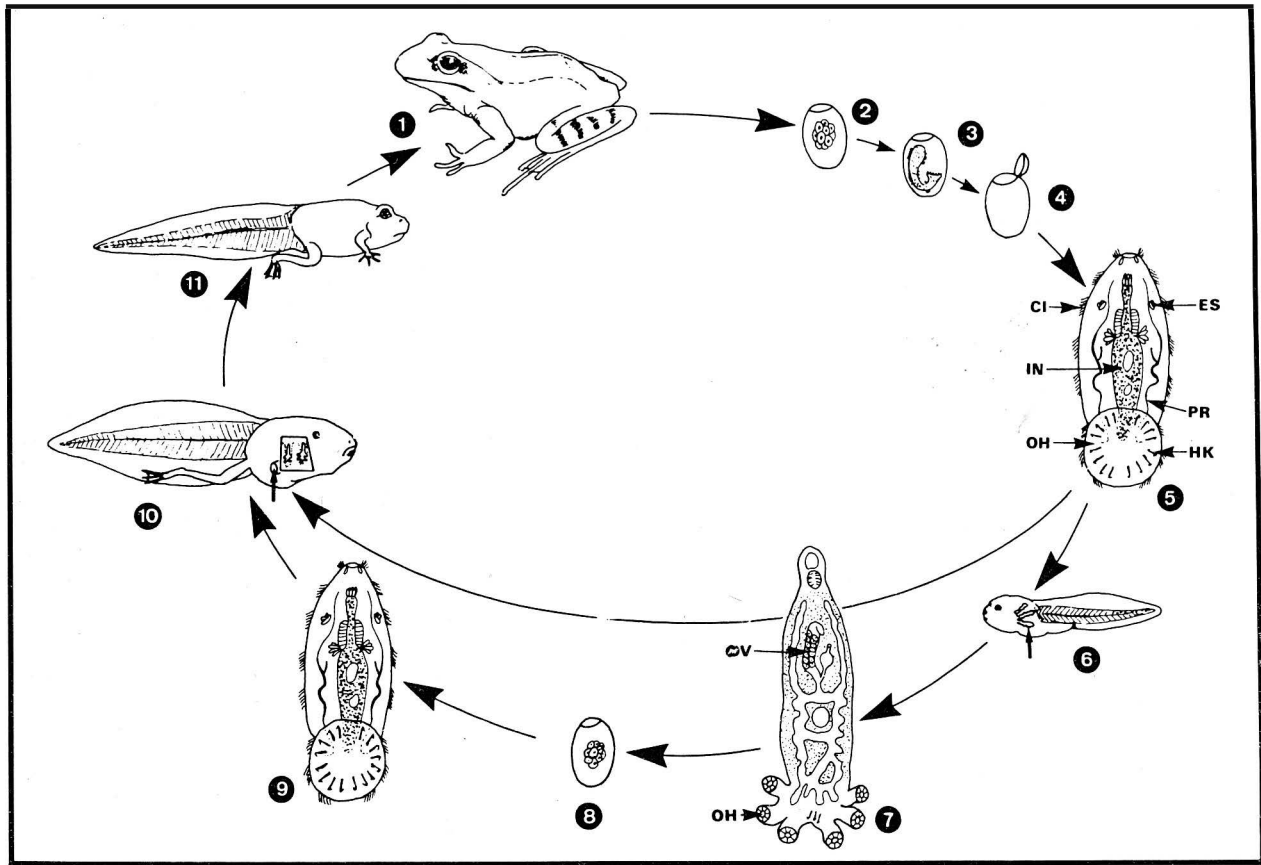


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THE RESIDUES IN THE EGGS OF SQUAMATE REPTILES AT HATCHING

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ABSTRACT

The residues present in hatched eggshells of captive-bred squamates were examined and their amounts recorded. Large amounts of a semi-gelatinous fluid were typically left in the eggshell at hatching. The amount of residues, but not hatching size, depended upon the uptake of water by the egg during incubation. In some instances egg yolk was also left in the eggshell at hatching. The role of these residues in the water relations of reptile eggs have largely been ignored.

INTRODUCTION

Water is absorbed by soft-shelled eggs of squamates and turtles during incubation (Packard and Packard, 1988) but its fate in the egg is unclear. In some squamate eggs albumen mass has been reported to increase during embryonic development (Clark, 1953; Badham, 1971) from initially low levels at oviposition (Tracy and Snell, 1985). The albumen in the eggs of *Amphibolus barbatus barbatus* oozed out during the hatching process (Badham, 1971). Considering that egg mass almost trebled during incubation, and that hatching mass was 15 per cent than initial egg mass, it is clear that there was considerable loss of albumen (Badham, 1971). By contrast, Subbo Rao (1987) reported that it was allantoic fluid that oozed from eggs of the crocodilian *Gavialis gangeticus* at the end of incubation. The amount of albumen in crocodilian and avian eggs is initially high, diminishes during incubation and is absent at hatching (Webb, Manolis, Whitehead and Dempsey, 1987; Manolis, Webb and Dempsey, 1987; Romanoff, 1967).

Reports of fluid loss at hatching are rare (Bustard, 1966; Badham, 1971; Subbo Rao, 1987; D. Ball, personal communication; Deeming and Ferguson, 1989) despite intensive studies of the water relations of reptile eggs (M. J. Packard, Packard and Boardman, 1980; G. C. Packard, Taigen, Packard and Boardman, 1980; G. C. Packard, Packard, Boardman, Morris and Shuman, 1983; G. C. Packard, Packard and Gutzke, 1985; Packard and Packard, 1984; Morris, Packard, Boardman, Paukstis and Packard, 1983; Ackerman, Dmi'el and Ar, 1985; Gutzke and Packard, 1986, 1987; Thompson, 1987). Obviously there is some confusion over the origin of this fluid but more importantly the quantities of fluid lost are unknown. This study examined the residues in the hatched eggshells from a species of lizard and four species of snake bred in captivity.

MATERIALS AND METHODS

Details of the eggs used in this study are shown in Table 1. All of the eggs were kept in sealed polyethylene bags containing vermiculite and water (1:1) as an incubation medium. At the Zoological Society of London the bags were kept in a room maintained between 26°C to 28°C. At both the University of Reading, and the University of Manchester, the bags were kept in a table top box oven (Laboratory Thermal Limited, Oldham England) maintained at 27°C. The bags were opened once or twice a week to replenish the air within the bag.

The studies were carried out during three seasons (1986, 1987 and 1988). In the first season eggs from *Eublepharis* and *Elaphe o. spiloides* were incubated at Reading. After the hatchlings had emerged the mass of the eggshell and the residues in the shell were determined to the nearest 10mg. Eggs of the other species (*Hydrodynastes*, *Pituophis* and *Python*) were incubated at the Zoological Society of London and were collected after hatching. On return to Reading the residues and the eggshell were weighed.

In the second season five freshly-laid eggs of *Eublepharis* were collected from London and incubated at Reading. In 1988 freshly-laid eggs of *Elaphe o. obseleta* were collected from the Manchester Museum and incubated at the department of Cell and Structural Biology. Each egg was weighed to the nearest milligram at the start of incubation and every seven days thereafter upto 35 days of incubation when the mass of each egg was determined every three or four days. The mass of the hatchling was determined after emergence from the shell. Any residues were removed from the eggshell which was weighed.

Species	No.	Origin
Lizards		
Gekkonidae		
<i>Eublepharis macularius</i>	10	The Zoological Society of London
Snakes		
Colubridae		
<i>Elaphe obsoleta spiloides</i>	3	Ms G. Rohan-Wild
<i>Elaphe obsoleta obsoleta</i>	2	The Manchester Museum
<i>Hydrodynastes gigas</i>	3	The Zoological Society of London
<i>Pituophis melanoleucus</i>	5	The Zoological Society of London
Pythonidae		
<i>Python molurus</i>	3	The Zoological Society of London

TABLE 1: Details of the number and sources of squamate reptile eggs examined.

Species	Egg Number	Shell	Fluids	Yolk	
<i>Eublepharis macularius</i>	A1	0.28	1.01	—	*
	A2	0.34	1.18	—	*
	B1	0.23	0.48	—	*
	B2	0.33	0.50	—	*
	C1	0.32	0.38	—	*
<i>Elaphe obsoleta spiloides</i>	A1	1.97	4.44	—	*
	A2	1.76	1.16	2.63	*
	A3	1.92	2.68	—	*
<i>Hydrodynastes gigas</i>	A2	—	3.49	15.14	
	A3	—	3.99	10.94	
	A4	—	1.25	13.57	
<i>Pituophis melanoleucus</i>	A1	2.95	1.75	—	
	A2	2.71	1.69	—	
	A3	3.16	3.12	—	
	A4	3.34	0.58	15.97	
	A5	3.45	1.62	—	
<i>Python molurus</i>	A1	10.09	26.54	25.25	
	A2	11.28	46.17	0.67	
	A3	19.91	43.98	0.77	

TABLE 2: The mass (grams) of the shell, residual fluids and residual yolk after the hatchling reptile has emerged from the egg.

* = Eggs incubated in Reading; other eggs incubated at the Zoological Society of London.

RESULTS

In the first season, neither the initial egg mass nor hatchling mass were available. The fresh mass of the hatched eggshell and the residues are shown in Table 2. Varying amounts of a semi-gelatinous fluid were found in eggshells of all the species examined. No details of possible leakage from the egg prior to collection were known. There were substantial amounts of yolk remaining in several snake eggs (Table 2).

Data collected from the *Eublepharis* eggs studied in the second season are shown in Fig. 1 and Table 3. The eggs increased in mass throughout incubation though after day 35 there was an increase in the rate of water

uptake. Final egg mass, recorded prior to hatching, was almost twice that recorded at the start of incubation (Fig. 1). After hatching (day 55) the average mass of the eggshell was 0.23g. As data was unavailable from oviposited eggs, initial eggshell mass was assumed to be the same as at the end of incubation. The total mass of the residues in the eggs was determined by difference (Table 3). Hatchling mass did not differ significantly from the initial calculated egg contents ($t = -1.70$, $p > 0.05$, two sample student's t test).

Eggs of *Elaphe o. obsoleta* likewise increased continuously throughout incubation; the first egg doubled in mass (after 57 days of incubation)

Variable	<i>Eublepharis</i>		<i>Elaphe</i>	<i>Elaphe</i>
	X	s.e.	1	2
Initial egg mass.	3.198	0.164	15.95	15.56
Final egg mass.	5.805	0.275	33.72	23.51
Shell mass.	0.230	0.016	2.33	1.29
Hatchling mass.	2.849	0.061	11.66	12.77
Residual mass at hatch.	2.725	0.249	19.73	9.76
Initial egg contents.	2.968	0.157	13.62	14.27

TABLE 3: Data from five *Eublepharis* eggs and two eggs of *Elaphe obsoleta obsoleta* at the beginning and end of incubation. Values for *Eublepharis* are means (X) in grams and standard errors (s.e.). Values for *Elaphe* are for the two individual eggs.

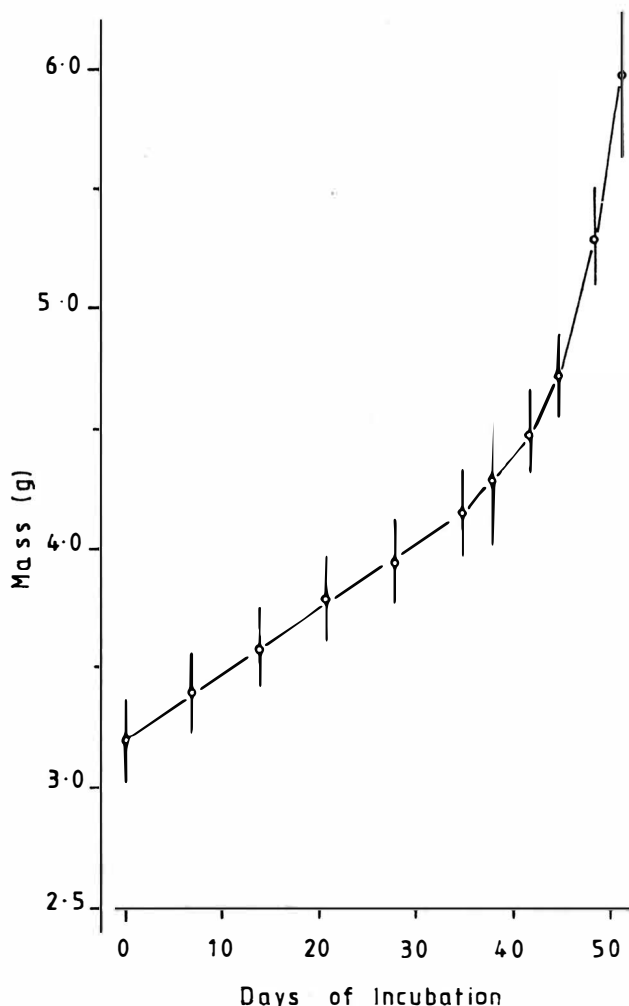


Fig. 1 The mass of five eggs of the gecko *Eublepharis macularius* during incubation. Values are means (grams) with standard error bars.

compared to the second egg which increased by half of its initial mass (Table 3). Despite this difference in water uptake hatchling mass was similar and less than the initial egg contents (85.6 per cent of initial egg mass, egg 1: 89.5 per cent, egg 2). The 10g difference in final egg mass was accounted for by the egg residues after hatchling emergence (Table 3).

DISCUSSION

Much residual material was present in the eggshells examined in the present study. Comparison of the residues found in eggs of *Eublepharis* in 1986, with those in 1987, highlighted a major problem in experimental technique. In 1986 neither the mass of the eggs prior to hatching, nor the mass of the hatchling, were recorded. Data collected in 1987 were more extensive and large amounts of residues were lost at hatching. It is clear that data collected in 1986 underestimated the actual amount of the residues present at the end of incubation in this species and it is likely that this result applies to all of the species shown in Table 2.

Residual yolk was easily recognised in eggs examined in the present study. It was surprising that such large amounts could be left in the eggshell. Normally, the initial mass of the yolk determines hatchling mass and larger hatchlings have better rates of survival (Tracy, 1982). The significance of the ability to leave residual yolk in the eggshell and its effects upon the size of the hatchling and its potential survival are not clear.

