(n = 109, r = -0.23, P<0.05)$$

Males: Growth rate = 0.057 - 00134 SVL   (2)
$$(n = 87, r = -0.21, P<0.05)$$

As the observed growth rates were so variable, no attempt has been made to fit the data to more complex growth formulae (Fukada, 1961; Andrews, 1982).
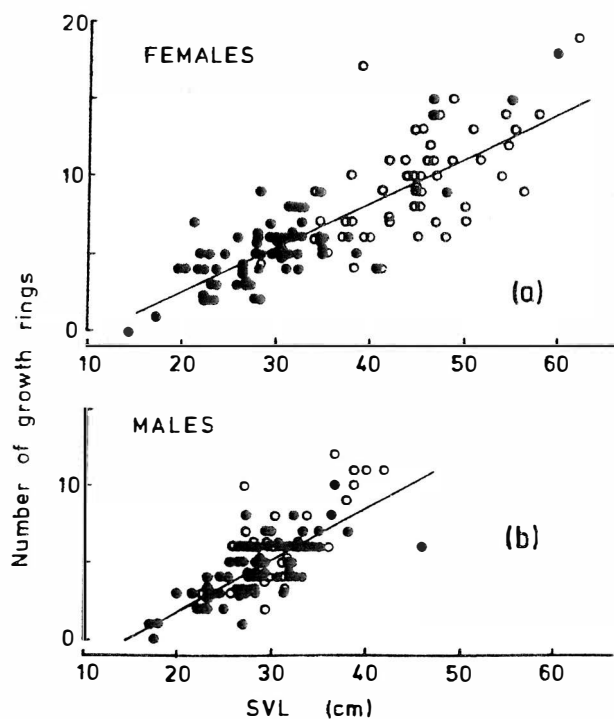

Fig. 4 Number of growth rings in the ectopterygoid of *N. maura* a) females, b) males. Source of specimens: ● Alcalali (Fig. 2, A-B); o pools 1-3, area B-C. Equations (3 and 4) in the text.

Growth rings

Narrow rings which would be expected to accompany slow growth were seldom seen. It is

therefore thought that most rings were produced during periods of faster growth, or remained from normal growth preceding the drought. The relationship between the number of growth rings and SVL (cm) is shown in Fig. 4, described by the equations:

Females: Growth rings = 0.291 SVL — 3.3   (3)
               (n = 119, r = 0.81, P<0.01)

Males: Growth rings = 0.342 SVL — 5.0   (4)
               (n = 105, r = 0.73, P<0.01)

If it is assumed that the number of growth rings equals the age in years, then equations 3 and 4 can be rearranged to show size *vs* age:

Females: SVL = 3.44 Age + 11.3   (5)
Males: SVL = 2.92 Age + 14.6   (6)

These equations predict growth rates of 3.4 and 2.9cm. year^{-1} and hatchling SVL of about 11.5 and 14.5cm in females and males, respectively.
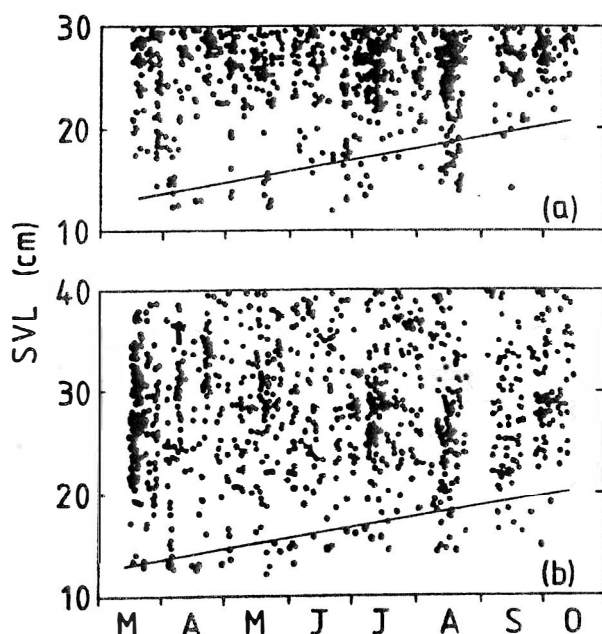

Fig. 5   Seasonal abundance of *N. maura* of different sizes (including recaptures), with inferred growth curve for the first full year fitted by eye. a) Males, truncated at 30cm, b) females, truncated at 40cm.

Growth of juveniles

No data are available on observed growth of juveniles as none were recaptured, and few heads were available to study growth rings of small snakes. Growth of juvenile snakes may also be estimated from the seasonal abundance of individual size (Fitch, 1961; Saint Girons, 1965). The smallest snakes found, of both sexes, had SVL of 12-14cm (Fig. 5), similar to the size of hatchlings (Davies, unpublished). Fig. 5 shows suggested growth during the first full year from 13 to 20cm.

Snakes of 12-14cm were commonly found under piles of rocks in early spring at two locations (Fig. 2), from where they dispersed, and slightly larger snakes were found in many places later in the year. No juveniles were found under these rocks, or anywhere else, in autumn, and the activities between hatching (probably in September, from eggs laid in July —

Hailey and Davies, 1987a) and the first hibernation are unknown. The lack of growth until the following spring suggests that they do not feed much, and they may remain near the nest.

MOVEMENT

Movements of marked snakes between captures are of interest in two respects, considered over different time scales. 1) Short term movements (<30 days between captures) show the scale of exploration and foraging during routine daily activity. 2) Long term displacements (captures in different years) show the overall extent of the area used, or home range. Only mature snakes are considered, as others were seldom recaptured. G-tests have been used to compare frequency histograms of displacements of males and females in different seasons (Fig. 6).

Short term movements of both sexes were greater in spring (March to May, Fig. 6b), when the stream connected the pools, than in the dry period (June to October, Fig. 6a) when the pools were isolated and movements would have to be over dry land (P<0.01 for each sex). It is therefore not possible to separate ease of movement from searching for mates as causes of increased movement in spring. There was no difference between the sexes in short term movements in either period (P>0.1).

Long term displacements (Fig. 6c) were greater in females (mode 80-320m) than males (mode 20-80m),
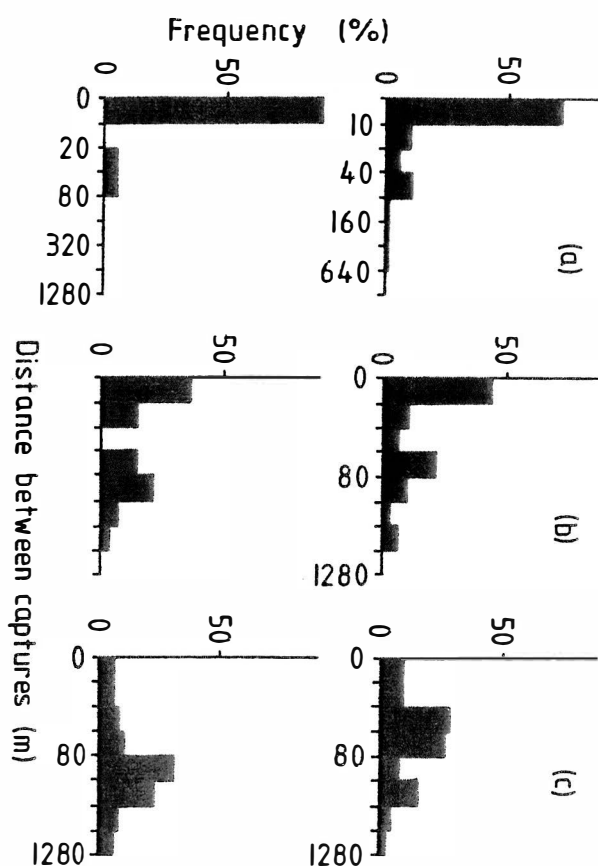

Fig. 6   Distance between captures of adult *N. maura*, males above, females below. a) Short term movements in summer, b) short term, spring, c) long term. Note the logarithmic distance scales; means and sample sizes in Table 1.

	Males	Females
Short term, summer	23 (132)	9 (18)
Short term, spring	68 (32)	76 (27)
Long term	113 (54)	204 (48)
Between successive captures*	66 (800, 66)	110 (950, 40)
Between first and last captures**	100 (300, 14)	180 (620, 10)
Minimum home range length**	170 (800, 14)	250 (950, 10)

TABLE 1: Movements of adult *N. maura*; mean displacements along the river, in m. Upper: total data, the variation of which is shown in Fig. 6 (with number of movements). Lower: snakes with four or more captures at intervals of >30 days (with maximum, number of movements* or individuals**).

P<0.001. These movements were all in one dimension, up or down the river, giving a linear home range. Few snakes were found in the river bed away from water, and these were usually between pools where there was no conneting stream. The length of the home range is estimated from snakes with four or more captures at intervals of >30 days. This was on average 170m in males and 250m in females (Table 1). The greater long-term movements and home ranges in females reflect the female> male size dimorphism in *N. maura* (Hailey and Davies, 1987a).

POPULATION STRUCTURE

The sex ratio and size distribution of males and females varied between different parts of the river (Fig. 7 and Table 2). In the area C-E slightly more males than females were captured. The sex ratio of adults was more heavily male-biased as they reach maturity at a smaller size (about 24 and 37cm in males and females, respectively; Hailey and Davies, 1987a). This area held the highest density of snakes and their prey, but snakes were also found in other places thought to be peripheral areas.

