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

### ADRIAN HAILEY\* AND P. M. C. DAVIES

Zoology Department, University of Nottingham NG7 2RD.

\*Present address: Department of Physiology, The Medical College of St. Bartholomew's Hospital. Charterhouse Square, London ECIM 6BQ, UK.

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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<sub>2</sub>) 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<sub>2</sub> accounted for 28 per cent of the energy in the food. VO<sub>2</sub> 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<sub>2</sub> 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 semimicro 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  $15^{\circ}$ 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<sub>2</sub> to compensate for low T<sub>b</sub> rather than lowered VO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> was measured four hours later. Thereafter VO<sub>2</sub> 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<sub>2</sub> during maximal activity was measured, to see if SDA would decrease performance. VO<sub>2</sub> 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 smallsnakes (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  $\langle 4g \rangle$ , suggesting that they are inactive and secretive in this state. Other snakes have been found to have lower selected T<sub>b</sub> 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)
МАМО	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 female	es		Others		Р	
June		11.0 (75)			6.0 (268)		>0.1	
Rest of year		5.3 (302)			6.3 (1820)		>0.5	
Р		>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<sup>-1</sup>) = 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 ImI  $0_2 = 20$ J:

Log SMR (KJ.day<sup>-1</sup>) = 0.75 Log Weight -1.35Thus 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.

°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<sup>-1</sup> (SD = 0.74). Dry weight accounted for 24.7 per cent (SD = 0.34) of live weight, giving 4.74 KJ.g live W<sup>-1</sup>. Sloughed skins had an energy content of 24.2 KJ.g dry W<sup>-1</sup> (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 =  $0.264 \text{ W}^{0.905}$ 



Fig. 1 Food consumption for maintaining weight in small cages at  $25^{\circ}$ C o males • females. Solid line is regression fit, dashed line is the energy equivalent of SMR (equations in text).

#### 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<sub>2</sub> 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)	 at
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<sup>-0.75</sup>.h<sup>-1</sup> (with coefficient of variation = SD  $\overline{x}$ , 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<sub>2</sub> after feeding was less (P<0.01) than AMR. VO<sub>2</sub> in ml.g<sup>-0.75</sup>.h<sup>-1</sup> (with SD, n) were:



Fig. 2 Time course of increased oxygen consumption after feeding at three temperatures. Mean  $\pm 1$  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<sub>b</sub> 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  $T_{h}$  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<sup>-0.75</sup>.h<sup>-1</sup> (Hailey & Davies, 1986c), so basking costs  $0.10ml.g^{-0.75}$ .h<sup>-1</sup>, = 11 J.h<sup>-1</sup> 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

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	Cost	of SDA		SMR	Extra VO <sub>2</sub>	Factorial
°C	(ml0 <sub>2</sub> )	(KJ)	(% Total)	(ml.g <sup>-0.75</sup> .h <sup>-1</sup> )	(ml.g <sup>-0.75</sup> .h <sup>-1</sup> )	SDA
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<sub>2</sub>, 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<sub>b</sub> raised by less than 2°C after feeding (Marcellini & Peters, 1982), though this species conserves heat by tight coiling after feeding. The raised  $T_{\rm b}$  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 K J.g live weight<sup>-1</sup>) 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<sub>2</sub> 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 K J.g<sup>-1</sup>, 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<sub>2</sub> during activity. Firstly, the total VO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> arising from SDA and from activity. If oxygen exchange were not limiting. VO<sub>2</sub> 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 K J.g<sup>-0.75</sup>.year<sup>-1</sup> for an active season of 245 days. After losses in digestion only 6 K J.g<sup>-0.75</sup>. year<sup>-1</sup> 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  $10 \text{ KJ.g}^{-0.75}$ . year<sup>-1</sup> 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<sub>2</sub> 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  $1.0 \times SMR$  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  $4.2 \times Lg^{-0.75}$ .year<sup>-1</sup>.

### 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<sup>-1</sup> for a 2g snake, or  $1.2 \text{ KJ.g}^{-0.75}$ .year<sup>-1</sup>. 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 snoutvent 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.glive weight<sup>-1</sup>. 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  $14.2 \text{ KJ}.g^{-0.75}.year^{-1}$ , 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<sup>-0.75</sup>. year<sup>-1</sup> before maturity and after growth ends, to about 28 KJ.g<sup>-0.75</sup>.year<sup>-1</sup> when both reproduction and growth occur (Table 6). If on average energy used is 24 KJ.g<sup>-0.75</sup>.year<sup>-1</sup>, and food intake occurs over 67 per cent of the year, then utilizable energy intake in *N. maura* is about 0.10 KJ.g<sup>-0.75</sup>.day<sup>-1</sup>. This may be

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

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

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 =  $0.22 \text{ KJ}.g^{-0.80}.day^{-1}$ 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  $0.06 \text{ KJ}.g^{-0.75}.day^{-1}$ . 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<sup>-1</sup>, equivalent to 46 KJ.g<sup>-0.75</sup>.year<sup>-1</sup>. Godley (1980) estimated digestible food intake of 7.3g *Regina alleni* to be 19.6 KJ.g<sup>-1</sup>.year<sup>-1</sup> (mean of spring, autumn and winter values), equivalent to 32 KJ.g<sup>-0.75</sup>.year<sup>-1</sup>. 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	2 55	24
Growth	13	21	<b>\$</b> 35	5 34
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)	Pg	Energy (KJ.g <sup>-0.75</sup> .ye P <sub>r</sub>	ar <sup>-1</sup> ) Total
0	13	1.8	0	Sandan Makatan Makatan Sanda Sanda		
1	20	5.4	0	6.5	0	21.9
2	25	9.5	0	4.3	0	19.7
3	29	14	0	3.2	0	18.6
4	22	21	0	3.8	0	19.2
4	55	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	2.5	е л 9 л	27.2
9	53	92	9.6	5.5	0.4	27.5
10	57	116	11.0	3.4	8.1	26.9
11	61	144	12.4	3.4	7.7	26.5
12	65	177	13.6	3.5	7.3	26.1
12.20	65	177	12.6	0	6.8	22.2
13-20	00	1//	13.0	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<sup>-1</sup>) from each value of VO<sub>2</sub>, then converting to ml.g<sup>-0.75</sup>.h<sup>-1</sup>. This was used because SDA was not obviously related to body weight. An alternative is to subtract weight-corrected mean SDA (0.73ml.g<sup>-0.75</sup>.h<sup>-1</sup>) 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	Correcti	ons to Ha	iley & D	avies (1986a.b)	
Page	Col.	Para.	Line	Should read	

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	2(b)	(P>0.05)