Although the present study was limited in its scope it highlights our poor understanding of the developmental physiology of reptile eggs. Unfortunately, this study cannot confirm the origin of the semi-gelatinous fluid in these eggs but examination of the literature suggests that it is allantoic fluid. Two reports have led to confusion over the role of albumen in squamate eggs (Clark, 1953; Badham, 1971). The albumen content of eggs of *Amphibolurus* (Badham, 1971) and *Coluber constrictor* (Clark, 1953) increased during incubation. The urea content of albumen in *Coluber* eggs increased during development and the fluid was seen as a major excretory store (Clark, 1953). In birds the normal storage compartment for nitrogenous waste (uric acid) is the allantoic fluid. Protein was present in the albumen of *Amphibolurus* eggs (Badham, 1971) but it only constituted less than 0.5 per cent of the total mass of the fluid measured. By contrast, albumen in eggs of birds (Romanoff, 1967) and crocodilians (Burley, Black, Wellington and Grigg, 1987) contains much more protein. Fresh albumen in reptile eggs is gel-like (Ewert, 1985; Ferguson, 1985) whereas allantoic fluid is much less viscous (Moffat, 1985) resembling thin albumen of birds eggs. The residual fluid in squamate

eggs was similar in appearance to allantoic fluid in eggs of *Alligator mississippiensis*; large amounts of allantoic fluid are present in these eggs at the end of incubation and it oozes from the egg during hatching (Deeming and Ferguson, 1989). Therefore, I agree with the suggestion of Packard and Packard (1988) that Badham (1971) and Clark (1953) mistook allantoic fluid in lizard eggs for albumen.

In both *Eublepharis* and *Elaphe* increases in egg mass during incubation were reflected in the amount of residues (allantoic fluid) at hatch and not in hatchling mass. Hatchling mass was similar to, or less than, the mass of the initial eggs contents. *Python* hatchlings weigh less than both the initial and final egg mass (Black, Birchard, Schuett and Black, 1984). Similarly, hatchlings of *Amphibolurus* weighed less than the initial mass of the eggs despite a three-fold increase in egg mass during incubation (Badham, 1971). It is interesting to note that crocodilian eggs also ooze allantoic fluid at hatching although they do not take up additional water from the nest substrate during incubation (Subbo Rao, 1987; Deeming and Ferguson, 1989). Eggs of *Crocodylus johnstoni* have around 10g of allantoic fluid present at the end of incubation (Manolis *et al.*, 1987) but all other fluids in the egg had disappeared. Unfortunately the fate of the allantoic fluid was not reported but as the combined masses of the hatchling and eggshell constituted only 72-76 per cent of initial egg mass it is likely that the fluid was lost from the egg at hatching.

Although many studies have examined the water relations of squamate eggs (Badham, 1971; Tracy, 1980; M. J. Packard, Packard, Miller, Jones and Gutzke, 1985; M. J. Packard *et al.*, 1980; Muth, 1981; Black, *et al.*, 1984; Gutzke and Packard, 1987; Packard and Packard, 1987) very few studies have examined the changes in the individual components of the egg during incubation. For example, various studies have shown that the urea content of chelonian and squamate eggs increases during incubation (Packard and Packard, 1983, 1987; G. C. Packard *et al.*, 1983; G. C. Packard, Packard and Boardman, 1984) but whole eggs were homogenised and the location of the urea was unknown. By contrast, Manolis *et al.* (1987) showed that urea increased in eggs of *Crocodylus* during incubation and that it was only present in large quantities in allantoic fluid. Indeed water absorbed during incubation may play an important role in diluting the large amounts of urea in reptile eggs allowing the embryo to develop for a longer period (Packard *et al.*, 1984). The toxic allantoic fluid would be released from the egg at hatching.

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ASPECTS OF THE MORPHOMETRY, GROWTH-RELATED PARAMETERS AND REPRODUCTIVE CONDITION OF AGAMA LIZARDS IN AGO-IWOYE, NIGERIA

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ABSTRACT

Immature, adult males and females of the lizard, *Agama agama* (L.) collected at Ago-Iwoye, Nigeria during the second and third quarters of 1987, differed most in snout-vent lengths (SVL). They averaged 59 ± 3 mm, 125 ± 2 mm and 104 ± 3 mm SVL, respectively and also differed in dimensions and weights of other body structures. These structures, including scales, eyes, tail and hind limb, correlated well with SVL and grow allometrically in relation to it. They can therefore be used to separate *Agama agama* into age-sex classes. Females are capable of breeding at 91mm SVL and those in breeding condition differed from non-reproductive members in weights and dimensions of gonadal structures ($P < 0.001$) but not SVL and body weight ($P > 0.10$). Males in reproductive condition differed from non-reproductive ones in SVL, body weight and reproductive parameters ($P < 0.001$).

INTRODUCTION

In tropical Africa, where it is widely distributed, the Agama or rainbow lizard, *Agama agama* (Family — Agamidae) is the most common reptile due to its tolerance of a considerable range of climatic conditions (Harris, 1963). Despite its abundance and common occurrence, this lizard has been little studied. Its breeding biology in Kenya (Marshall and Hook, 1960), growth and cyclic behaviour in Liberia (Daniel, 1960), and general biology in Ghana (Chapman and Chapman, 1964) have been studied and reported. Tinkle (1969) reviewed life history strategies of lizards and postulated that *Agama agama* is early-maturing, short-lived, multiple-clutched and acyclic in breeding.

Reported investigations of *Agama agama* in Nigeria were carried out in widely-separated periods of time. Harris (1963, 1964) described the anatomy, general habits, territorial behaviour and reproductive biology of the lizards collected from Ibadan and Lagos, Nigeria. The diurnal activity pattern, and population density were investigated by Halstead (1970) and Ekundayo and Otusanya (1969). Male *Agama agama* are usually bigger than females in size and are polygynous. The ratio of males to females varies between 1:3 in the rainy season to 1:4 in the dry season. These lizards are inactive at dawn. Thereafter, activities increase and peak in the late afternoons.

The size distribution and morphometrics, growth rate, and reproductive parameters of this species have been little studied. Information on sizes of lizards at specific stages of sexual maturity and known ages are required by those conducting field research on population and general ecology of these lizards. Life history data are also needed to test hypothesis on reproductive strategy of *Agama agama*.

In this paper, results of a preliminary investigation of the growth relationships and morphometrics, age-

sex differentiation criteria and reproductive condition of *Agama* lizards collected between March and August 1987 on the Ogun State University Mini-Campus, Ago-Iwoye, Nigeria, are presented.

STUDY AREA AND METHODS

The study site, the Ogun State University Mini-Campus, Ago-Iwoye, occurs in the southern Nigerian Rain Forest belt. Open spaces between buildings on the Mini-Campus are interspersed with grasses and planted shrubs and the roads are bordered by unpainted concrete drains.

Eighty-two lizards collected from different sites on the Mini-Campus were each studied as a unit for morphometric features, growth and its indices and reproductive activity. Lengths of the following expressed to the nearest mm or 0.1mm were recorded for each lizard caught: snout-vent (SVL), hind limb (HLL), intact tail (TL), eye diameter (ELD), and scale (SL) removed from the dorsal part of the tail near its junction with the trunk. Dimensions of ovarian follicles or oviductal ova were recorded for females.

Weights of: the whole body (GBW), eye (ELW), paired ovaries and oviduct with follicles and eggs, paired testes (TW) and the epididymis (EW) were recorded to the nearest 0.1g or 0.01g for the applicable sex. The epididymis: testis weight ratio (ETR) was determined for males.

Lizards were categorised as immature, and adult (sexually-mature) males and females on the basis of gonadal maturity. Breeding females were either vitellogenic with developed, yolked ovarian follicles; or ovigerous with oviductal eggs. Non-breeding females were those which had undeveloped, milky-white ovarian follicles and no oviductal eggs. Male

Attribute	Immature (14)	Adult males (40)	Adult females (28)
SVL (mm)	59 ± 3 ^c	125 ± 3 ^a	104 ± 2 ^b
Scale length (mm)	1.1 ± 0.1 ^b	3.5 ± 0.1 ^a	2.8 ± 0.1 ^a
Eye diameter (mm)	4.2 ± 0.1 ^b	8.1 ± 0.1 ^a	7.4 ± 0.1 ^a
Eye weight (g)	0.12 ± 0.01 ^b	0.36 ± 0.02 ^a	0.28 ± 0.01 ^a
Body weight (g)	8.2 ± 1.4 ^c	68.1 ± 3.4 ^a	40.2 ± 1.7 ^b
TL:SVL ratio	1.78 ± 0.06 ^a	1.44 ± 0.04 ^b	1.65 ± 0.05 ^a
HLL:SVL ratio	0.30 ± 0.01 ^a	0.27 ± 0.01 ^b	0.25 ± 0.01 ^b

TABLE 1: Mean dimensions, weights and morphometric measurements (\pm S.E.) of body structures of Agama lizards belonging to different age-sex classes. Number of lizards in each category is shown in parentheses.

Mean along rows with same superscript are not different ($P > 0.05$).

Agama agama were placed in breeding categories on the basis of their body weights, testes weights and ETR. Breeding males were those that had higher-than-average values of the 3 parameters while non-breeding ones had lower values.

Frequency distributions of lizards according to their SVLs, TL:SVL and HLL:SVL ratios were inspected to determine the utility of the variables as age-sex class indicators. The relationship between some of these and other variables where lengths were expressed in cm and weights in g., was examined by correlation and regression. The occurrence of allometry between any 2 body dimensions compared was proven by: (i) testing for deviations of observations from simple size allometry (Simpson *et al.*, 1960), and (ii) testing the homogeneity of regression and correlation coefficients of juveniles, adult males and females by means of an F-test and a χ^2 -test criterion respectively (Steel and Torrie, 1980). Constants of the allometric growth formula, $Y = bX^a$ are indicated.

Pair-wise and multiple comparisons were made using the t-test and one-way analysis of variance (ANOVA). Mean separations were accomplished with Duncan's New Multiple Range Test. Results of statistical tests were considered significant at $P < 0.05$; highly significant at $P < 0.01$.

RESULTS

SIZE DISTRIBUTION OF *Agama agama*

The snout-vent length (SVL) showed the sharpest modal separation of the lizard age-sex classes. The general distribution modes of low SVL, intermediate SVL, and high SVL fitted those of immature (55mm), adult females (105mm), and adult males (135mm) respectively (Fig. 1a). The smallest-sized juvenile was 45mm SVL while the biggest was 75mm SVL. Sizes for adult males and females were between 84-148mm and 89-119mm SVL respectively. The TL:SVL distribution was trimodal (Fig. 1b), while the general distribution of HLL:SVL quotients was unimodal (Fig. 1c).

Means of snout-vent length, body weight and other variables for sampled lizards categorised into the 3

age-sex classes are shown (Table 1). Immature, adult male and adult female lizards differed in SVL, eye diameter, eye weight, scale length and gross body weight which were highest in adult males (all tests one-way ANOVA, $P < 0.01$). They also differed in HLL:SVL and TL:SVL ratios (F tests, $P < 0.01$), which were greatest in immature lizards.

Body weight ranges were 2.5-18.4g for the immature, 22.6-54.0g for adult females and 21.1-107.8g for males. The upper limits of ranges of the eye diameter, eye weight, scale length, hind limb length and tail length for immature lizards were respectively 5mm, 0.2g, 1.5mm, 21mm and 142mm. The minimum values of these parameters for the sexually-mature were 6mm, 0.1g, 1.0mm, 22mm and 122mm consecutively.

GROWTH RELATIONSHIPS AND MORPHOMETRIC ANALYSIS

There was no systematic deviation of observations from a simple allometric relation for each dependent variable versus the snout-vent length, as no trend or curvature was apparent from a plot of these deviations. Regression coefficients, a , for relationships considered for each age-sex category, which also constitute the constant of allometry since all values were log-transformed, were homogeneous for the regressions on SVL of scale length ($F_{2,76} = 0.02$, $P > 0.10$), eye diameter ($F_{2,76} = 0.11$, $P > 0.10$) and eye weight ($F_{2,76} = 0.33$, $P > 0.10$).

The correlation coefficients and constants which specified the growth relationship between the SVL and these dependent variables are shown (Table 2). Allometry constants were positive and above 1 for scales, eye weight, and pooled body weights, but, below 1 for the eye diameter, the tail, and the immature lizards' hind limb length in relation to the SVL. The allometry constant was negative for adult hind limbs. Correlation between snout-vent length and each of the following: scale length, eye diameter, eye weight, and tail length; was significant ($P < 0.05$) for juvenile and adult *Agama agama* except for eye diameter of females whose correlation with SVL was not significant ($P > 0.10$). Body weights of the individual age-sexes correlated poorly with total body length ($P > 0.10$).