In the polluted area at Jalon (E-F) there were fewer small or large snakes (Fig. 7b), most being in the range 25-35cm, i.e. adult males and subadult females. The overall sex ratio was even, but the adult sex ratio was heavily male-biased (Table 2). A similar pattern was found at Alcalali (A-B), though there were more adult females (Fig. 7c).
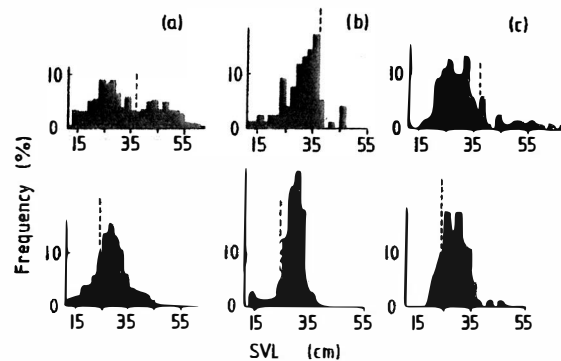

Fig. 7 Size frequency histograms of *N. maura*, females above, males below; recaptures excluded. a) Central study area, Fig. 2 part C-E, b) polluted area at Jalon, E-F, c) Alcalali, A-B. Sample sizes in Table 2. ---- Size at maturity.

POPULATION SIZE AND TURNOVER

The number of snakes in the area C-F was estimated using Bailey's triple catch method (Begon, 1979) on three main sampling sessions: August-September 1981, April-May and September-October 1982, June-August 1983. Although the September-October 1982 sample was large, it was from a restricted area due to an extremely low water level at that time and lack of snakes elsewhere. It was therefore unsuitable for use separately, and was pooled with the spring 1982 sample.

The results for mature males and females are shown in Table 3. A large proportion of the estimated

Area	All individuals				Adults			
	Males	Females	Males Females	P	Males	Females	Males Females	P
C-E	672	593	1.1	<0.05	567	250	2.3	<0.001
E-F	72	76	0.95	>0.05	64	9	7.1	<0.001
A-B	85	119	0.71	<0.025	72	23	3.1	<0.001

TABLE 2: Sex ratios of individuals found in different parts of the river. The number of different males and females, the ratio of males per female, and the probability (X^2 test) that the true ratio is 1.0, are shown for all snakes and for adults only.

	Males	Females
Sample	numbers captured: released	
1981	129 : 128	53 : 53
1982	327 : 309	173 : 166
1983	240 : 238	74 : 65
Last previous capture	number	
1981-1982	20	16
1981-1983	6	3
1982-1983	38	22
Estimate (with SE)		
Population size 1982	1060 (360)	390 (140)
Survival 1981-1982	0.53 (0.16)	0.71 (0.25)
Recruitment 1982-1983	0.52	0.42

TABLE 3: Mark-recapture data and population estimates for adult *N. maura* in the area C-F. Sample numbers in 1982 and 1983 include those recaptured from previous years.

population were handled, 60 per cent of 1060 males and 66 per cent of 390 females. The sex ratio of adults is 2.7 males per female from the population estimates. The data also allow estimates of survival and recruitment of adults between samples (Table 3).

POPULATION DENSITY

The density of animals which are found along rivers is not a simple concept (Turner, 1977), and cannot be reduced to a single value. Two densitites are considered, of value in different contexts, depending on the definition of the area occupied.

Ecological density

This is concerned with the number of animals in the area where they are active (Odum, 1959), and should be used when considering rates of contact with prey, predators and conspecifics. In *N. maura*, all foraging occurred in or close to the water, and mating and basking snakes were almost always within 2m of the water, often overhanging it (Hailey and Davies, 1986a, 1987a,b). The ecological density is therefore based on the area of surface water, 0.3 ha, i.e. about 4800 adults ha⁻¹.

Crude density

This covers the area used at all times of the year, and any pockets of unused habitat (Odum, 1959), i.e. the area which would have to be protected to conserve the population undamaged. In *N. maura* this includes daily refuges in the river bed and rock piles and walls above the river bed used for nesting and hibernation (Hailey and Davies, 1987a,b). It is based on the area of the river bed plus a band 5m wide on each side including stone walls of the lowest terrace of farmland, a total of 6 ha, i.e. about 240 adults ha⁻¹. *N. maura* were not found in the surrounding farmland, either by us or by the farmers, who readily distinguished them from the commonly seen 'culebra bastarda' (*Malpolon monspessulanus*).

DISCUSSION

GROWTH AND AGE AT MATURITY

The results from Jalon are compared with those for *N. maura* in central France, based on the seasonal distribution of length, gonad histology and growth in enclosures (Duguy and Saint Girons, 1966). Their results have been converted from total length to SVL using the equations of Hailey and Davies (1987a), and are summarised in Fig. 8. Histology revealed that males underwent the first, abortive, spermatogenesis at two years old, and were mature at three. Duguy and Saint Girons had less data for females, but suggested that they were mature at four.
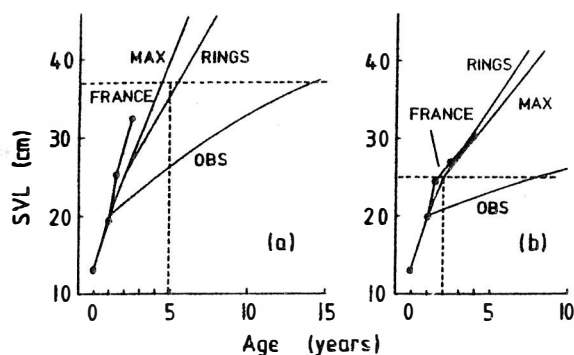

Fig. 8   Growth curves of *N. maura*, a) females, b) males. OBS) Observed growth above 20cm, equations 1 and 2, MAX) maximum observed, rates of 0.2 and 01.mm.day⁻¹ in females and males, respectively, RINGS) from growth rings, equations 5 and 6, FRANCE) from Duguy and Saint Girons (1966) study of *N. maura* in France. ---- size and age at maturity.

The size of hatchlings in France, 13cm, is similar to that of the smallest snakes found at Jalon, where they were first seen in spring. Growth to 20cm after the first full year is suggested by the seasonal distribution of SVL (Fig. 5). Observed growth above 20cm in 1981-1983 was slow (Figs. 3 and 8), presumably the result of

drought and low food supply. Snakes with two growth rings had SVL of about 25cm (Fig. 4), and it is thought that both sexes normally grow to 25cm after two years. These snakes were from Alcalali, where worms were abundant near the polluted area even during the drought — these are a common food of small snakes (Hailey and Davies, 1986a).

The growth ring data (equations 5 and 6) suggest constant growth of SVL above 25cm, at rates of 2.9 and 3.4cm.year^{-1} in males and females, respectively. The maximum observed growth rates were about 0.1 and 0.2mm.day^{-1} in males and females (Fig. 3), or 2.5 and 5.0cm.year^{-1} over an active season of 245 days. These rates are shown as growth curves in Fig. 8 — they are slightly lower than those found in France. It is concluded that: 1) The drought severely reduced growth, particularly above 20cm, and that in normal years; 2) Males reach adult size at two years old (in the autumn) and breed the following spring in their third year as in France; 3) Females reach adult size and first breed in their fifth year.

POPULATION DYNAMICS

The dynamics of the population are now explored to calculate the juvenile survival rate needed for stability and make predictions for further study. The results suggest that the adult female population was increasing at the proportional rate $e^r = 1.13$ per year (survival 0.71 + recruitment 0.42, Table 3). This seemed unlikely during a drought and so, as it is not apparent which is an overestimate, both survival and recruitment have been divided by 1.13, to give 0.63 and 0.37 respectively and a stable population (i.e. $e^r = 1.0$). This gives an annual turnover of 0.37 x 390 = 145 adult females. A similar adjustment for males ($e^r = 1.05$) gives both survival and recruitment values of 0.50.

Mean fecundity was 7.1 viable eggs per adult female per year (Hailey and Davies, 1987a), or 2770 eggs for the whole population, half of the eggs are assumed to be female. In the five years to maturity this number must be reduced by a factor of 0.105 for recruitment of 145 adults. This is equivalent to constant survival at the rate $0.105^{1/5} = 0.64$ year^{-1} over this period, i.e. similar to that of adult females.

Survival of immature males and females should be similar; what is the effect of a survival rate of immature males of 0.65 year^{-1} on the male population dynamics? This would give annual recruitment of 380 three year olds, 0.36 of the adult population. The difference between this value and recruitment calculated by mark-recapture, 0.50-0.36 = 0.14, could be due to immigration. In that case there should be a similar loss in emigration, and the survival rate within the study area from mark — recapture (0.50) plus this emigration would give a total survival rate of adult males of 0.64 year^{-1}.

Three conclusions can be drawn from this discussion:

1) The adult male and adult female populations were stable or increasingly slightly.

2) There was dispersal of adult males but not of adult females.

3) Total survival (including emigrants) of adults was about 0.65 year^{-1} for both sexes, and immature snakes would have to survive at the same rate for the population as a whole to be stable.

The second conclusion is a prediction from the model, and is supported by the population structure data. Dispersal of adult males (and of subadult males and females, immigration balancing emigration), but not of adult females or juveniles, would produce the population structure found in peripheral areas (Fig. 7b,c). In the near absence of adult females, these areas must be stocked by dispersal.