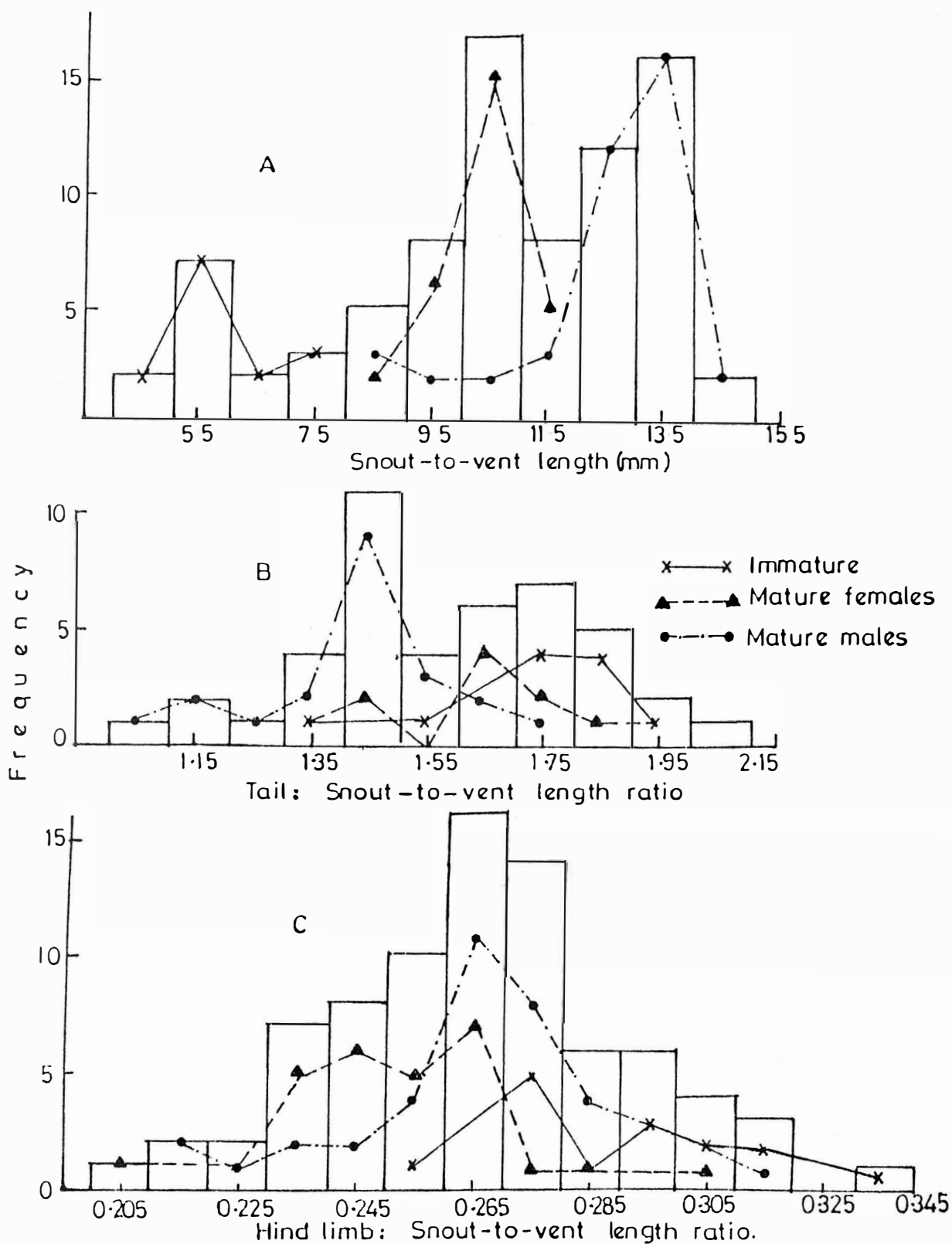


Fig. 1 Distribution of all sampled Agama lizards (histogram) and of the component age-sex classes (frequency polygons) according to their Snout to vent lengths (A) TL:SVL ratio (B) and HLL to SVL ratio (C).

Dependent variable (Y)	r	Males			r	Females			r	Immature			Overall (pooled)		
		b	a			b	a			b	a		r	b	a
Scale length	0.69 **	0.01	1.37		0.65 **	0.01	1.44		0.63 *	0.01	1.40		0.91 **	0.01	1.55
Eye diameter	0.84 **	0.22	0.52		0.31 n.s.	0.15	0.70		0.69 **	0.14	0.60		0.89 **	0.10	0.82
Eye weight	0.48 **	0.02	1.12		0.47 *	0.02	1.66		0.76 **	0.01	1.38		0.83 **	0.01	1.41
Hind limb length	0.97 **	33.57	-1.02		(males and females pooled)				0.94 **	0.45	0.75		0.48 **	1.02	0.42
Tail length	0.53 *	3.30	0.68		0.63 **	3.02	0.74		0.72 **	3.02	0.71		0.75 **	4.73	0.52
Body weight (versus t. body length)	0.14 n.s.	10.14	0.58		0.36 n.s.	10.91	0.38		0.51 n.s.	0.05	1.79		0.88 **	0.01	2.76

TABLE 2: Correlation coefficients and constants of the allometric growth relationship, $Y = bX^a$ between SVL or total body length (X) and other variables (Y) for the 3 Agama lizard age-sex classes. n.s., not significant; * significant ($P < 0.05$); ** highly significant ($P < 0.01$).

There was distinct discontinuity in the regression lines fitted for the SL-SVL relationship, between juveniles and adults (Fig. 2). The correlation coefficients ($X^2 = 0.49$, 2 d.f., $P > 0.75$) and regression

slopes ($F_{2,76} = 0.02$, $P > 0.10$) of each age-sex category did not differ from each other and from the composite. The pattern was the same for eye diameter and weight, which were not plotted.

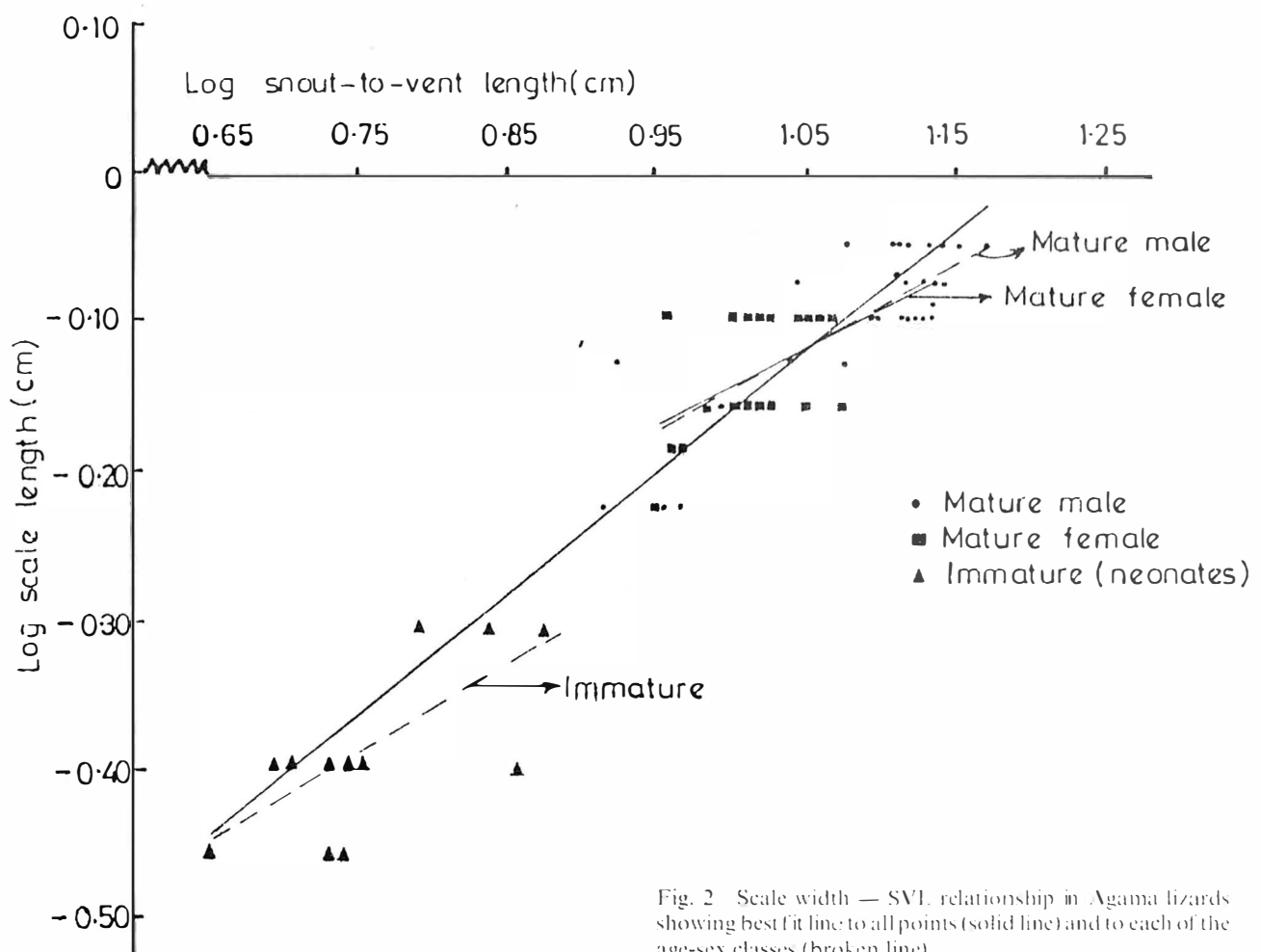


Fig. 2 Scale width — SVL relationship in Agama lizards showing best fit line to all points (solid line) and to each of the age-sex classes (broken line).

Breeding category	SVL (mm)		Body wt. (g)		Ovary wt. (g)		Oviduct wt. (g)		Ovum length (mm)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
		\pm S.E.		\pm S.E.		\pm S.E.		\pm S.E.		\pm S.E.
Ovigerous (8)	91	103	32.4	38.7	0.15	0.20 ^b	3.41	7.05 ^a	16.0	18.4 ^a
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	111	2	44.1	1.3	0.30	0.02	10.70	0.92	24.0	1.3
Advanced vitellogenic (8)	100	108	36.2	45.4	3.20	4.45 ^a	0.60	0.86 ^b	7.0	8.8 ^b
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	116	2	60.0	3.0	4.80	0.25	1.00	0.05	10.0	0.4
Early vitellogenic (7)	92	102	26.7	38.1	0.80	1.21 ^b	0.20	0.44 ^b	4.0	5.8 ^{bc}
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	109	2	55.3	3.9	1.90	0.17	0.90	0.08	7.5	0.5
Non-breeding (5)	89	104	22.6	37.4	0.10	0.23 ^b	0.01	0.05 ^b	2.0	2.5 ^c
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	119	7	52.7	5.9	0.40	0.05	0.10	0.02	3.5	0.4

TABLE 3: Dimensions and weights of the body and reproductive parameters of female *Agama* lizards belonging to different breeding categories. Number for each category is shown in parentheses.

Means along columns with same superscript(s) are not different ($P > 0.05$).

REPRODUCTIVE STATE AND SIZE AT MATURITY OF *Agama agama*

We observed that breeding females constituted 82 per cent of females caught while males in breeding condition made up 55 per cent of males sampled. Breeding lizards belonging to both sexes were found during the months of study (April–August).

Female:

There was no difference in the SVLs ($F_{3,24} = 0.85$, $P > 0.10$) and body weights ($F_{3,34} = 1.25$, $P > 0.10$) of non-breeding, early-vitellogenic, late-vitellogenic, and ovigerous females who differed significantly (F -tests, $P < 0.001$) in weights of the ovary and oviduct, and size of follicles or ova (Table 3). Among breeding females with mean SVL of 103 ± 2 (S.E.) mm, none less than 91 mm SVL contained vitellogenic follicles or oviductal eggs. Advanced vitellogenic females had the greatest ovary weights while oviductal weight was highest in ovigerous females whose ova were largest.

Mean ova per ovigerous female lizards sampled was 6. Three non-breeding females (mean SVL 103 mm)

with distended oviducts had mean oviductal and ovarian weights of 0.01 g and 0.15 g respectively. Six eggs laid by a gravid female lizard on 22 June hatched on 18 and 19 August, 1987. The snout-vent lengths of the hatchlings at emergence ranged between 37–39 mm (Mean 38 ± 3 mm).

Male:

Males in breeding condition differed from the non-breeding in SVL ($t = 4.15$, d.f. 37, $P < 0.001$), body weight ($t = 5.69$, d.f. 37, $P < 0.001$), and epididymis: testes weight ratio ($t = 6.96$, d.f. 37, $P < 0.001$). They had consistently higher values of these variables than the non-breeding males (Table 4). The smallest male in breeding condition had a snout-vent length of 125 mm and 3 other males had SVLs greater than 125 mm but lower than 130 mm. Four non-breeding males with atrophied testes and epididymis had SVLs ranging between 131 mm and 142 mm (Mean 136 ± 2 mm) and ETR and testes weights averaging 0.08 ± 0.02 and 0.25 ± 0.05 g respectively.

Breeding category	SVL (mm)		Body wt. (g)		Testis wt. (g)		Epididymis wt. (g)		ETR	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
		\pm S.E.		\pm S.E.		\pm S.E.		\pm S.E.		\pm S.E.
Breeding (22)	125	133	64.2	81.5	0.30	0.56	0.10	0.12	0.25	0.22
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	148	1	107.8	2.6	0.90	0.04	0.20	0.01	0.33	0.01
Non-breeding (18)	84	117	19.6	53.6	0.10	0.25	0.01	0.02	0.03	0.08
	—	\pm	—	\pm	—	\pm	—	\pm	—	\pm
	142	4	75.0	4.4	0.50	0.03	0.05	0.01	0.25	0.02

TABLE 4: Dimension and weights of the body and reproductive parameters of breeding and non-breeding male *Agama* lizards. Number for each category is shown in parentheses.

DISCUSSION

The snout-vent length has utility as an age predictor in *Agama agama* because it differed well between immature and adults. However, the TL:SVL and HLL:SVL distributions are poor indicators of age or age-class because there was considerable overlap between the tails of the individual distributions of immature, adult male and adult females.

On the basis of SVL only, juveniles can be easily separated from sexually-mature lizards on the field since these are individuals with SVLs of 75mm or less. Adult males with sizes greater than 125mm SVL can be differentiated from females whose maximum recorded dimension in Ago-Iwoye was 119mm SVL, a greater length than the 116mm SVL for females in Ibadan (Harris, 1964). Males and females within the 84-120mm SVL range can be partially separated on the basis of body weight since no female heavier than 60g was sampled, neither has any been reported in earlier studies. Chapman and Chapman (1964) used mostly weight as criterion of size in their study although body weights alone may not be reliable for this purpose because they are affected by the condition of the animal. Finally, presence of anal pads in the vent region of males (Harris, 1963) can be employed in identifying the sexes where there is overlap in size or weight of the animals.

Overlap in the tail lengths of immature and adult lizards might be due to the differential growth rate of each age-sex tail. Chapman and Chapman (1964:122) observed that the rate of increase in tail length was less in old females compared to males so that female tails were shorter. Overlap in tail length between older juveniles and sub-adult females might thus occur. Similar overlaps occurred for eye weight and scale length the implication of which is that these variables cannot be used in isolation to separate lizard age-classes.

The tests of deviation of observations from allometry and of homogeneity of allometry constants indicated the occurrence of an allometric growth relationship between the dependent variables and SVL of *Agama* lizards. The ontogenetic changes in the dimensions of the eye, tail and hind limb in relation to the SVL indicate that there was decrease in the sizes of these, relative to the latter. These structures grew at a slower rate although, they did not cease growth because their absolute dimensions were greater in older and larger-sized lizards than in younger, smaller-sized ones. A negative coefficient of allometry indicates that the organ or structure showing it grows smaller as the dimension of the other structure it is being compared with increases (Simpson *et al.*, 1960: 404). It is highly unlikely that the hind limbs of adults decreased as their SVLs increased, rather, the hind limbs probably ceased growing altogether on, or after adulthood was attained. This readily explains the positive allometry constants for immature lizards and all the lizards sampled since, the immature phase represents the period of most active hind limb growth. The scale length, eye weight and overall body weight increased at a faster rate than the SVL.