COMPARISONS WITH OTHER SNAKES

Comparison with previous population studies of snakes suggests two areas for particular study at Jalon. 1) Growth and age at maturity of females in normal conditions. The five years suggested here seems rather long for a small colubrid — females of most small snakes are mature at 2-4 years (Turner, 1977). 2) Survival of juveniles. Most studies have suggested that survival of juvenile snakes is very low (Turner, 1977), although numerical values have rarely been obtained, and low probability of recapture may also reflect the difficulty of finding them.
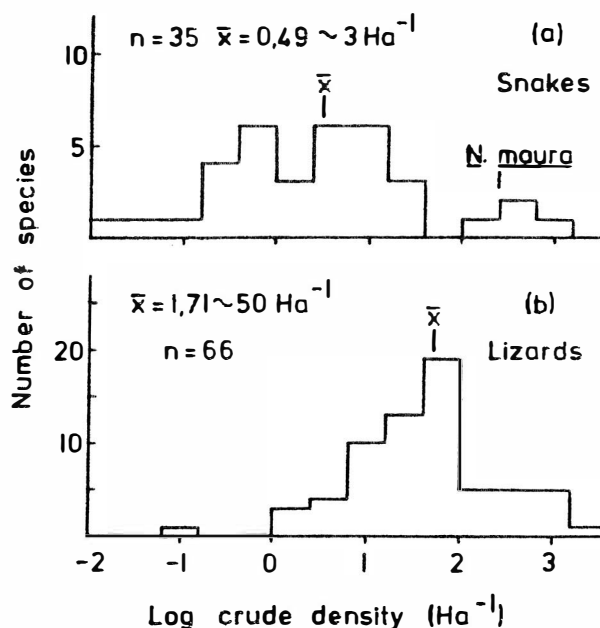

Fig. 9 Frequency distribution of reported crude population densities of a) snakes and b) lizards. Data from Table IX and Fig. 1 of Turner (1977). Note the logarithmic density scale. The position of the *N. maura* crude density of adults is shown in (a).

Density

The crude density can be compared to those reviewed by Turner (1977), which had a geometric mean of about 3 Ha^{-1}, an order of magnitude lower than for lizards — Fig. 9. The high value in *N. maura* is not surprising in view of the rich food supply normally associated with water.

The very high ecological density shows a high potential for contacts with conspecifics around the water. *Natrix maura* did not seem to have complex

social or reproductive behaviour; courtship, aggression or territoriality were never seen, and mating accounted for only about 0.3 per cent of all sightings. Snakes usually seemed to ignore each other, though on two occasions they were seen competing for food, by simultaneous ingestion. Hailey and Davies (1987a) calculated that females mated several times per year by observing sperm in cloacal fluid — this would be interesting to compare in a less dense population.

Survival

There are not sufficient data on snake survival to allow firm conclusions to be drawn, but the 14 populations reviewed by Turner (1977) are suggestive. Survival of these ranged from 0.25 to 0.86 year^{-1}, mean 0.61. Small colubrids (*Carphophis, Diadophis, Heterodon, Rhabdophis, Thamnophis*) had relatively low survival (0.25-0.63, mean 0.43), large colubrids (*Coluber, Elaphe, Masticophis*) were intermediate (0.40-0.86, mean 0.67) and viperids had highest values (0.70-0.82, mean 0.75). The survival of adult *N. maura* is thus greater than that of other small colubrids. This, together with the high population density, is probably due to the scarcity of predators (see Conservation below).

EFFECTS OF DROUGHT

The adult population as a unit was resistant to drought, possibly even increasing. Female reproduction was also little affected, assuming that females have a fixed number of follicles developing each year according to body size; on average only 18 per cent of these follicles were atretic (Hailey and Davies, 1987a). In contrast growth was very slow (Fig. 8), and most adults did not grow at all.

Annual differences in reproduction within populations, correlated to food supply, have been shown in a number of reptiles (Ballinger, 1977; Swingland, 1977; Andren and Nilsson, 1983; Seigel and Fitch, 1985). Annual variation in growth has been shown in long-lived reptiles (Peabody, 1958; Stubbs and Swingland, 1985). Among female reptiles, only snakes and crocodiles show substantial growth after maturity (Hailey and Davies, 1987a), suitable to show clear trade-offs between growth and reproduction with different food supply. This study shows that growth is reduced before reproduction in adult female *N. maura*; it is suggested that they grow only after their reproductive capacity for the year has been completed.

MOVEMENT

Table 4 summarises data on the movements of non-migratory natricine snakes; those which migrate to hibernacula may move much further, for example 11 km in *Thamnophis sirtalis* in Canada (Gregory and Stewart, 1975).

The widely foraging grass and garter snakes move further than the more sedentary water snakes, both between successive daily radio fixes and between captures at longer intervals. This correlates with the activity metabolism of these ecological types, active natricines having a greater capacity for sustained aerobic activity (Hailey and Davies, 1986 c).

Home ranges show no pattern, as expected as these should be related to the amount of food available within an area (Mace, Harvey and Clutton-Brock, 1983) rather than to the distance moved during foraging within that area. All of these natricines are found in productive marsh or riparian habitats.

Widely foraging			Sit-and-wait		
(a) Distance between captures (m)					
Thamnophis sirtalis	300	(1)	*Natrix maura**	44	(4)
Thamnophis butleri	115	(2)			
Thamnophis butleri	72	(3)			
Thamnophis sirtalis	62	(3)			
Thamnophis sirtalis	58	(2)			
(b) Daily displacements of radio-tracked snakes (m)					
Natrix natrix	30	(5)	*Nerodia sipedon*	4	(6)
Thamnophis sirtalis	10	(6)			
(c) Home range (ha)					
Natrix natrix	12	(5)	*Nerodia* spp	5.7	(5)
Thamnophis sirtalis	11	(1)	*Natrix maura***	0.6	(4)
Thamnophis sirtalis	0.8	(2)	*Nerodia sipedon*	0.5	(7)
Thamnophis butleri	0.3	(2)			

TABLE 4: Studies of movement in natricine snakes according to foraging mode. A simple (unweighted) mean is used where data were originally divided by sex or season. References: 1) Fitch (1965); 2) Carpenter (1952); 3) Freeman and Catling (1978); 4) this study; 5) Madsen (1984); 6) Fitch and Shirer (1971); 7) Fraker (1970).

* Short term, as other data are for successive captures.

** Assumed to be 30m wide, corresponding to the area used for the crude population density.

CONSERVATION

The study population is clearly large, dense, and of ecological interest — is it likely to survive? Many snakes were killed by people, particularly large females which were though to be poisonous — 32 of these were found decapitated or battered on paths close to the stream or in the water. However, this is probably not a new occurrence, and the population seems able to withstand it. The high density is indeed likely to be due to human interference, on predators of snakes. There were very few predatory birds or mammals in the river, and no terrapins (one *Pseudemys* (!) was found at Jalon, but several stuffed *Mauremys* were seen on sale at nearby coastal resorts).

The main threat is further urbanisation of the Jalon valley and increasing pollution, eventually killing the fish in the river. These are probably necessary prey for large *N. maura*, although small snakes commonly take worms which are common in polluted areas (Hailey and Davies, 1986 a). This has probably already happened at Gata (Fig. 1) and other places in Alicante and Valencia provinces, which are vulnerable because of low normal rainfall.

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A REVIEW OF GEOGRAPHICAL VARIATION IN *GERRHOSAURUS MAJOR* DUMÉRIL (SAURIA : CORDYLIDAE)

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ABSTRACT

Examination of most of the available material of *Gerrhosaurus major* indicates that only two geographical races should be recognised, the typical form (with *grandis* Boulenger as a synonym) in eastern Africa and *G.m. bottegoi* Del Prato (with *zechi* Tornier as a synonym) ranging from northern Somalia west to Ghana.

In the last revision of the genus, Loveridge (1942) recognised four races, but did not realise that the name *bottegoi* was applicable to the dark form which he called *zechi*. The range of variation in the typical form includes all the material that Loveridge assigned to *bottegoi* and *grandis*.

INTRODUCTION

When the genus *Gerrhosaurus* was last reviewed by Loveridge (1942) most of the available material of *G. major* was from East Africa, and he assigned it to three races based on colour pattern, using the following key:

'7. Head above, buff, each scale spotted with black . . 8

Head above, uniform buff or fulvous brown . . . 9

8. Above head, body and tail almost black, each scale with a small buff spot or streak arranged to form interrupted lines on back and sides; belly streaked with dusky; range Belgian Congo and Togo . . . . *m. zechi*

Above, head and body buff, each scale (except those forming an ill-defined, buff, dorsolateral line) heavily streaked with black or dark brown in regular lines on back and sides with a tendency to

coalesce posteriorly and on tail where the buff survives only as spots; belly streaked with dusky; range: Central Tanganyika north through Kenya to Ethiopia and Eritrea . . . . *m. bottegoi*

9. Above, head only buff through back anteriorly largely so, while posteriorly, as also on sides and tail, many scales are streaked with black or dark brown among which large buff blotches or spots are prominent; belly usually streaked with dusky; range Zululand and Transvaal north to Morogoro, Tanganyika Territory . . . . *m. grandis*

   Above, head and body uniform buff or fulvous brown; belly uniform yellowish; range Northern Rhodesia (?) and Mozambique north to Zanzibar along eastern Tanganyika Territory and eastern Kenya Colony. . . . . *m. major'*

Later in 1942, H. W. Parker published his monograph on the lizards of British Somaliland and independently reviewed the geographical races of *Gerrhosaurus major*. He regarded *zechi* as a synonym of *bottegoi* and, after examining the 'rather scanty' material in the British Museum, recognised three races as follows:

'I. Uniform brownish above, or with only irregular dark markings; tail with alternating darker and lighter annuli. This form is confined to Kenya Colony, Zanzibar and northeastern Tanganyika Territory and is the typical form. *G. major major* Duméril.

II. Black above, with longitudinal series of yellow spots between the dorsal scales; a more or less distinct yellow dorsolateral stripe; flanks brown with longitudinal light flecks forming regular series. Head black above with small yellow spots. This is a northern Sudanese subspecies, ranging from the Gold Coast to Eritrea and Somaliland. It enters the savannahs of the Congo around Garamba (Schmidt, 1919), Uganda (Kyagwe and Kaiso) and probably northeastern Kenya (? USNM 42216 recorded by Loveridge, 1929, p.66). In British Somaliland it appears to be confined to the mountains from the Boroma district as far east as the Golis Range: *G. major bottegoi* del Prato.

III. Similar in colour posteriorly to the preceding, but anteriorly the light markings are more extensive, obliterating the darker colour and the whole of the upper surface of the head is pale brown, uniform or with small black or chocolate-brown spots. This race occurs in Zululand, Transvaal, Mozambique and Tanganyika Territory and should apparently be known as *G. major grandis* Boul'.

Loveridge (1957) persevered with his own arrangement, although admitting that there was a wide zone of overlap between *grandis* and typical *major*.

I have long regarded *grandis* as a synonym of the typical form (Broadley, 1971), but it was not until I began work on a checklist of the reptiles of Tanzania that the divergent views of Loveridge and Parker with regard to the status of *G.m. bottegoi* attracted my attention. It was obviously desirable to establish the correct application of this name and to update Schmidt's 1919 distribution map.

MATERIALS AND METHODS

The Natural History Museum of Zimbabwe has a series of 60 specimens of *G.m. major* from Zimbabwe, Moçambique and Zambia. During a three month tour of museums in the United States in 1985, I took the opportunity to examine additional material of *G. major* and I was also able to check the specimens in the British Museum (Nat. Hist.) during a brief stopover on my way back to Zimbabwe. Subsequently I was supplied with data for an additional 115 specimens of *G. major* by several other museums in Europe, the United States and South Africa.

As no geographical variation in morphological characters has been detected in *G. major*, this study was restricted to colour pattern.

The following acronyms were used to indicate the institutions holding *G. major* material for each listed locality: AMNH = American Museum of Natural History, New York; BM = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco; CM = Carnegie Museum, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; JPT = J.P. Tello Collection, Maputo, Moçambique; MCZ = Museum of Comparative Zoology, Harvard; MHNP = Museum National d'Histoire Naturelle, Paris; MZUF = Museo Zoologico de 'La Specola', Florence; NMZB (+ UM) = Natural History Museum of Zimbabwe, Bulawayo; TM = Transvaal Museum, Pretoria.

RESULTS

Loveridge (1942, 1953) regarded the uniform buff or tawny typical form (Fig. 1, above) as an 'East African coastal form' replaced by the black streaked *grandis* inland, but even one of the Zanzibar syntypes of *major* (MHNP 6539) has black infuscations in the mid-dorsal region, increasing posteriorly. I have examined 27 of the Tanzanian specimens from Mangasini (= Kwa Mtoro) and Dodoma which Loveridge identified initially (1933) as *zechi* and subsequently (1942) as *bottegoi*, because of the black markings on head and body. These vary in extent from 5 to 50 per cent on the head, from 10 to 50 per cent on the body anteriorly and from 50 to 90 per cent posteriorly.

The lizards from Zimbabwe show almost the full range of colour patterns found in Tanzania. The most extensive dark markings are found in juveniles. UM 17904 from Tanganda Bridge, with a snout-vent length of 78mm, has symmetrical black head markings, most extensive on the frontal, frontoparietals and parietals. UM 18705, a 100mm SVL juvenile from Mahenya, and UM 27553, a 128mm SVL subadult from Mutare, also show these markings in a reduced form. Most adult specimens have no dark head markings, but the body is more or less streaked with black, increasing posteriorly, there is much variation within a population. The only specimens with no dark markings on the body are two from Kapami in Hwange District (the most westerly locality), one from Triangle and one from Mahenya, where most adults are heavily streaked with black. Most Moçambique
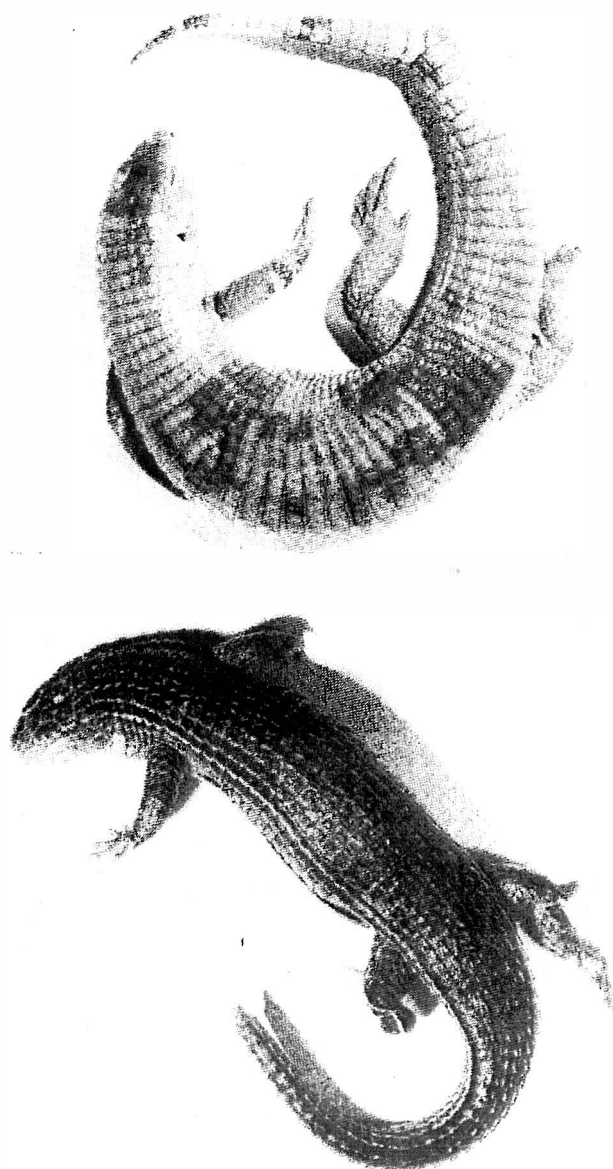
and usually a continuous yellow dorsolateral stripe; the flanks and ventrum are usually light brown, sometimes with yellow streaks (Fig. 1, below). Dunger (1967) reports that males from Jos, Nigeria, have a distinctive slate-blue chin and throat.

GERRHOSAURUS MAJOR BOTTEGOI Del Prato

Gerrhosaurus Bottegoi Del Prato, 1895, *Atti. Soc. ital. Sci. nat.*, **35**: 19, fig. 1-1a. Type locality: Valley of Ghinda, Eritrea (= Ethiopia). Reprinted in 1929 by the Instituto di Zoologia, Museo Bottego, Regia Universita di Parma, with an additional plate.

Gerrhosaurus maior var. *zechi* Tornier, 1901, *Arch. Naturgesh.*, **67**: 74, fig. 1. Type locality: Kete Kratje, Togo (= Ghana).

Gerrhosaurus zechi Schmidt, 1919: 509, fig. 21, pl. xx, fig. 2.

Gerrhosaurus major Loveridge, 1929: 66 (part, Kenya); Böhme, 1975: 36.

Gerrhosaurus major bottegoi Loveridge, 1942: 498 (part); Parker, 1942: 77; Wermuth 1968: 12 (part); Lanza, 1983: 214 (part).

Gerrhosaurus major zechi Loveridge, 1952: 241; Dunger, 1967: 176, pl. 3; Wermuth, 1968: 12.

Habitat. Rock outcrops (Dunger, 1967; Böhme, 1975) and open savanna, where they live in burrows (Schmidt, 1919).

Distribution. Northern Ethiopia, northwestern Somalia and western Kenya west to Ghana (Fig. 2).

Recorded localities. GHANA: Kete Kratje (ex Togo) (Tornier, 1901), Mole National Park (BM), Wa (BM, CAS, NMZB). BENIN: Koussokoingu (Loveridge, 1952). NIGERIA: Bauchi (Dunger, 1967), Jos Plateau (Dunger, 1967; BM), Waka (Dunger, 1967). CAMEROUN: Mokolo (Böhme, 1975). CENTRAL AFRICAN REPUBLIC: Bozo (MHNP). ZAIRE: Garamba (AMNH). SUDAN: Ngangala (FMNH), Torit (FMNH). UGANDA: Bagungu (BM), Kaiso (BM), Mabira Forest (BM). KENYA: no locality (Loveridge, 1929: USNM 42216); 8km SSW of Amaler (MCZ), Kampi-ya-Samaki, Lake Baringo (CAS). ETHIOPIA: Valley of Ghinda (Del Prato, 1895). SOMALIA: Borama District (BM), Wagar, Golis Mts (BM).