The composite regression equations for the growth relationships of *Agama agama* considered can be used to fit all lizards because the correlation and regression coefficients of the individual age-sexes were homogeneous.

Compared to the incubation period of 58 days for eggs in this study, eggs brooded in the laboratory by Harris (1964) whose oviposition dates were unknown, hatched before 32 days. The sizes of the hatchlings at emergence were, however, similar in both cases. Growth trajectories based on data from these two studies shows that females of size 90mm SVL are about 14 months old while males at 125mm SVL are aged circa 22 months.

The lack of disparity in body weights of the breeding and non-breeding females suggests compensatory weight loss by breeding females aimed probably at reducing the risk involved in carrying a weight heavier than the normal for the population. The values of some reproductive parameters for females in Ago-Iwoye is in consonance with those for female *Agama agama* in Ghana (Chapman and Chapman, 1964). In both instances, females with maximum ovary weight of 4.0g and oocyte dimension of 12mm were advanced vitellogenic; those with ovary weight circa 0.16g were ovigerous; while an ovary weight of 0.5g or less was characteristic of non-breeding females. As evident from this study, females that have recently oviposited have; ovary weights similar to ovigerous ones, no oviductal eggs, oocytes with same dimensions as non-breeding members and oviducts more distended than those of vitellogenic and non-breeding female *Agama agama*. These criteria are useful in delineating breeding categories of female lizards.

Lizard testicular condition and weight vary with spermatogenic activity (Licht *et al.*, 1969). Occurrence of spermatozoa in the testicular lumina, hypertrophy of the epididymis, and subsequent spermiation are indicative of reproductive readiness. The epididymis: testes weight ratio and testicular weight are, therefore, good indicators of breeding condition of male lizards. We separated male *Agama agama* into breeding categories on these basis. The occurrence of males in breeding condition in all our monthly samples in the southern Nigerian Rain Forest where, the lizard has been observed to breed all the year round (Harris, 1964, Ekundayo and Otusanya, 1969), probably attests to the acyclic nature of breeding reported for the species (Tinkle, 1969, Tinkle *et al.*, 1970).

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IDENTIFICATION OF INDIVIDUAL ADDERS (*VIPERA BERUS*) BY THEIR HEAD MARKINGS

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ABSTRACT

During a study of adders (*Vipera berus*) in Wyre Forest, a systematic method was developed to identify individuals in the field. It was revealed that no two adders possessed identical head markings. It was shown that a photographic record was a reliable aid to identification. Furthermore it was observed that over the period of study adders retained their individual head markings.

INTRODUCTION

This paper originates from a study of the adder, (*Vipera berus*), in Wyre Forest, Worcester, U.K., which began in 1981 and is now in its 8th year. During the early stages of this work the great diversity of head markings found on the adder became apparent. In attempting to follow the movements and specific seasonal behaviour of a sizeable population of adders, it was preferable if a simple method of identifying adders in the field was available, which allowed for positive identification of individuals without the associated problems of handling and disturbance.

STUDY AREA

The study area was centred upon a plantation of Japanese Larch (*Larix kaempferi*), in which a number of old coppice stools remained from a previous stand of sessile oak (*Quercus petraea*) that occupied the site prior to 1970.

METHOD

During the active period regular visits were made to the main study area. Notes were taken recording time, weather conditions, ambient and ground temperatures.

details of each adder, and significant events observed during that day.

To investigate the possibility of adders possessing an individual head marking, the markings on the head were divided into three basic components, as follows:

- A. *Eye-lines*.
 - B. *Inverted V*.
 - C. *Apex of zig-zag*.
- as illustrated in Fig. 1.

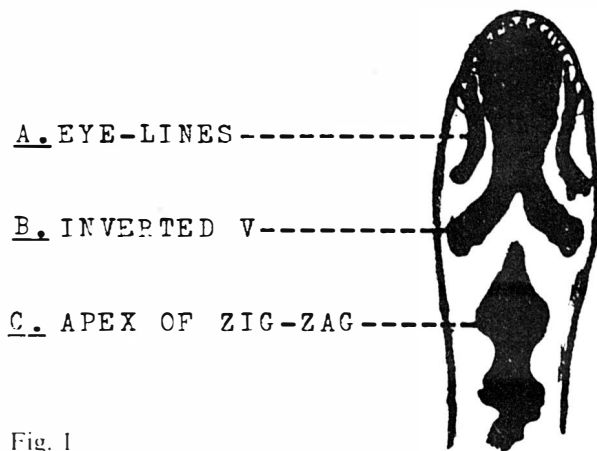


Fig. 1

If A, B or C proved subject to individual variation then this would provide the variables by which individual head patterns could be identified.

Colour photographs of each adder, specifically of the head were obtained, and fixed into a 11 x 13cm mini-file for immediate reference. In conjunction with shed skins (the pigment is retained in the scales and clearly visible when viewed with transmitted light against a white background), this allowed for detailed analysis.

Of the 92 adders photographed, 64 were in the main study area, and the remaining individuals at various locations throughout the Wyre Forest.

RESULTS

It proved possible to resolve the individual scales which comprise each component A, B and C and to place the head marking of each adder into one of two categories.

For the purpose of this study these categories have been labelled:

1. *Visually Identical*. Where the pigmented scales which comprise A, B and C and their respective positions prove impossible to distinguish apart as from one adder to another in a field situation.
2. *Individual*. Where one or more of the components A, B, C, which constitute the head pattern is obviously different.

Further, using the same components A, B, C the head pattern of adders within the study area were compared as they appeared in 1981 when the study first began, or alternatively, when first identified/photographed, and through each successive season until the present, (1988). Colour photographs and, where possible, shed skins were carefully examined for signs of any structural change (changes in shape or position of components A, B, C) over the years.

It was convenient to identify individual adders by name, in addition to each being allocated a number. For example, the two males illustrated in Fig. 2, A and B, and Fig. 3, A and B, were named Pawn and Knight because of the remarkable similarity of component C to the corresponding pieces in a chess set. Fig. 2, C and D, and Fig. 3, C and D, show two other males where component C resembles a Pyramid and a Mushroom. Figs. 2 and 3, E-P illustrate a sample of other head markings.

It was possible to identify individual adders in practically any situation provided that:

- A. A clear view of each head marking was obtained, and
- B. The observer was familiar with the various head markings of individuals within the study area.

As Table 1 shows, in five cases, two adders (set of two) shared a component which was visually identical, each set distinct from the others, significantly, in no two individuals were all three components A, B, C, (which comprise the head pattern) visually identical. Indeed only one adder was found with two components visually identical to the corresponding components on another adder, in this case the third component was the readily identifiable feature.

CHANGES IN HEAD MARKINGS OVER SUCCESSIVE SEASONS

In just one solitary male, (Fig. 2,K and Fig. 3,K) a single pigmented scale to the left of apex appeared in 1984, this was not apparent in 1983. This was the only positive change detected over a period of eight years in a sizeable population of mature adders which have been regularly monitored.

Category of Head Pattern	Component (A) Eyelines	Component (B) Inverted V	Component (C) Apex of Zig-Zag	Components Any Two A, B, C.	
1. Visually Identical	1 Set	2 Sets	2 Sets	1 Set	0
2. Individual	90	88	88	90	92

TABLE 1: Showing number of adders within the study area possessing head markings considered:

1. *Visually identical*.
2. *Individual*, classified according to components A, B, C.

Note: A 'Set' is defined as two individuals who share a component which is visually identical.

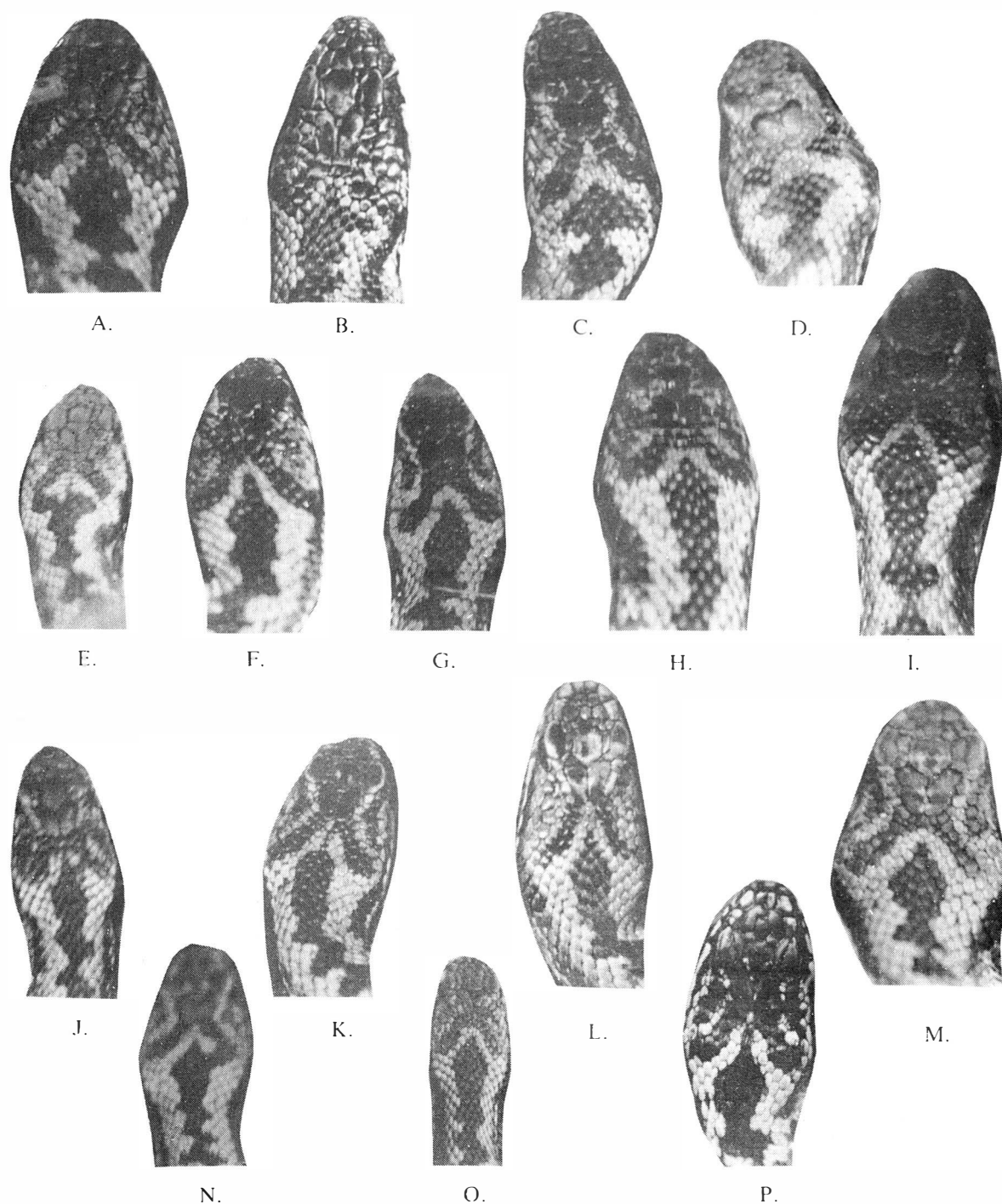


Fig. 2 A-P, showing variations in head markings.

CONCLUSIONS AND DISCUSSION

Leighton (1901) observed the wide variety of head markings in adders, but did not pursue this as a means of identification.

When studying a population of grass snakes *Natrix natrix* in Sweden, Carlstrom and Edelstam (1946) discovered 'the black and white pattern which is found on the underside of the grass snake has an infinite range of variation', and further state 'photographs of the back pattern can be used for *Coronella* and *Vipera* species' to identify individual snakes.

More recently Andren and Nilson, University of Goteborg, used a similar method to identify juvenile *V. berus* and *C. austriaca*, which were too small to mark with ventral scale cuts, but have not published anything specifically on their method.

In Britain the use of head markings for individual recognition has been used for the smooth snake *Coronella austriaca*, Goddard (1984), although details of the work are to be found in his Ph.D. thesis only.

After eight years our research is still continuing with particular attention being paid to juvenile adders, and, if circumstances permit, it is intended to monitor these individuals over many successive seasons to investigate more fully their behaviour in the wild.

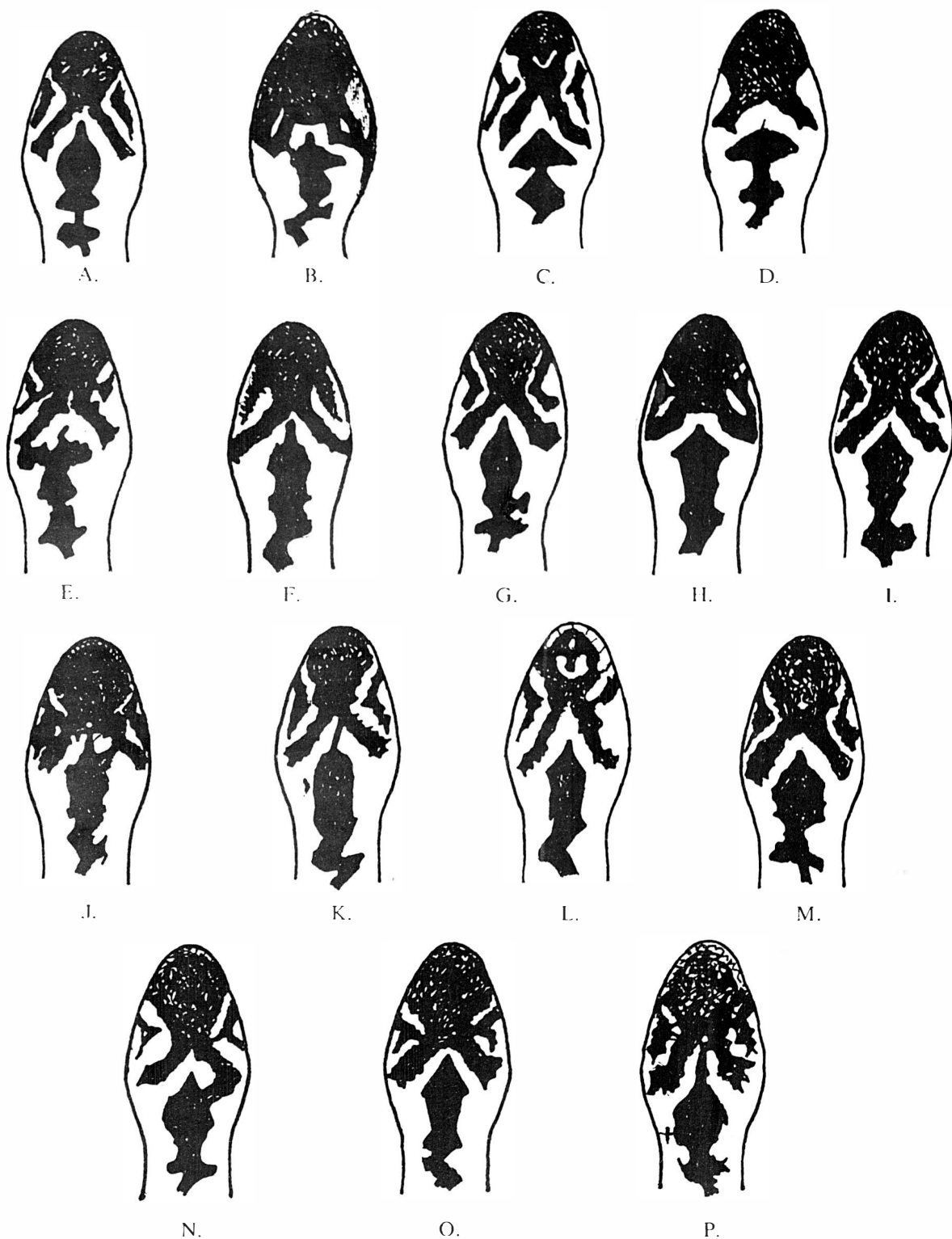


Fig. 3 A-P. Sketches illustrating variations in head markings.