GERRHOSAURUS MAJOR MAJOR Duméril

Gerrhosaurus Major A. Duméril, 1851, *Cat. méthod. Coll. Rept. Mus. Paris:* 139. Type locality: Zanzibar; Loveridge, 1929: 66 (part).

Gerrhosaurus zanzibaricus Pfeffer, 1889, *Jahrb. hamburg. wiss. Anst.*, **6**: 7. Type locality: Kibueni, Zanzibar.

Gerrhosaurus bergi Werner, 1906, *Zool. Anz.*, **30**: 54, fig. 1-3. Type locality: Usambara Mts., Tanzania.

Gerrhosaurus grandis Boulenger, 1908, *Ann. Natal Mus.*, **1**: 225, 233, pl. xxxvi. Type locality: Ubombo, Zululand.

Gerrhosaurus major major Loveridge, 1933: 311, 1936: 64, 1942: 502, 1953: 225 and 1957: 224; Wermuth, 1968: 11; Broadley, 1971: 59; Broadley & Blake,

Fig. 1 Dorsal views of (above) *Gerrhosaurus major major* (CAS 123161 Laisamis, Marsabit District, Kenya) and (below) *G. major bottegoi* (CAS 140367 Kampi-ya-Samaki, Lake Baringo, Kenya). These are the nearest adjacent localities for the two subspecies. Photos by courtesy of R. C. Drewes.

lizards have black streaks on the body at least posteriorly (including MCZ 50997 from Tete, identified as *G.m. major* by Loveridge, 1953), the only uniform buff specimen is UMMZ 61418 from Lumbo. Specimens from Zululand (Pooley, 1965, pl. 5) and the Transvaal (Pienaar, 1978, pl. 37, 37A) are usually heavily streaked with black on the body.

At the northern end of its range, specimens of *G.m. major* from southern Somalia vary from having the dorsum heavily streaked with black to completely devoid of dark markings (photos supplied by B. Lanza).

G. major bottegoi does not show appreciable geographical variation in colour pattern. The head is about 70 per cent and the dorsum 80 per cent dark brown or black with symmetrical yellow spots on the dorsal head shields, lines of yellow spots on the back
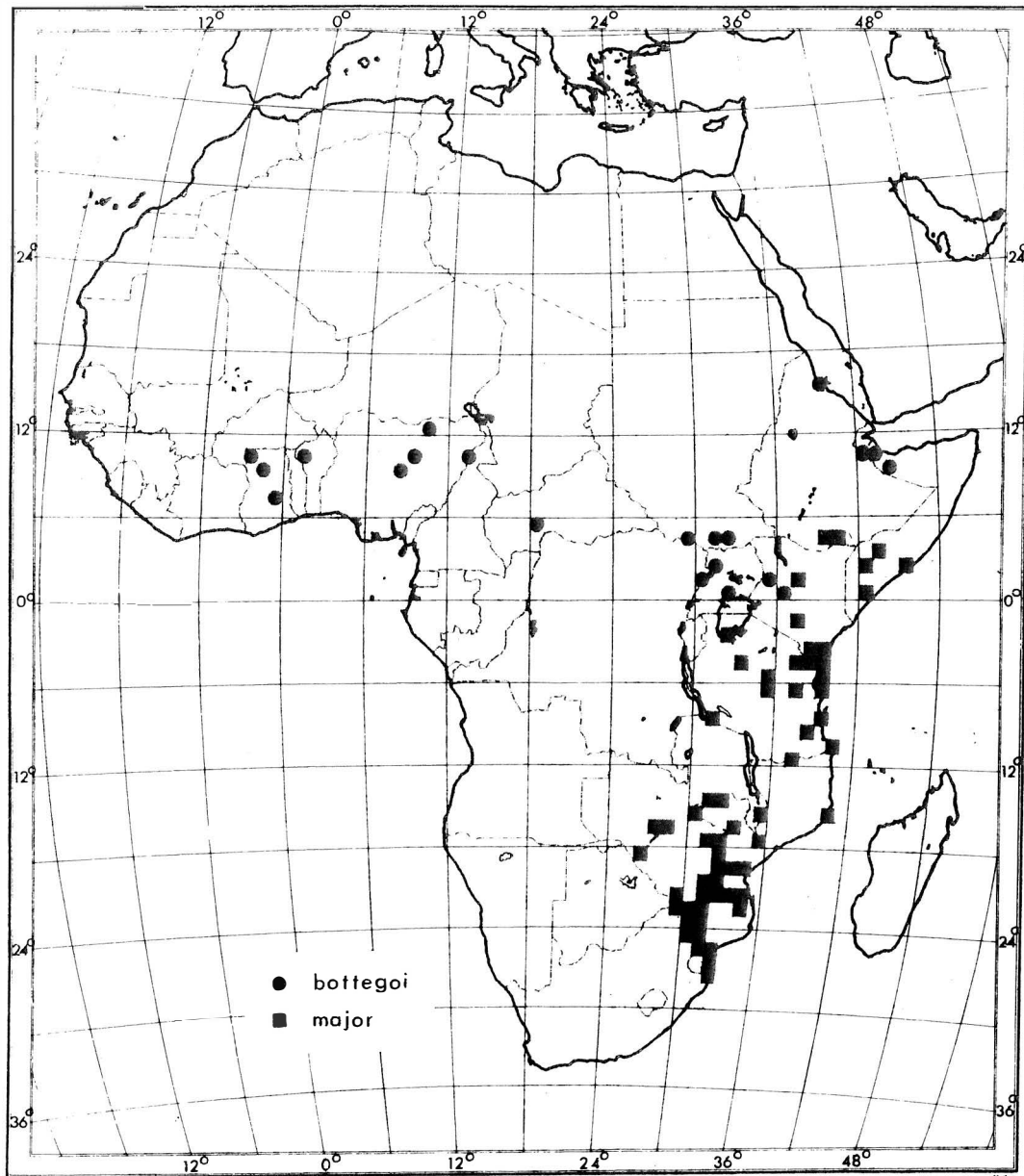
Fig. 2 Distribution of *Gerrhosaurus major* by degree squares.

1979; 8; Pienaar, 1978: 94, pl. 37, 37A; Pakenham, 1983: 20; Pienaar, Haacke & Jacobsen, 1983; 85, pl. 30, 30A.

Gerrhosaurus major zechi (not Tornier) Loveridge, 1933: 311 and 1936: 64.

Gerrhosaurus major bottegoi (not Del Prato) Loveridge, 1942: 498 (part); Witte, 1952: 16; Loveridge, 1957: 224 (part); Wermuth, 1968: 12 (part); Lanza, 1983; 214 (part).

Gerrhosaurus major grandis Loveridge, 1942: 500; FitzSimons, 1943: 280, fig. 162-4; Loveridge, 1953: 224, 1955: 175, 1956: 6, 1957: 224 and 1959: 34; Broadley, 1962: 819; Pooley, 1965: 45, pl. v; Pienaar, 1966: 79, pl. 27, 27A; Rowe-Rowe, 1968: 32, pl.; Wermuth, 1968: 12.

Habitat. Savannas, usually living in rock crevices or old termitaria.

Distribution. Southern Ethiopia and southern Somalia south to Zululand, reaching its western limits in the Hwange District of Zimbabwe (Fig. 2).

Recorded localities. ETHIOPIA: Bisan River (FMNH). SOMALIA: Afgoi (MZUF), Alessandra Island (MZUF), Baidoa (Lanza-photo); Belad (MZUF), Dinsor (MZUF); Giohar (= Villaggio Duca degli Abruzzi: Scortecci 1931); Mareri (CAS). KENYA: Ithanga Hills (MCZ); Ithumba (BM), Kilibasi (AMNH), Kilifi (BM), Laisamis (CAS), Lukenya Hills (USNM), Maji ya Chumvi (MCZ, USNM), Mariakani (NMZB), Mazeras (USNM), Merelle River (USNM), Mt. Mbololo (MCZ), Mt. Sagalla (MCZ, USNM), Murri (BM), Sokoke Forest (Loveridge, 1936b), Taita (Peters, 1878), Takaungu (BM), Tiwi (FMNH), Voi (MCZ, FMNH), Yatta Plain (BM). TANZANIA: Dodoma (MCZ), Kasanga (Witte, 1952), Kilosa (Loveridge, 1923), Kilwa (MCZ), Kwa Mtoro = Mangasini (MCZ, UMMZ), Liwale (MCZ), Luguo & Mkindo River (Loveridge, 1923), Morogoro (AMNH, BM, UMMZ), Mount Kirui (Loveridge, 1923), Mwanza (Loveridge, 1933), Tunduru (MCZ), Ulugu (Loveridge, 1923), Wembere (NMZB), Zanzibar (BM, MCZ). ZAMBIA: Feira District (Boulenger, 1907),

Gwembe Valley (NMZB), 30km West of Katete (NMZB). MALAWI: Lake Chilwa (TM), Libabula River (AMNH, MCZ). MOÇAMBIQUE: Amatongas (BM), Caia (Cott, 1934), Jorge (NMZB), Lumbo (UMMZ), Mkurrumbane, Morera and Muabsa (JPT), Muda-Lamego (NMZB), 10km SSE and 25km SE of Ressano Garcia (NMZB), Tete (MCZ, NMZB), Xiluvo (NMZB), Zinave (JPT). ZIMBABWE: Bangala Ranch (NMZB), Birchenough Bridge (TM) and 30km West (NMZB), Chipoli Farm, Doddieburn Ranch, Hot Springs-Chimanimani District, Jemembi Hill, Kapami, Lake Kariba, Mahenya, Malonga Bridge, Matowa, Mutare, Odzi, Ruenya River Drift, Rupisi Hot Springs, Ruware, Sabi Experimental Station, Siyanje, Tanganda Bridge, Triangle (NMZB). TRANSVAAL: Epsom Farm (TM), Griffin Mine and Hectorspruit (MCZ, TM), Kaapmuiden (TM), Komatipoort (CM), Klaserie (TM), Kruger National Park (Pienaar, 1966), Leydsdorp, Malelane (TM), Messina (FitzSimons, 1943), Middlesex Farm (TM), Newington (FitzSimons, 1943), Schelm & Malta Farms, Sekororo, Thulamila (TM), Waterpoort (FitzSimons, 1943). ZULULAND: Ndumu Game Reserve (TM), Ubombo (BM).