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THERMAL ECOLOGY OF *CYRTODACTYLUS KOTSCHYI* (STEINDACHNER, 1870)
(SAURIA-GEKKONIDAE) IN THE INSULAR ECOSYSTEMS OF THE AEGEAN

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ABSTRACT

Initial data on the thermal ecology of *Cyrtodactylus kotschyi* from two insular ecosystems of the Aegean are reported. *C. kotschyi* is a thermoconformer. *C. kotschyi* is an eurythermic gekko and is active all the year in the ecosystems of the Aegean archipelago.

INTRODUCTION

The family Gekkonidae is one in which a high proportion of the species are nocturnal (Avery, 1982). Thermoregulatory patterns within the Gekkonidae include active control of body temperatures at night by selection of appropriate substrates, passive control of body temperature achieved by modification of activity times and diurnal basking (Avery, 1982).

Cyrtodactylus kotschyi (Steindachner, 1870) (Sauria-Gekkonidae) is the most widespread lizard in the insular ecosystems of the Aegean archipelago. Although the distribution and the systematics of this gekko are well known (Werner, 1930, Wettstein, 1953, Beutler, 1981, *et al.*), on the contrary its ecology in the Aegean ecosystems has been studied less. Some data on its ecology are referred by Beutler (1981), Beutler and Gruber (1977, 1979) and recently by Valakos and Vlachopanos (1987).

The initial data on the thermal ecology of *C. kotschyi* are reported in the present study from two insular ecosystems of the Aegean during July and November of 1987 and February and March of 1988.

of the small village of Moutsouna, during July, November and March. The main characteristics of the area are the rocky terrain and the vegetation which is maquis. The most predominant plant species is the *Juniperus phoenicea*; however *Pistacia lentiscus* and *Olca europea* are abundant.

Seventy nine of the gekkos were collected from ecosystems located on the small island of Antikythira (SW Aegean), during February. The main characteristics of these ecosystems are the rocky terrain and the vegetation which is degraded maquis, where *Juniperus phoenicea*, *Pistacia lentiscus*, *Thymus capitatus* and *Genista acanthoclada* are abundant.

Gekkos were collected by airgun or hand. For every gekko, date, time, length (snout-vent), position in the environment when first observed, body temperature (Tb) (with quick reader cloacal thermometer, Muller & Co), air temperature (Ta), 5cm above the position of gekko and substrate temperature (Ts) (with digital thermometer) were recorded.

For statistical analysis, Mann-Whitney U-tests, Student t-tests and regression analyses, were used as described by Zar (1984).

LOCALITIES AND METHODS

One hundred and thirty gekkos were collected from two insular ecosystems of the Aegean archipelago.

Fifty one of the gekkos were collected in the eastern part of the Naxos island (Central Aegean), 6 km south

RESULTS

Average cloacal (Tb), air (Ta) and substrate temperatures (Ts) are given in Table I. (Twenty three cases which were recorded in winter when the gekkos were in their burrows motionless were not included.)

Months	Tb°C			Ta°C			Ts°C			N
	x	SD	Range	x	SD	Range	x	SD	Range	
July	30.7	3.2	26.6-37.2	27.5	1.6	24.5-31.0	28.8	2.3	25.0-33.8	31
November + March	22.2	3.1	16.5-29.3	17.0	2.1	12.0-20.2	19.3	2.9	15.4-25.1	20
February	15.6	3.1	9.0-22.0	13.9	2.7	8.0-20.1	14.3	2.5	10.0-21.0	56
All the months	21.2	7.3	9.0-37.2	18.4	6.3	8.0-31.0	19.5	6.7	10.0-33.8	107

TABLE I: Descriptive statistics for body (Tb), air (Ta) and substrate (Ts) of *C. kotschyi*.

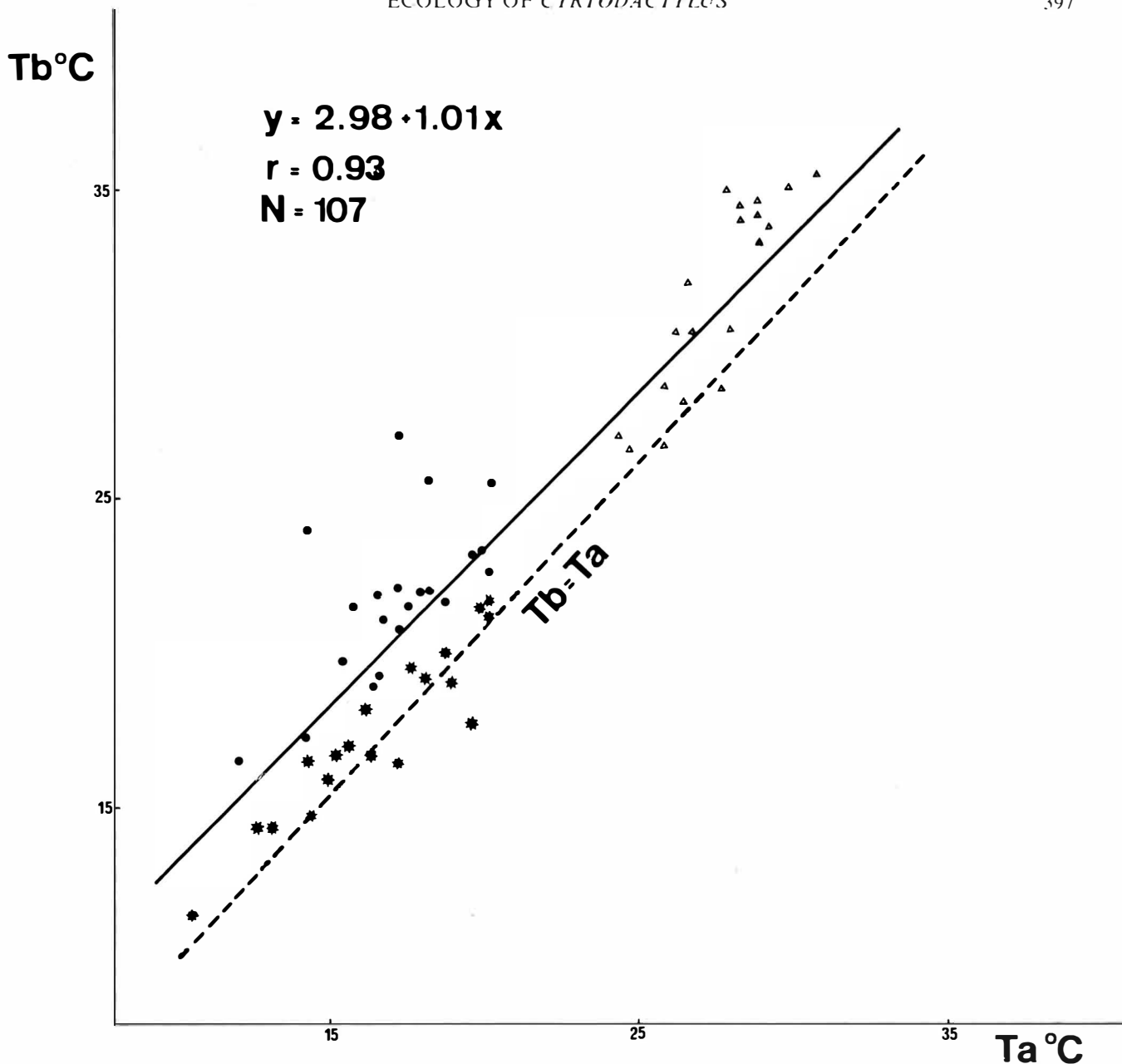


Fig. 1 Relationship between body temperature (Tb) and air temperature (Ta), in *C. kotschyi*. Solid line = line for equivalence, i.e. Ta = Tb, dots = November + March, stars = February, triangles = July.

There was a significant correlation between Tb and Ta (Fig. 1 $r = 0.93$ $P < 0.05$). Also there was a significant correlation between Tb and Ts (Fig. 2 $r = 0.96$ $P < 0.05$).

The slopes Tb versus Ta and Tb versus Ts did not differ from 1 (Tb ver. Ta $t = 0.37$ $P < 0.05$ — Tb ver. Ts $t = 1.91$ $P < 0.05$).

	Tb vs Ta				Tb vs Ts			
	b	r	r ²	P	b	r	r ²	P
July	1.50	0.77	0.60	<0.05	1.12	0.82	0.66	<0.05
November + March	0.83	0.55	0.31	<0.05	0.79	0.74	0.55	<0.05
February	1.06	0.94	0.88	<0.05	1.02	0.95	0.89	<0.05
All the months	1.01	0.93	0.87	<0.05	1.04	0.96	0.95	<0.05

TABLE 2: Correlation between body temperature (Tb) and air (Ta) and substrate temperatures (Ts) in every season (b = slope of the curves). Number of cases as in Table 1.

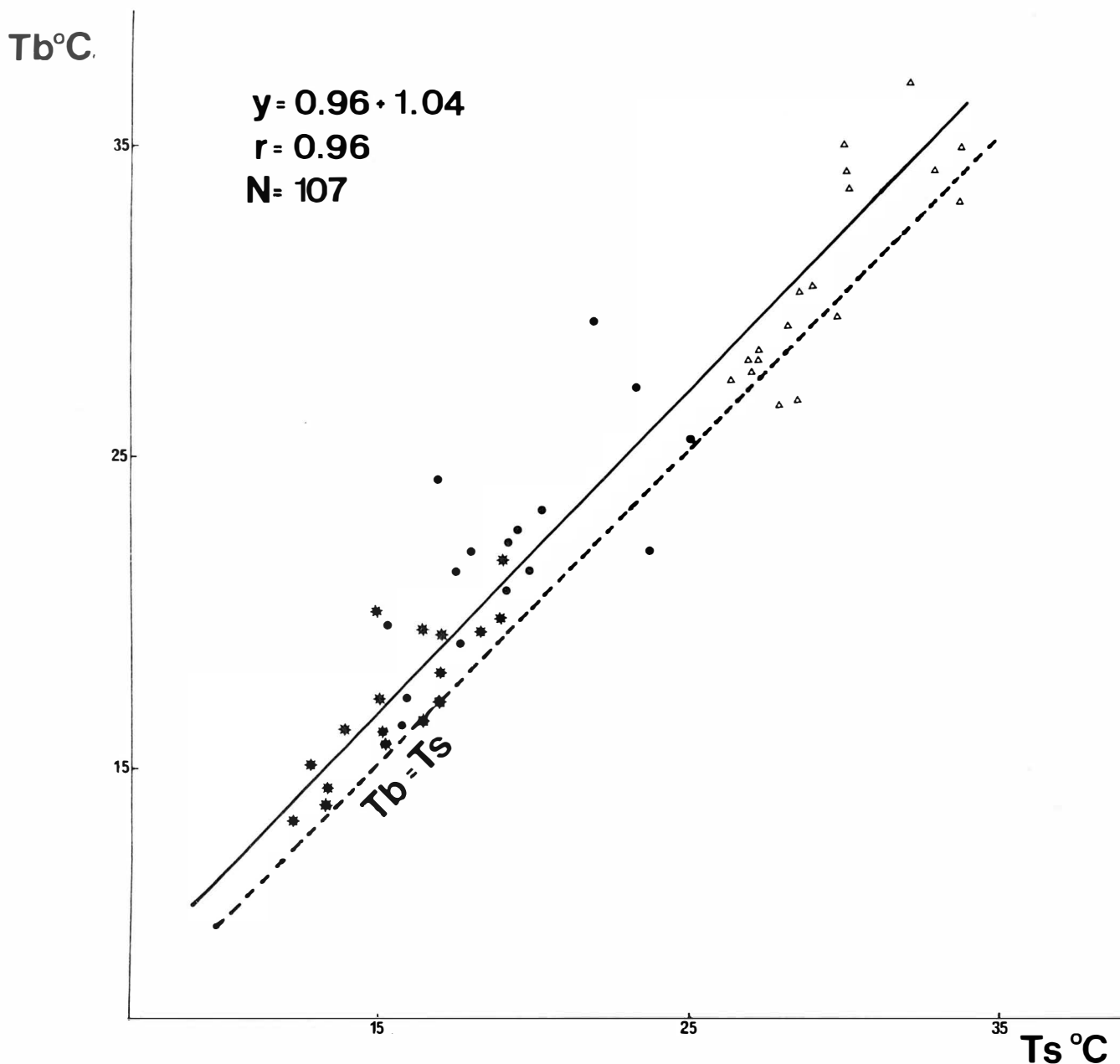


Fig. 2 Relationship between body temperature (Tb) and substrate temperature (Ts), in *C. kotychyi*. Symbols as in Fig. 1.

Also in Table 1 are given average cloacal, air and substrate temperatures. There was no difference between Tb's between November and March (Mann-Witney U test $U = 68$ $P < 0.05$) so the data were pooled. There was a significant correlation between Tb and Ta and also between Tb and Ts every month (Table 2). The slopes of the regression Tb ver. Ta and Tb ver. Ts in every month did not differ from 1 (Tb ver. Ta, November plus March $t = 0.58$ $P < 0.05$, February $t = 1.42$ $P < 0.05$ July $t = 2.14$ $P < 0.01$; Tb ver. Ts, November plus March $t = 1.24$ $P < 0.05$, February $t = 1.02$ $P < 0.05$ July $t = 0.83$ $P < 0.05$).

ACTIVITY PERIODS

In July the geckoes appeared in two periods during the day. One period between sunrise (6.30 a.m.) until 10 a.m. and a second period between sunset (7.00 p.m.)

until 10 p.m. Tb in the first period ranged from 26.6°C to 37°C and in the second period from 26.9°C to 30.7°C. During these periods the individuals basked on the stones.

In the other months the animals had a unimodal activity. In November and March the geckoes appeared and basked on the stones from 10 a.m. until 4.30 p.m., when Tb ranged from 16.5°C to 29.3°C, Ta from 12°C to 20.2°C and Ts from 15.4°C to 25.1°C.

In February the geckoes appeared and basked on the stones or in the holes between the stones from 10 a.m. to 3 p.m. Tb's ranged from 9°C to 22°C, Ta's from 8°C to 20.1°C and Ts's from 10°C to 21°C.

Twenty three motionless animals were captured in their burrows and their body temperatures ranged from 8°C to 12°C (mean 9.8°C) Ta ranged from 8°C to 12°C (mean 9.19°C) and Ts ranged from 8°C to 12°C (mean 9.08°C).

DISCUSSION

C. kotschy is a thermoconformer. The slope of the curve Tb ver. Ta did not differ from 1 (Huey and Slatkin, 1976). Also the slopes of the curves Tb ver. Ta in every season did not differ from 1 (Huey and Pianka, 1977). Thermally passive lizards seem to have longer activity times than thermoregulatory ones (Tanaka, 1986). *C. kotschy* was active in the biotope of Naxos island even in the cloudy days when the sympatric thermoregulatory species *Podarcis erhardii* (Sauria-Lacertidae) was inactive (per. obs.).

The different mean body temperatures among the seasons showed that *C. kotschy* is an eurythermic lizard. The eurythermic lizards are also eurytopic (Ruibal *et al.*, 1970). This fact is in agreement with the wide distribution of this gekko in all the Aegean insular ecosystems.

Gekkonidae belongs to the thigmotropic lizards (Spellerberg, 1972). *C. kotschy* uses the substrate temperature to maintain its body temperature. There was significant correlation between Tb and Ts, and also the value- r^2 was higher than 0.5 every season.

C. kotschy is the most diurnal gekko in the Europe (Beutler, 1981). Valakos and Vlachopoulos (1987) reported that *C. kotschy* was active in the summer in the twilight zone of the day while in spring and fall, its activity depended on the ambient temperature. From the winter observations it seems that the activity of this gekko depended on the light conditions because it was active even in low ambient temperature. It is known that the activity of lizards is related not only to ambient temperature but also to photic conditions (Heatwole, 1976). The *C. kotschy* is active in summer at such times so that it avoids the high temperatures during the day, but in other seasons it is active in a wide range of a ambient temperatures and its activity depends also on the light conditions.

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NOTES ON THE BIOLOGY OF THE HIGH ALTITUDE LIZARD *LACERTA BEDRIAGAE*

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ABSTRACT

We report preliminary data on the natural history and biometry gathered during a short-term study in a Corsian population of the lizard *Lacerta bedriagae*. Lizards were encountered at heights of 1650-1950m. Main characteristics of its habitat are the presence of large rocks, boulders and rock pavements. Three size (age) classes were distinguished. Adult males average larger in body size and have larger heads and limbs than females. Females mature at a body size of 66-68mm. Earth-worms, arthropods and plant leaves were recorded as food items.

INTRODUCTION

The lizard *Lacerta bedriagae* is an endemic species of the mediterranean islands Corsica and Sardinia. In Corsica, its distribution is largely restricted to heights above 1000m, although it has been reported from sea-level in the extreme southwest of Corsica and on small islets between Corsica and Sardinia (Schneider, 1984, Fretey, 1987). The natural history of this species appears little studied: much of the information reviewed by Schneider (1984) is anecdotal or based on observations made in captive conditions.

In an attempt to partially fill that gap, we recently made a short-term field study of a high-altitude population of this species in Corsica. Our aim here is to present limited information on habitats, size distribution, sex-ratio, ontogenetic and sexual variation of morphometric traits, reproductive characteristics and food items. Although remaining fragmentary and preliminary, these data are the first to become available for a natural population of this lizard. Data on activity rhythms and body temperatures are presented elsewhere (Bauwens *et al.*, in press).

MATERIAL AND METHODS

Field work was carried out on 25 May and from 31 May to 3 June 1988 near Haut-Asco (42° 25' N, 8° 55' E; département Haute-Corse, Corsica, France). The study area was situated on the steep east-facing slope of the Mont Mufrella, on either side of the hike-path GR 20. We searched for lizards from Haut-Asco (1450m) up to the mountain-pass 'Bocca Alla Culaja' (1950m) that gives access to the top of the Mont Mufrella.

Active lizards were captured with a noose. Each lizard was marked individually by toe-clipping, sexed and weighed (to nearest 0.1g on a portable electronic Sartorius balance). We also measured (to nearest 0.1mm) snout-vent length (SVL), tail length (original

and regenerated portions separately), length of pileus (tip of snout to posterior end of parietal scales), width of pileus (at widest point on parietal scales), width and height of head (at widest and highest points, by closing the calipers until resistance was felt), and length of the stretched left fore (arm-pit to base of fourth toe) and hind-limb (first femoral pore to base of fourth toe). Reproductive condition of females was assessed by noting the presence of mating scars; the presence of oviductal eggs was detected by palpation of the abdomen. We collected and analysed the contents of some faecal pellets that the lizards excreted during manipulation.

Relative size of morphometric traits (length and width of pileus, width and height of head, length of fore and hind-limb, weight) versus SVL, was investigated through application of the allometric equation ($Y = a \text{ SVL}^b$ or $\log Y = \log a + b \log \text{SVL}$). The parameters, and their standard errors, of this equation were estimated through least-square regression analysis of *log-log* transformed data. To determine whether a given body dimension deviates from geometric similarity during ontogeny, we compared the estimate of the corresponding regression slope (b) with the expected value ($=1$ for length measurements, $=3$ for weight). If b equals the expected value, growth is isometric and geometric similarity is maintained. When $b >$ expected value growth is positive allometric; whereas a $b <$ expected value indicates negative allometry. Differences between sexes in the parameters of the allometric equation were assessed by analysis of covariance (ANCOVA).

RESULTS AND DISCUSSION

ALTITUDINAL DISTRIBUTION AND HABITATS

Within our study area, we did not encounter *L. bedriagae* at altitudes $<1650\text{m}$. We exclude the local presence of this species at heights between 1450 and 1500m as we extensively searched there for lizards during a parallel study of *Podarcis tiliguerta* (Van

Damme *et al.*, in press). The incidence of *L. bedriagae* from a height of 1650m, coincided with a rather abrupt change in vegetation composition and habitat structure. An open *Pinus nigra* forest dominates at the lower altitudes. Trees are absent above 1650m, the scanty vegetation there is composed of dwarf-shrubs (dominant species: *Juniperus nana*, *Genista labelli*, *Berberis acnensis*) and grasses that grow patchily between large boulders, screes and extensive zones of rocky outcrops. In this zone, we found *L. bedriagae* up to an elevation of 1950m. As our searches were restricted to that height, we cannot dismiss its presence at higher altitudes. Although quantitative data are lacking, no obvious altitudinal variation in sighting frequency of this lizard was evident within the elevational range 1650-1950m.

Almost all lizards were seen on large and exposed boulders, rocks and bare rock pavement, although they stayed often near some vegetation cover. During the midday hours some individuals foraged under cover of dwarf-shrubs.

Throughout its local altitudinal range, we found *L. bedriagae* to be sympatric with *P. tiliguerta*. However, frequency of sightings of the latter species was distinctly highest at heights between 1450 and 1600m, where this lizard was ubiquitous and very conspicuous, and dropped sharply above 1650m altitude. In the area where both lizards occurred, *P. tiliguerta* tended to occupy microhabitats with a

relative high cover of dwarf-shrubs, was often observed on piles of small rocks and stones, but was virtually absent from large boulders and rocky outcrops.

BODY SIZE DISTRIBUTION, SEX-RATIO AND TAIL-BREAK FREQUENCY

Snout-vent length of 73 captured lizards ranged from 35.6mm to 84.8mm for males and 79.8mm for females (Fig. 1).

The smallest individuals, with SVL of 35.6 and 36.3mm, could not be sexed. They had brown back colours and blueish tails, characteristic for the youngest age-class in some *Lacerta* and *Podarcis* (Arnold *et al.*, 1978). As newborns of *L. bedriagae* have a SVL of ca. 30mm at hatching (Schneider, 1984), we suggest that these individuals were born at the end of the preceeding activity season. Lizards with SVL of 50-63mm could easily be distinguished in the field from their larger conspecifics by their back coloration, which was brown or grey-brown, whereas the larger had green, olive-green or brownish green back colours. This size class probably represents lizards that were in their third activity season. Lizards with SVL ≥ 66 mm were considered as adults, although some females with SVL of 66-68mm did not evidence signs of sexual activity (see further). We suggest that adults were in their fourth activity year or older, although (some of) the smaller individuals of this size class might have

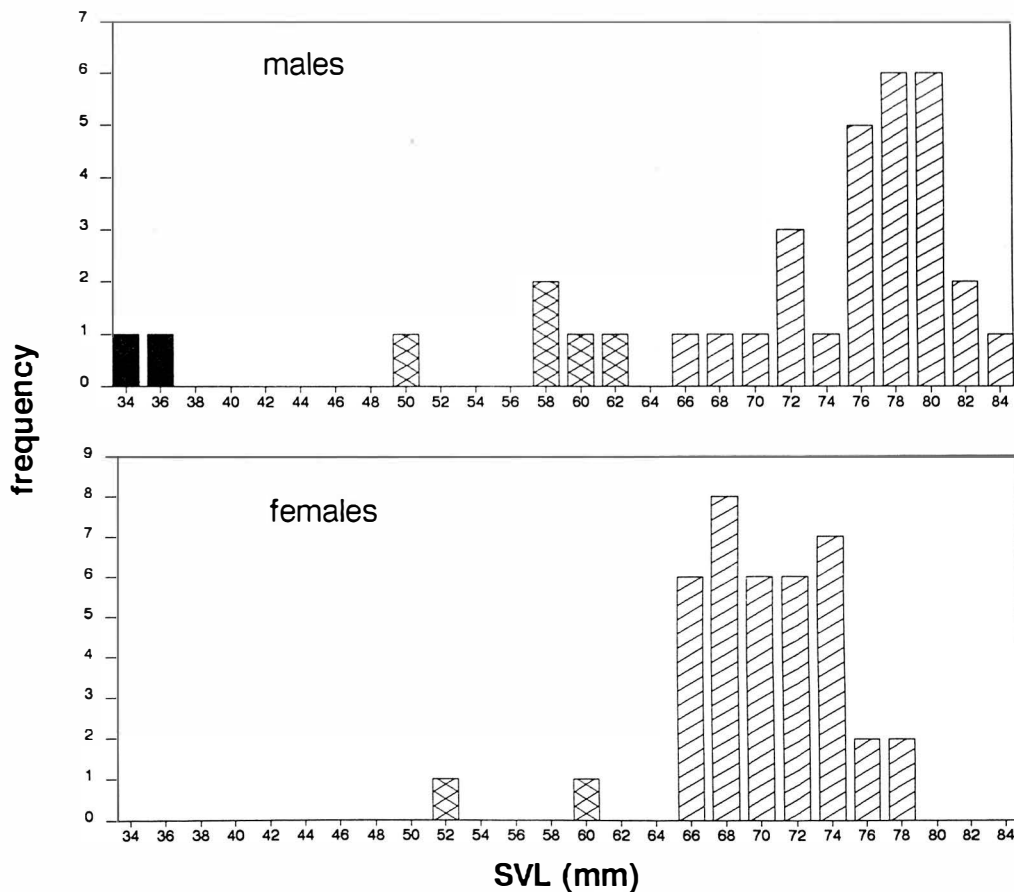


Fig. 1 Distribution of body size in male and female *Lacerta bedriagae*. Black : unsexed individuals; cross-hatched : lizards with brownish back colours; hatched : adults.

been in their third activity season. Mean SVL of adult males was significantly larger than that of the adult females (males : $\bar{x} = 77.6$, $SD = 4.2$, $n = 27$; females : $\bar{x} = 71.9$, $SD = 3.6$, $n = 37$; $t = 5.982$, $P < 0.001$).

Sex ratio (males/females) within the adult size class was 0.73 (27/37), which does not differ significantly from unity ($\chi^2 = 1.563$, $P > 0.20$).

The percentage of lizards with regenerated tails was high and increased with body size (SVL < 50 mm: 0% ($n = 2$), 50–65 mm: 43% ($n = 7$), ≥ 66 mm: 81% ($n = 64$); $\chi^2 = 11.3$, 2 df, $P < 0.01$). Incidence of natural tail breaks was not different in adult males (89%, $n = 27$) and females (76%, $n = 37$; $\chi^2 = 2.7$, $P > 0.05$).

RELATIVE SIZE OF MORPHOMETRIC TRAITS

The smallest, unsexable lizards ($n = 2$, see Fig. 1) were not included in subsequent analyses. Our data, which consist of a cross-sectional sample, hence only represent part of the range of body sizes that can be encountered in this lizard. Parameter estimates for the allometric equations are presented in Table 1.