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HERPETOFAUNA OF THE SWANTON MORLEY SITE (PLEISTOCENE: IPSWICHIAN), NORFOLK

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ABSTRACT

The Swanton Morley Ipswichian site yielded fossils of *Bufo bufo, Rana arvalis arvalis, Rana temporaria, Rana* sp. indet., *Emys orbicularis,* and *Natrix natrix.* This is the first British fossil record of *Rana arvalis arvalis* which today occurs in the European low countries adjacent to England. A second continental form, *Emys orbicularis,* has previously been reported from the site. The nearest to Swanton Morley that these herpetological species could be found living together today would be in the Mecklenburg District of northern East Germany.

INTRODUCTION

A detailed report on amphibians and reptiles from an Ipswichian interglacial age site has never been presented, although Stuart (1979, 1982) reported *Emys orbicularis* from six Ipswichian sites in Britain, including Swanton Morley. Through the kindness of Dr. A. J. Stuart who collected the fossils, and Dr. J. Clack who now is in charge of the fossils at the University Museum of Zoology, Cambridge, I was given the privilege of studying the Swanton Morley herpetological fossils in the summer of 1986.

The Ipswichian Interglacial Age. The Ipswichian age may be defined as the temperate interglacial sequence between the cold Wolstonian glacial age (exact dates unknown) and the cold Devensian glacial age which began about 110,000 years before the present. In terms of the human fossil record, the Ipswichian would represent mid Palaeolithic times. Stuart (1982) has provided a general discussion of Ipswichian sites and their vertebrate faunas. The Ipswichian is the best known interglacial age, and many of its sites have yielded the African hippo (*Hippopotamus amphibius*). The type site is Bobbitshole, Essex.

The Swanton Morley Site. The Swanton Morley Site (Fig. 1) lies on the right bank of the River Wensum, about 2km north of the village of Swanton Morley, Norfolk. All of the herpetological material came from pits (A, B, C, etc.) that were described in detail by Coxon *et al.* (1980). Pollen and faunal analysis (Coxon *et al.,* 1980; Phillips, 1976; and Stuart, 1976, 1979, 1982) all verify that the vertebrate assemblage is from several subzones within the Ipwichian age. The fossils and sediments indicate a back channel of a meandering river. Bone of *Hippopotamus amphibius* and *Emys orbicularis,* and fruits of a water chestnut (*Trapa natans*) indicate a warmer climate than that of today.

Herpetological fossils are all from either Pit A or from Pit C. Fossils from Pit A all represent the Ip11b subzone of the Ipswichian and fossils from Pit C all represent the Ip11a subzone of the Ipswichian.
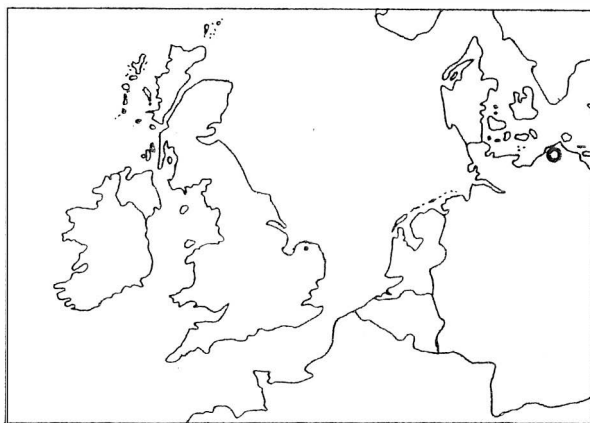

Fig. 1   The dot indicates the location of the Swanton Morley Site, Norfolk. The open circle indicates the nearest area where all of the Swanton Morley herpetological species can be found living together today.

SYSTEMATIC PALAEONTOLOGY

The fossils reported below all reside in the collections of the University Museum of Zoology, Cambridge. Specimen catalogue numbers are prefixed by the letters SM which designate the Swanton Morley site.

Class Amphibia

Order Salientia

Family Bufonidae

Bufo bufo Laurenti

Identified Material. Pit C1 (Zone Ip11a), Sample 4: right ilium SM 273.

Remarks. Holman (1985) has discussed the identification of *Bufo bufo* on the basis of ilial characters. *Bufo bufo* occurs in the area today (Frazer, 1983).

Family Ranidae

Rana arvalis arvalis Nilsson

Identified Material. Pit C1 (Zone Ip11a), Sample 4: left ilium SM 268; left ilium SM 271; sacral vertebra SM 272.

Remarks. This is the first fossil record of *Rana arvalis* from Britain. *Rana arvalis* does not occur naturally in Great Britain today, but occurs in the adjacent low countries of the European Continent (Arnold and Burton, 1985, p. 258, map 37). The ilium of *Rana arvalis arvalis* (Fig. 2) has been shown to be distinguishable from other British and European species (Böhme, 1977). The ilium of *Rana arvalis arvalis* has a smooth, elongate, unelevated tuber superior (term of Böhme, 1977, Fig. 1) that separates it from *Rana arvalis wolterstorffi, Rana graeca, Rana latastei, Rana lessonae,* and *Rana temporaria. Rana arvalis arvalis* has a well-developed ilial blade (vexillum of Böhme, 1977, Fig. 1) that separates it from *Rana temporaria.* The ilium of *Rana arvalis arvalis* has a very small pars descendens (term of Böhme, 1977, Fig. 1) that separates it from *Rana arvalis wolterstorffi, Rana dalmatina,* and *Rana graeca.* Finally, *Rana arvalis arvalis* has a well-developed ventrolateral ridge on the ilial (vexillum) that separates it from *Rana dalmatina, Rana esculenta, Rana latastei,* and *Rana ridibunda.* The sacral vertebra is assigned to *Rana arvalis arvalis* as it differs from *Rana temporaria* in having its sacral diapophyses directed much more anteriorly.

Today, *Rana arvalis* occurs in damp fields, fens, and sphagnum bogs, often in the same area as *Rana temporaria* (Arnold and Burton, 1985), but it is said to prefer wetter habitats. It rarely occurs at high altitudes.

Rana temporaria Linnaeus

Identified Material. Pit A1 (Zone IpIIb) 1971 Sample: right ilium of a juvenile specimen SM 407. Pit C1 (Zone IpIIa) Sample 4: left ilium SM 269; right ilium SM 270.

Remarks. The ilium of *Rana temporaria* (Fig. 2) is easily separated from other British and European species in that it has a very poorly developed ilial blade and an elevated, sometimes roughened tuber superior. *Rana temporaria* occurs in the area today (Frazer, 1983).
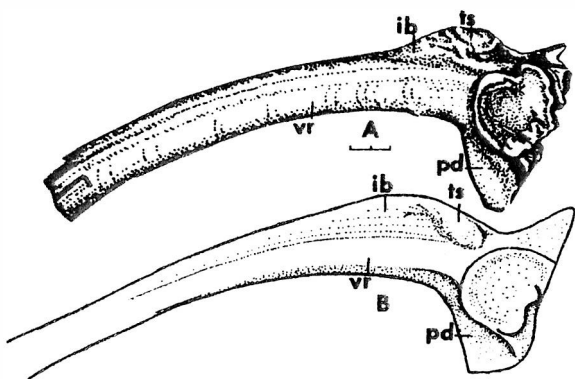

Fig. 2 Left ilia of *Rana* in lateral view. A, male *Rana temporaria* drawn from Michigan State University Museum Specimen Number 3867; the line equals 2mm. B, *Rana arvalis arvalis* redrawn from Böhme (1977); no scale was given. Symbols: ts, tuber superior; ib, ilial blade, pd, pars descendens; vr, ventrolateral ridge.

Rana sp. indet.

Identified Material. Pit C1 (Zone IpIIa) Sample 4: left humerus.

Remarks. The humerus of *Rana* may be distinguished from *Bufo* on the basis of its rounded rather than distally flattened distal condyle. The fossil may represent *Rana arvalis, Rana temporaria,* or possibly a third species.