All four dimensions of head size exhibited sexual dimorphism. In males, positive allometry occurred for length of the pileus and head height, indicating that relative size of these traits increases with SVL. In females, length and width of the pileus showed negative allometry and hence decrease in relative size during ontogeny. As a result of these relations, sexual differences in length and width of the pileus and in head height are most pronounced in the larger lizards (Fig. 2). Relative growth of head width was isometric in both sexes. The sexual difference in regression intercepts indicates that head width is largest in males over the entire body range span (Table 1, Fig. 2). In summary, males have larger and more robust heads than females and, except for head height, differences in head dimensions tend to increase with body size. Comparable sexual differences in relative head size, have previously been described in representatives of different lizard families (e.g. Iguanidae: Schoener *et al.*, 1982; Scincidae: Vitt and Cooper, 1985, 1986; Lacertidae: Wermuth, 1955, Castilla and Bauwens, in prep.).

	males		females		ANCOVA	
	log a	b + SE	log a	b + SE	b	a
length pileus	-2.120	1.180 \pm 0.040***	-0.576	0.793 \pm 0.049***	***	
width pileus	-2.233	1.009 \pm 0.083	-1.000	0.701 \pm 0.090**	*	
height head	-5.072	1.634 \pm 0.094***	-2.800	1.072 \pm 0.178	***	
width head	-2.320	1.132 \pm 0.080	-1.532	0.916 \pm 0.085	ns	***
length forelimb	-0.956	0.878 \pm 0.060*	0.137	0.596 \pm 0.109***	*	
length hindlimb	-0.830	0.932 \pm 0.049	-0.295	0.782 \pm 0.080**	ns	***
weight	-11.462	3.178 \pm 0.128	-11.902	3.274 \pm 0.203	ns	ns

TABLE 1: Allometric equations with snout-vent length as independent variable. Shown are estimates for intercepts (log a) and slopes (b) of *log-log* regression equations, results of comparisons of slopes with expected values (see methods) and of comparisons between the sexes of the regression equations through ANCOVA. (ns : $P > 0.05$, * : $P < 0.05$, *** : $P < 0.001$).

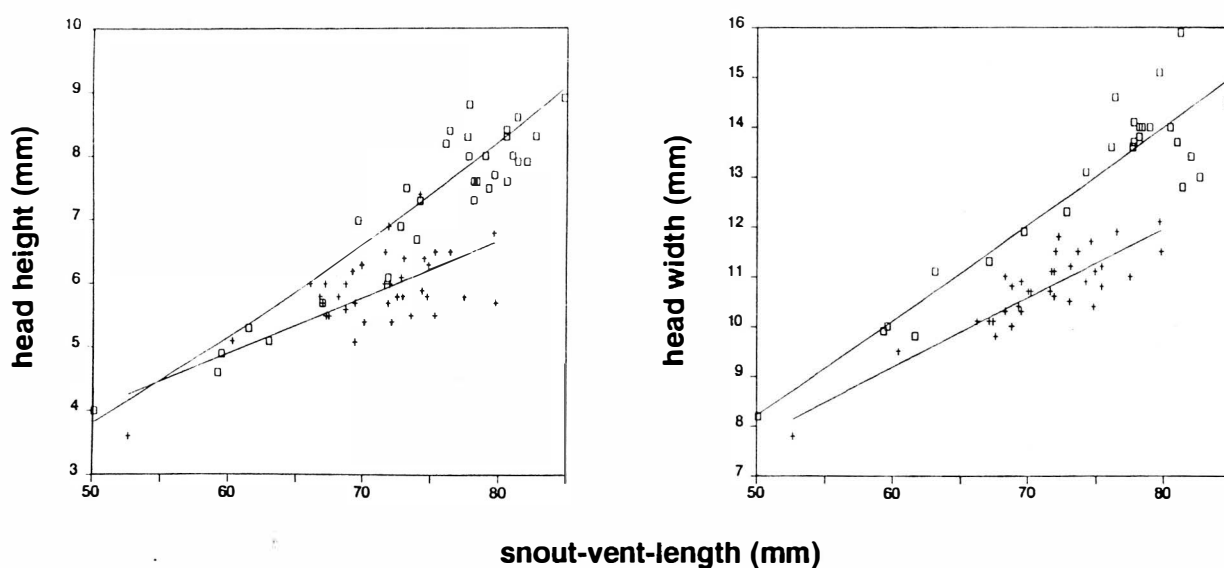


Fig. 2 Relations of head height and head width to snout-vent-length in male (squares) and female (crosses) *Lacerta bedriagae*. See Table 1 for regression equations.

Negative allometry of limb sizes was seen in three of four cases (Table 1). Relative size of fore and hindlimbs was largest in males. Negative allometry of limb dimensions seems to be rather common in lizards (e.g. Kramer, 1951, Laerm, 1974, Pounds *et al.*, 1983, Garland, 1985).

In spite of sexual differences in head and limb sizes, no sexual difference in weight-size relations were evident.

REPRODUCTIVE CHARACTERISTICS AND BEHAVIOUR

None of the females with a SVL <66mm had mating scars and they were therefore considered to be non-reproductive. The smallest reproductive female had a SVL of 66mm, whereas four females with SVL of 66-68mm showed no signs of sexual activity. All females >68mm were reproductive. A SVL of 66-68mm can therefore be considered as the minimum size of reproductive females.

Most reproductive females beared numerous mating scars, to the extent that these scars almost completely coloured the ventral side of the pelvic region and the anal scale. These observations are considered as evidence for the occurrence of multiple matings in individual females. A direct relation between the number of mating scars and mating frequency has been observed in the closely related *L. vivipara* (Bauwens, unpubl. obs.).

We observed a copulation on 25.5.1988 at 10.30h (MET). The behavioural sequence described hereafter took place on a large exposed rock, in full sun. An adult male was seen running over a distance of ca 3m towards an adult female. The male obtained a mouth-hold on the posterior part of the female's tail and maintained the grip while the female moved forward ca 2m. When the latter halted, the male displaced his grip toward the female's trunk and obtained a hold just anterior to the pelvis. After exhibiting some jerky movements, the female layed down. The male then arched his body, curling its tail underneath the female's and moving his cloacal region toward that of the female. Both lizards maintained this position during ca. 6 min. The observed copulatory posture is similar to that of other species of *Lacerta* and *Podarcis* (Verbeek, 1972). The absence of any preliminary courtship displays is noteworthy.

Oviductal eggs were detected in three females with SVL of 74.2, 74.6 and 79.7mm.

FOOD

Limited data on diet composition, were obtained through direct observations of foraging lizards and the analysis of faecal pellets. These evidenced the consumption of Oligochaeta, Aranea, Coleoptera, Hymenoptera and Lepidoptera. We frequently observed lizards feeding on ants, which were also the most numeric prey type encountered in the faecal pellets. Remnants of vegetables, mainly grass-leaves, were present in 6 out of 12 faecal pellets, and were the exclusive contents of two of them. More detailed data are however needed to establish the degree of herbivory in *L. bedriagae*.

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THE COMPARATIVE POPULATION ECOLOGY OF HERMANNS TORTOISE, *TESTUDO HERMANNI* IN CROATIA AND MONTENEGRO, YUGOSLAVIA

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ABSTRACT

Following initial studies on the population ecology of *Testudo hermanni* in Montenegro, Yugoslavia (Meek, 1984; 1985; 1988a) new demographic observations have been made on additional populations of these tortoises in Croatia and Montenegro. Results indicate that Montenegrin males attain a greater size than Croatian males, but there were no significant differences between the sizes of females. Adult sex ratios were in good agreement with equal numbers of males and females in Croatia; in Montenegro the ratio was 1.33:1. A large proportion of individuals in both populations exceeded 19 years although the proportion was higher in Montenegro as a result of Montenegrin males attaining greater age than Croatian males. Equations to describe growth trends indicate that in general females grow faster than males and that Montenegrin females grow faster than Croatian females. Population and biomass densities, biomass production and relative biomass turnover were higher in Croatia. Survivorship was higher and mean annual recruitment lower in Montenegro but males have a higher survivorship than females in both regions. Females sustained greater shell damage and physical injuries than males although generally Croatian tortoises of either sex sustained injuries at earlier ages. Sexually active males were smaller than their female partners and there were no inter-population differences between the sizes of males or females. Allometric equations describe morphometric characters, confirming sexual dimorphic trends found earlier in Yugoslavia and additionally show that males have longer tails. Only male plastron length, which was relatively greater in Croatian males showed inter-population differences.

INTRODUCTION

Studies on the ecology of Mediterranean tortoises have developed principally out of a concern that commercial exploitation for the food and pet trades may have detrimental effects on wild populations (Lambert, 1980). The earliest work examined the impact of pet trade collection on *Testudo graeca* in North Africa and indicated serious declines in population levels over large areas of its range (Lambert, 1980, 1982). Further studies concerned *Testudo hermanni* in Europe. In Greece the effects of deliberate burning and ploughing of the habitat resulted in a dramatic reduction in numbers (Stubbs *et al.*, 1985) and in southern France a slow decline in population levels was attributed to the abandoning of traditional agricultural practices by the local people (Stubbs and Swingland, 1985). Clearly many factors could be involved in a species decline and thus demographic information concerning Mediterranean tortoise populations are important conservation tools, since it is conceivable that the dynamics of each population may differ even when these are closely situated to one another; indeed, distinct differences in the thermal ecology of *T. hermanni* have already been found between various populations (review in Meek and Avery, 1988). This paper presents new observations on the comparative population ecology of *T. hermanni* in Yugoslavia and compares a Montenegrin population living in close association with humans with one living in a relatively undisturbed area in Croatia. The paper forms part of a series of field studies on the

ecology of *T. hermanni* which have to date after an initial general survey in Montenegro (Meek and Inskeep, 1981), examined thermal ecology (Meek, 1984, 1988a, 1988b) and population ecology (Meek, 1985).

STUDY AREAS

The observations were obtained from tortoise populations inhabiting scrubland areas with partly wooded perimeters on the Adriatic coast. The northern site was in Croatia where the dominant vegetation, *Quercus pubescens*, *Agrimonia eupatoria*, *Paliurus spina-christi*, *Ficus carica*, *Prunus domestica* and *Olea europaea* were used by *T. hermanni* as shade plants. Typically there were open grass covered clearings with limestone rocky outcrops (Fig. 1b) where growth of *Hedera helix* was also found. Such clearings in the summer months could experience air temperatures around 41°C. Wet Autumn weather saw the appearance of fungi (*Basidiomycetes*) on the clearings.

The main feature of the Montenegrin site was the agricultural activities (e.g. cabbage, lettuce and olive cultivation) which accounted for about 30 per cent of the land area (Fig. 1a). In the remaining natural zones the dominant vegetation was *Vicia*, *Arundinkria*, *Rubus*, *Pteridium* and *Pistacia*. The whole area was covered by a series of irrigation ditches (mostly of concrete construction) about 1 metre wide.

The adults were mostly found in scrub habitat generally in both areas. In contrast, hatchlings and

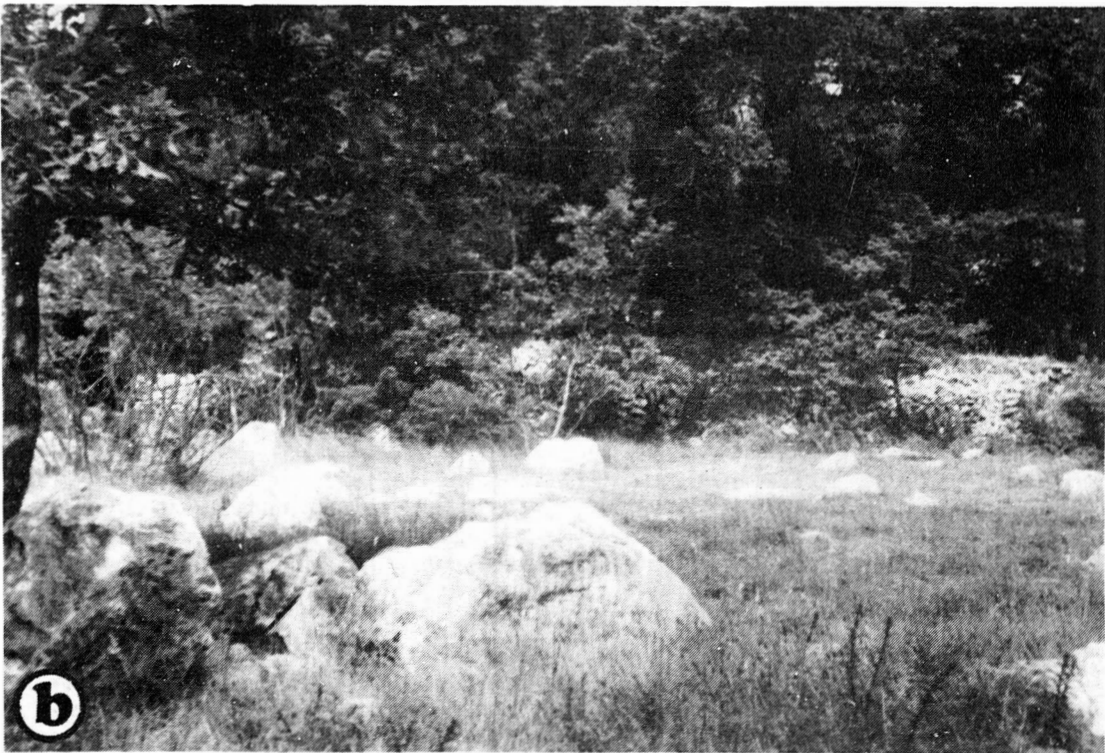
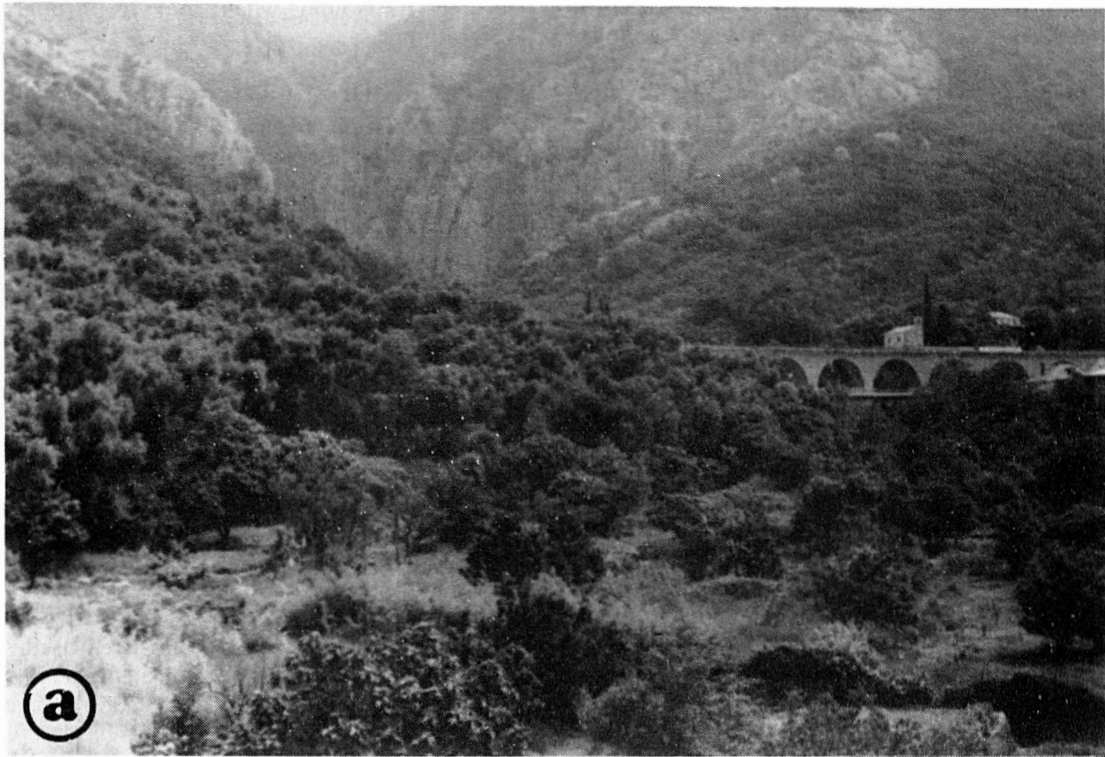


Fig. 1 Views of study areas in Montenegro (1a) and Croatia (1b). Fig. 1a shows the cultivated areas in the foreground and the heavily wooded eastern section. Fig. 1b shows an open clearing with characteristic limestone outcrops.

very young tortoises (<5 years) were when found, usually in association with *Spartium junceum* (Croatia) and *Brachypodium* sp. (Montenegro). These tall (app. 1 m) narrow stemmed plants provide the benefits to small tortoises of both cover and sunlight penetration.