<div align="center">

Class Reptilia

Order Testudines

Family Testudinidae

Emys orbicularis Linnaeus

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Identified Material. Pit C1 (Zone IpIIa) 1977-78 Samples: vertebra SM 192; right humerus SM 177; second right pleural plate SM 179; peripheral plate SM 178. This material was seen by J. A. Holman in August, 1986, but was originally identified by A. J. Stuart (1979).

Remarks. The pond tortoise does not occur in Britain today, but occurs on the European Continent (Arnold and Burton, 1985, p. 259, map 48). *Emys orbicularis,* however, does not occur in the adjacent low countries of Europe as does the other exotic Swanton Morley species, *Rana arvalis arvalis.*

<div align="center">

Order Squamata

Family Colubridae

Natrix natrix (Linnaeus)

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Identified Material. Pit C1 (Zone IpIIa) Sample 2, 1977: four vertebrate SM 68, SM 69, SM 70, and SM 71.

Remarks. Holman (1985) and Szyndlar (1984) have provided discussions and illustrations of how to distinguish the individual vertebrate of *Natrix natrix* from other British and European species. *Natrix natrix* appears to be separate from *Natrix tesselata* on the basis of the rounded (rather than a truncated) hypapophysis in *Natrix natrix* and on the less gracile parapophyseal process in *Natrix natrix* (Szyndlar, 1984). This species occurs in the area today (Frazer, 1983).

DISCUSSION

The previously reported biota and sediments of the Swanton Morley Site have indicated an ecological setting of a back channel of a meandering river (Coxon *et al.,* 1980; Phillips, 1976; and Stuart, 1976, 1979, 1982) and the herpetofauna is consistent with this interpretation. *Emys orbicularis* could have lived in the slow-moving back channel waters, and *Bufo bufo, Rana arvalis arvalis, Rana temporaria,* and *Natrix natrix* could have inhabited the adjacent wetlands.

Two of the five herptile species from Swanton Morley do not occur in Britain today. The moor frog, *Rana arvalis arvalis* occurs in the adjacent lowland countries of the European Continent; the European pond tortoise, *Emys orbicularis,* occurs further inland on the continent (Arnold and Burton, 1985, p. 258, map 37 and p. 259, map 48). It is noteworthy that the nearest to Swanton Morley that these herptiles could be found living together today would be in the Mecklenburg District of northern East Germany (Fig. 1 this paper and Arnold and Burton, 1985, maps 31, 36, 37, 48, and 114). Thus, the Swanton Morley

herpetofauna may well suggest a more continental type climate for Britain during Ipswichian times.

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FORUM:

(1) SEXUAL SELECTION IN AMPHIBIANS: A REPLY TO HALLIDAY AND VERRELL

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The evolutionary interpretation of sexual dimorphism in amphibians has long been of interest to biologists. Charles Darwin (1874) noted of frogs that 'although cold-blooded, their passions are strong', and suggested that dimorphism should be common. However, he lacked the data to investigate further. Over one hundred years later, I reviewed available published literature to see whether any correlation was apparent between male-male combat and (i) large male body size relative to female size, and (2) the presence of enlarged spines or tusks in males. Such correlations were evident at the familial, subordinal and ordinal levels within the Amphibia and I interpreted these correlations as supporting the Darwinian hypothesis that male-male combat provided a selective advantage to large body size and weaponry in males (Shine, 1979). A recent review by Halliday and Verrell (1986), primarily a critique of my 1979 paper, concluded that both my specific results and my general approach were in error (e.g. 'attempts, such as that by Shine, to find correlations between behavioural and morphological characters are not useful', p. 90). I regret that I did not know of Halliday and Verrell's paper until after its publication, because most of their criticisms can easily be shown to be invalid.

The primary criticism levelled by Halliday and Verrell is that the data base and methodology for my 1979 paper are unreliable because (1) the information came from a wide variety of published sources, with highly variable samples sizes, techniques of measurement, and preparation of material; (2) placing any species in a single category introduces error because of possible intraspecific variation in sexual size dimorphism or reproductive behaviour; (3) analyses should have been done separately for various subgroups of amphibians (e.g. aquatic *versus* terrestrial species; prolonged *versus* 'explosive' breeders); (4) I compared dimorphism among amphibian species known to show combat, to dimorphism among species in which combat had not been recorded. Inevitably, future studies will show that many of these latter taxa also display combat behaviour.

I agree that all of these factors introduce potential error into my 1979 analysis; indeed, I pointed this out in the original paper (pp. 300, 302). Importantly, this error will introduce random 'noise' into the analysis rather than systematic bias. Thus, it will make it less likely for any statistically significant correlations between behaviour and morphology to be demonstrated. The existence of strong correlations between these variables in several amphibian taxa, despite such problems with the data, suggests that the underlying correlations must be very strong indeed. Thus,

Halliday and Verrell's main criticism reinforces the conclusions of my 1979 paper, rather than casting doubt on them.

A second major criticism by Halliday and Verrell (1986) is to point out that there are several well-studied amphibian species which are clearly exceptions to the general correlation I found between large male size and male-male combat: that is, where males fight with each other, but are smaller than females. Halliday and Verrell are correct in viewing these cases as real exceptions rather than statistical 'noise', but the important point is that the general correlations exist (and are statistically significant) despite exceptions such as these. Neither are these cases directly contradictory to the Darwinian hypothesis. All that the hypothesis predicts is that large male body size is likely to evolve if combat is important in determining male reproductive success. Whether or not males grow larger than females will depend on other factors as well, including sexual differences in survivorship and selective pressures on female body size (see p. 302 of Shine 1979). The hypothesis makes no specific prediction about the size of males relative to females. The only basis for introducing sexual size dimorphism as a dependent variable in the analysis, rather than absolute male size, is essentially to use female size as a control. Hence, the prediction is that adding an extra selective pressure for larger male body size will tend to make it more likely (but certainly not inevitable) that males will grow larger than females, compared to a species where male body size is not under that pressure. Thus, many 'exceptions' (species with male combat, but with males smaller than females) would be expected *a priori*, and are completely consistent with the Darwinian hypothesis.

Halliday and Verrell (1986) also criticise my analysis on the grounds that it did not consider other behavioural strategies of males (e.g. mating interference), in which large body size may confer no advantage to males. Neither did I investigate other sexually dimorphic aspects of morphology (e.g. certain glands) or physiology (e.g. energetics of vocalisation). These criticisms misinterpret the intended scope of my paper. I set out to consider only those attributes of male amphibians (large body size and possession of 'weapons') which could readily be postulated to increase success in male-male combat, and to derive and test predictions from this hypothesis. Other sexually dimorphic attributes of amphibians also deserve attention, but were outside the scope of my 1979 paper. I specifically dealt only with the role of physical combat between males, not with any other form of male-male competition. This misunder-

standing by Halliday and Verrell seems to be the basis for much of their discussion.

A fourth criticism by Halliday and Verrell is that I did not consider that sexual size dimorphism could result from survivorship differences between males and females, rather than resulting from natural selection for different body sizes. Their assertion is incorrect. I argued that differential survivorship may be an important proximate cause of observed patterns of sexual size dimorphism in amphibians (p. 302).

Finally, Halliday and Verrell correctly point out an omission in my data for *Plethodon glutinosus*, in which I had overlooked records of male-male combat. The direction of sexual size dimorphism in this taxon is uncertain (and perhaps geographically variable), because published accounts disagree with each other. More detailed data on this species would be of value.

I do not wish to imply that my 1979 analysis lacks flaws. For example, recent methodological suggestions for such comparative studies (e.g. Harvey and Mace 1982) convince me that there are real dangers in using species as the units in such analyses; a more detailed consideration of the extent of phylogenetic conservatism among the variables studied would add to the value of my 1979 work. The other obvious difficulty is my reliance on an essentially anecdotal data base. The problem is not one of random error, but of the possibility of systematic bias (if, for example, behavioural studies — and therefore records of male combat — had concentrated on some 'type' of amphibian which also, for some unrelated reason, tended to have males larger than females). Such systematic biases are unlikely to be a major problem, because (a) there is no *a priori* reason to expect them, (b) they cannot explain the observed correlations between large male size and presence of 'weapons', and (c) further studies, as they accumulate, will readily show whether these correlations are indeed valid.

Despite these reservations about methodology, I disagree strongly with Halliday and Verrell's cavalier dismissal of the general approach of comparative analysis. I see nothing in their criticisms to make me doubt the basic results from my 1979 study: large male body size (relative to female size) and 'weapons' are more common in amphibians known to show male-male combat, than in amphibians where no such combat has been described. This correlation strongly suggests that these attributes have evolved because they increase male reproductive success by promoting success in combat. I agree with Halliday and Verrell (1986) that no single hypothesis can explain the phenomenon of sexual dimorphism in amphibians: the interplay of various ultimate and proximate influences is bound to be extremely complex. Nonetheless, I remain convinced that comparative analyses of correlations between behaviour and morphology offer a powerful technique for discovering some of the most important of these influences.

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(2) SEXUAL SELECTION IN AMPHIBIANS: A REPLY TO SHINE

Our most important criticism of Shine's (1979) paper was of his comparison between two categories of species, those with male combat and those in which combat may or may not occur. In his reply, Shine suggests that this will involve random 'noise' rather than systematic bias; I disagree. The first category includes species where fighting has been observed and described and there is no reason to suppose that future research will show that it does not occur in any of these species. The second category, however, may include many species in which fighting does occur but for which it has not yet been described because they have been inadequately studied. If fighting is described for any species in this second category, those species would have to be reallocated to the first category. This inbalance in the status of the two categories is surely a systematic one. Only the accumulation of future studies will determine how significant is this source of error in Shine's analysis.

On the point that Shine excluded dimorphic characters that are not related to combat because they were outside the scope of his 1979 paper, I can only observe that the title of that paper was highly misleading. Sexual selection theory, since its original development by Darwin, has generally been regarded as having two major components, male competition and female choice. Many recent studies of sexual behaviour have shown that these two components, intrasexual and intersexual selection, are often acting together within a mating system such that it is difficult if not impossible to differentiate their effects (Halliday, 1978; Partridge and Halliday, 1984).

Behind our critique of Shine and his reply to it lies a basic question: whether or not cross-species statistical tests are a valid test of evolutionary theory. Provided, as Shine acknowledges in his reply, such tests control for the confounding effect of phylogeny, they may reveal biologically significant patterns. They can, however, only reveal correlations between characters and cannot prove a causal relationship between those characters. Neither can they necessarily shed light on the situation in a particular species, such as *Bufo bufo*. The uncritical use of evolutionary generalisations about the relationship between body size and sexual selection has been attacked in a recent paper by Greenwood and Adams (1987). They discuss what they describe as two fallacious assumptions: first, that if large size is favoured by sexual selection, males will be larger than females and, second, that if males are larger than females, this must be evidence of intrasexual selection among males. Our contention is that there is now so much evidence that body size is the product of many selection pressures in amphibians, that further research should be directed towards estimating accurately the strength of these pressures in individual species, not in seeking generalisations across species.

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BOOK REVIEWS:

(1) *Heathlands*, Nigel Webb (1986). Collins. 223pp., £20: paperback £9.95.

Anyone interested in lowland heaths will enjoy and benefit from this book. Confining his survey to land below 800 feet, Dr. Webb describes the probable history of heaths in the UK, with some reference to those in Europe and elsewhere. He outlines the formation and maintenance of the characteristic podsolic soils found there and deals in considerable detail with heathland plant and invertebrate communities: his treatment of the vertebrates is less thorough. He concludes with an excellent chapter on management and conservation and provides a list of references and of heathland nature reserves.

On podsol formation, Dr. Webb's chemistry is absurd: thus (p. 23) he writes: 'bases such as calcium, magnesium, sodium and potassium are leached by chemical processes in which they are replaced by hydrogen ions'. How can chemical processes leach anything? In no chemical sense can the metal ions be classified as 'bases': here Dr. Webb is using concepts abandoned by physiologists and the like at least 20 years ago. It is disturbing that this nonsense perhaps still forms part of ecology courses. Understanding the acidification of heathland soils will require chemical understanding too: hence Dr. Webb's muddled remarks have more than academic importance. The use of 'phosphorous' (unknown in nature) instead of its invariable form as 'phosphate' in describing plant nutrition, etc. is widespread but chemically deplorable.

I found Dr. Webb's account of the heathland plants beautifully clear and quite fascinating: he rightly pays most attention to Heather (Ling) (*Caluna vulgaris*), describing in detail the long succession from seeds to degenerate plants. Renewal of this final cover by burning (suggesting later), is fatal for reptiles and amphibians: it is a relief to read (p. 169) 'Management of heathland by burning must now be considered inappropriate for . . . rare reptiles'. Herpetologists will oppose all burning of areas where reptiles and amphibians occur; the peril is greater for the Sand lizard, with its poor dispersal habits, than for the Smooth snake, contrary to Dr. Webb's assessment (p. 194). Dr. Webb stresses the importance of Common gorse (*Ulex europaeus*) as shelter and food for the Dartford warbler: although gorse is a fire hazard, we must not add to the threats to this rarest heathland vertebrate by clearing too much of it. On the rare herptiles, Dr. Webb surprisingly does not mention *The ecology and conservation of amphibians and reptile species endangered in Britain* (Nature Conservancy Council, 1983), a most valuable source of information on the Natterjack toad, Sand lizard and Smooth snake. If he had read this, he might have modified his statement on the Sand lizard (p. 166) that 'it will not be possible to provide prescriptions for the conservation of the species'. BHS has provided such prescriptions and using them has successfully preserved and increased Sand lizard populations.

The style of writing is quite clear if somewhat repetitive: the print is unduly small. The book is well produced and illustrated, although some of the diagrams are hard to understand. There are good photographs, including excellent coloured ones. I recommend this work to those interested in British wild life and its protection, especially to all who enjoy the loveliness of our lowland heaths.

G. A. D. Haslewood

(2) *Handbuch der Reptilien und Amphibien Europas. Band 2/II. Echsen (Sauria) III (Lacertidae III: Podarcis).* Edited by Wolfgang Böhme (1986). Wiesbaden: AULA-Verlag, DM 216.

The *Handbuch* is a bit like a tortoise: its progress is slow (I reviewed the first volume in *British Journal of Herpetology* in 1982) and steady, it is solidly put together, and it will probably endure.

This is the third volume in the series and deals with seventeen species of lizards which Arnold (1973) defined as *Podarcis* sensu stricto — wall lizards. Arnold and Burton in the *Field Guide* (1978) included 14 species within this category: here we have three more due to the inclusion of Medeira (so adding *P. dugesii*), the acceptance of *P. gaigeae* as a full species (it was originally described as a subspecies of *P. erhardii*) and the transfer of *P. perspicillata* from the genus *Lacerta*.

The format of the book follows that of the previous volumes. Each species has been assigned to a separate author, who discusses it under a set sequence of headings from 'diagnosis' through 'variation in marking' to 'behaviour: communication' followed by a list of relevant literature. Distribution maps are given. Where it has seemed appropriate these show the records which outline the edges of the range of a species; for species with extensive insular distributions, separate maps give the details. The book does not attempt to give a comprehensive account of such aspects as the biochemistry or endocrinology of each species — it is a *Handbuch* and not an *Enzyklopädie* —but I have the impression that relatively more space is devoted to ecological and physiological topics than in previous volumes. It is difficult to judge whether this reflects changing emphases in European herpetology or results from the fact that some *Podarcis* are particularly well-studied species.

Many of the species are immensely variable and innumerable subspecies have been described. This has given rise to a vast, daunting and confused literature, and there are probably almost as many views about what should be done about it as there are herpetologists who have studied the problem. A extreme view, as represented by Thorpe (1980), is that the whole approach is misconceived, should be abandoned, and replaced by multivariate analyses which emphasise similarities and possible evolutionary relationships, but do not involve the naming of taxa

below the species level. I have a great deal of sympathy with this approach, and was therefore most interested to see how the Editor and authors have dealt with the problem. So far as I can judge (this is not an area in which I am expert) they have taken an uncommitted stance: subspecies and their distribution are listed at great length, but alternatives, including reference to Thorpe's work, are also mentioned.

This book maintains the very high standards set by the previous two volumes, and will be indispensable as a reference for serious herpetologists. It must have been an immense labour to gather such a large and scattered literature together — there are more than 400 references to *P. sicula* alone — and many of us will continue to be grateful to W. Böhme and the fourteen authors for understanding the task. Credit to the publishers, too: the book is well-produced. English readers will regret that there is not a translation, and that the weakness of sterling makes buying it an expensive undertaking.

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R. A. Avery

OBITUARY: HUGH COTT

It would be appropriate, sadly, to record the death of Dr. Hugh B. Cott on 18th April at the age of 86. Originally trained at Sandhurst as an army officer, he later graduated in zoology at Cambridge and went on to become an eminent naturalist in the Darwinian tradition and one of the finest animal artists in the black and white medium.

Cott's book *Adaptive Coloration in Animals*, first published in 1940, is a classic and his later books *Uganda in Black and White* (1959) and *Looking at Animals* (1975) exemplify both his knowledge of East Africa and his artistic talent.

Much of Cott's work contains references to amphibians and reptiles, but he will be chiefly remembered by herpetologists for his monumental study of the ecology of the Nile crocodile and its exploitation by man (*Trans. zool. Soc. Lond.*, 1961, vol. 29). This was a truly seminal work, concerned with every aspect of the life-history of this magnificent reptile. It has provided a baseline for all subsequent studies of crocodilian ecology and conservation, such as those of Pooley in southern Africa, and of Messel and of Webb and their collaborators in northern Australia.

It would be fair to say that Cott never quite achieved the scientific recognition which he deserved, but his reputation and personality will live on in his publications and pictures. Hugh was a wise, talented and lovable person who will be missed by all who knew him.

Angus Bellairs

THE HERPETOLOGICAL JOURNAL

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1. The *Herpetological Journal* publishes original articles, short notes and mini-reviews on all aspects of herpetology. Faunistic lists and letters are not published. Short notes should include a single data set. Mini-reviews will in general be solicited by the editor, who should in any case be consulted before such a review is written.

2. Two copies of papers and illustrations should be sent to the Editor.

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5. The usual rules of zoological nomenclature apply.

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

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

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

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From December 1987 the Herpetological Journal will in addition to existing features, publish short articles on contentious or generally controversial matters in Herpetology. Details of relevant procedures for submitting such articles (to appear under the heading of 'Forum') can be obtained from the editor.

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