METHODS

Field work was carried out in Montenegro over an eight day period in late May 1986 and over a two week period in early June 1986 in Croatia. Additional general information was gathered over a three week period in Croatia from late September to mid-October 1984. When located each tortoise was given a unique mark using the method of scute notching; also noting the date and time of capture. Other procedures in the field, that is methods for gathering plant samples, body measurements, assessment of age and physical condition are those given in Meek (1985). Sampling was carried out throughout the daily period, by making daily routine patrols of the study area usually by two observers, but each working alone. Most tortoises were located by sight although a small number of individuals, particularly juveniles were

located by sound when moving through dense vegetation.

POPULATION DENSITY ESTIMATES

Density estimates have been made using the triple catch method in which recaptures are grouped according to the time at which they were marked. In this system the three samples were taken at short intervals of time and although it is not required that the time intervals between sampling should be equal (Ricker, 1958) in this study two day sampling periods were separated by one day non-sampling intervals.

STATISTICAL ANALYSIS

Regression analysis has been used for calculating mathematical models of age related and relative growth after transforming the data into logarithmic form (Sokal and Rohlf, 1981). To estimate the number of growth annuli on the coastal scutes from carapace length Model (1) regression has been used which treats y , the number of annuli, as dependent on carapace length (x). To describe relative growth Model (2) regression (geometric mean) has been used. This is considered a more appropriate method for relating variables when neither can be regarded as truly

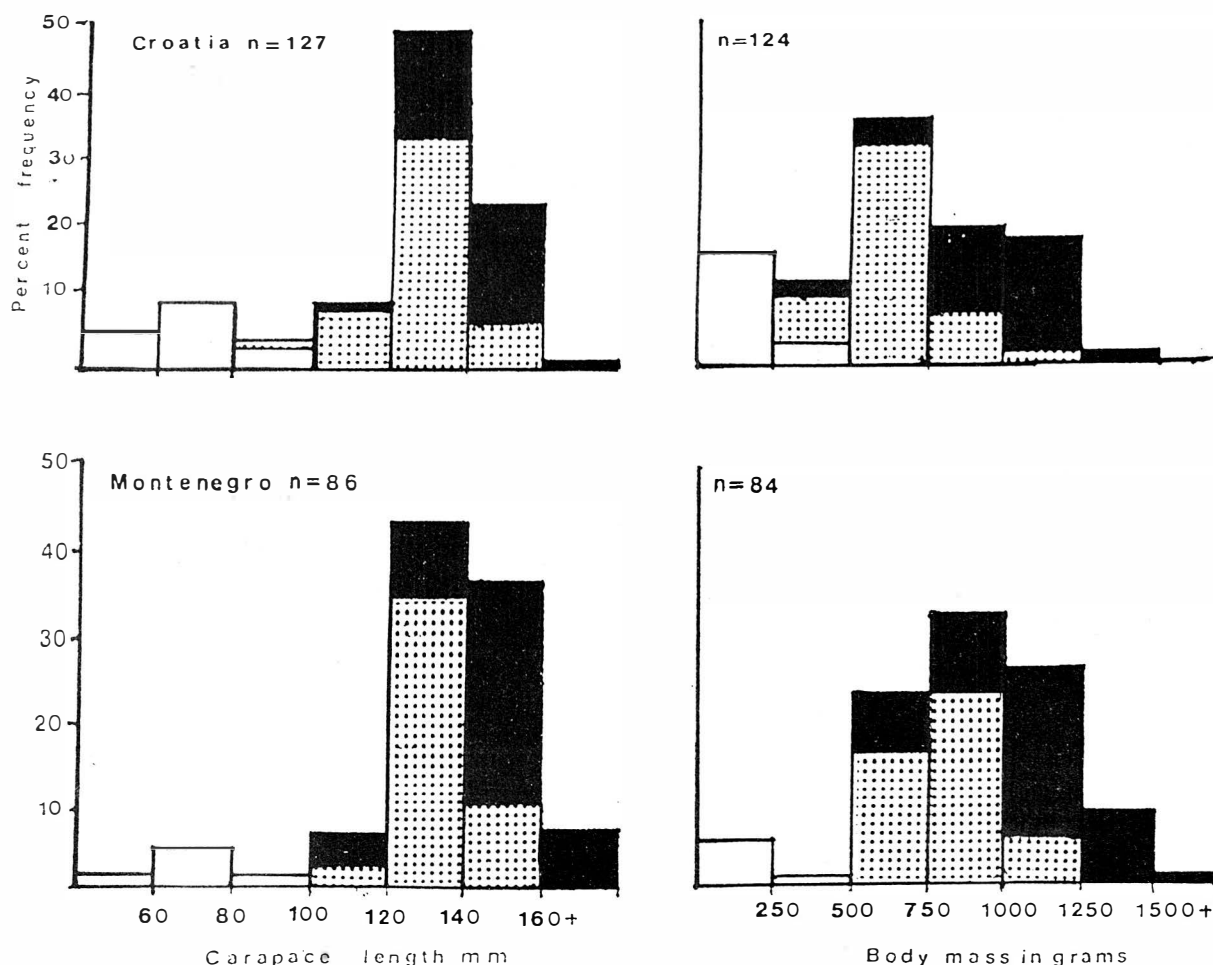


Fig. 2 Size frequencies of *T. hermanni* in Croatia and Montenegro. Solid histograms represent females, stippled bars males and open bars immatures.

	Mean and (maximum) carapace length ± 1 S.E. in mm		Mean and (maximum) body mass ± 1 S.E. in grams	
	males	females	males	females
Mont. (1)	135.4 \pm 7.8 (148)	147.6 \pm 16.8 (190)	822.9 \pm 136.6 (1038)	1075.7 \pm 276.5 (1680)
Mont. (3)	126.4 \pm 8.6 (143)	147.0 \pm 12.1 (170)	609.0 \pm 105.3 (740)	989.0 \pm 208.9 (1410)
Mont. (4)	140.9 \pm 11.3 (170)	159.3 \pm 14.6 (175)	— — —	— — —
Croa. (2)	127.7 \pm 9.8 (145)	141.7 \pm 9.6 (164)	631.9 \pm 144.8 (1025)	990.9 \pm 184.8 (1300)
Cor. (5)	140.6 \pm 7.9 (150)	164.6 \pm 19.6 (190)	724.3 \pm 131.4 (879)	1056.0 \pm 276.5 (1417)

TABLE 1: Details of size characteristics of *T. hermanni* populations in this study in Yugoslavia (1,2) and also data from (3) Budva (Meek, 1985) (4) Petrovac (Wallace and Wallace, 1985) and (5) Corfu (Wallace and Wallace, 1985). The calculations are based on tortoises exceeding 100mm carapace length.

independent. A basic description of the differences between the two methods has been given in Meek (1987).

Confidence intervals have been calculated for the constants in the equations at the 95 percent interval. In Model (2) regression the confidence limits are expressed for b and y_0 , in Model (1) regression for b and a . The expression x/\div in the intervals for a and y_0 indicates for example in equation (1) in Table 2, from 0.0004×1.07 to $0.0004 \div 1.07$. Tests for significant differences between exponents have been made using the t -distribution in the way described by Bailey (1981). Other population characters have been analysed at the 95 per cent interval using the t and F -distributions at appropriate degrees of freedom.

RESULTS

POPULATION STRUCTURE

The frequency distributions of carapace lengths and body masses of both populations are shown in Fig. 2 with details of the means and ranges given in Table 1. The samples were skewed towards larger animals with females larger than males in both populations: Carapace lengths {Croatia} $F\{1.103\} = 48.74, P < 0.0001$ and {Montenegro} $F\{1.78\} = 16.05, P < 0.001$; body masses {Croatia} $F\{1.100\} = 118.59, P < 0.0001$ and {Montenegro} $F\{1.76\} = 25.53, P < 0.0001$. Males from Montenegro had significantly longer carapace lengths $\{F\{1.99\} = 15.51, P < 0.001\}$ and greater body masses $\{F\{1.95\} = 41.59, P < 0.001\}$ than Croatian males, but there was no significant difference between the carapace lengths or body masses ($P > 0.05$) of females from the two populations.

SEX RATIOS

From a total of 127 identified tortoises in Croatia, 60 were males 45 were females and 22 immatures or hatchlings. This indicates an adult sex ratio of 1.33:1 in favour of males and an adult: immature ratio of 4.77:1. Eighty six tortoises were identified in Montenegro of which 41 were males, 39 were females and 6 immatures. This gives an adult sex ratio of almost parity (1.05:1) and adult: immature ratio of 13.33:1.

AGE STRUCTURE

Based on the limitations of growth ring number as a means of determining age (Castanet and Cheylan,

1979). Age structure has been limited at 19 years with older animals shown as more than 19 years. The age distributions are shown in Fig. 3. In both populations most tortoises were above 16 years (Croatia 75.5 per cent; Montenegro 87.1 per cent). However, whilst in Croatia 42.5 per cent exceeded 19 years a much larger proportion (67.4 per cent) of Montenegrin tortoises exceeded 19 years. In animals aged more than 19 years males predominated (Croatia, males 27.5 per cent, females 14.9 per cent; Montenegro, males 39.5 per cent, females 27.9 per cent), although in both

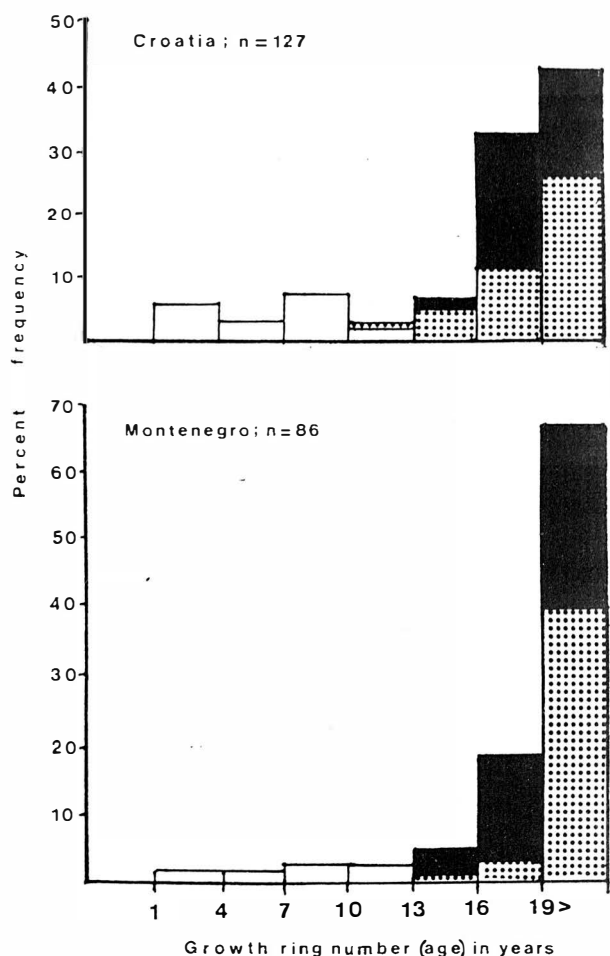


Fig. 3 Age frequencies of *T. hermanni* in Croatia and Montenegro. Other details are given in Fig. 2.

Eqn. No.	Independent variable x	Pop.	Factor a	95% con. interval	Exponent b	95% con. interval	n
(1)	C. length (males)	C	0.0004	1.07	2.23	0.18	82
(2)	C. length (females)	C	0.0011	1.07	1.99	0.16	67
(3)	C. length (males)	M	0.0011	1.06	2.02	0.29	47
(4)	C. length (females)	M	0.0096	1.05	1.54	0.25	45

TABLE 2: Allometric equations of the form $y = ax^b$ relating the number of growth annuli on the coastal scutes y with the straight length of the carapace x in mm in *T. hermanni* from Croatia (C) and Montenegro (M). The 95% confidence intervals attached to factor a are the x/\div type, to the exponent b the \pm type. The number of observations on which the equations are based (n) are also given.

populations females were more numerous between 16-19 years. Based on growth ring counts there was no significant difference between the ages of females in the two populations (Croatia $\bar{x} = 20.2$; Montenegro $\bar{x} = 20.3$; $F\{1.82\} = 0.01$, $P > 0.05$) but Montenegrin males ($\bar{x} = 23.6$) were apparently older than Croatian males ($\bar{x} = 21.3$) with the difference significant ($F\{1.99\} = 4.07$, $P < 0.05$). Immatures from Croatia ($\bar{x} = 5.7$) were younger than those from Montenegro ($\bar{x} = 7.6$) but the differences was not significant ($P > 0.05$).

AGE MODELS

The simplest model which relates the logarithms of carapace length y in mm with the logarithms of growth ring number x , is a model 1 allometric equation of the form:

$$y = ax^b$$

where a and b are constants. Data for these variables are shown in Table 2. The highest correlations were found for Montenegrin tortoises (males $r = 0.94$;

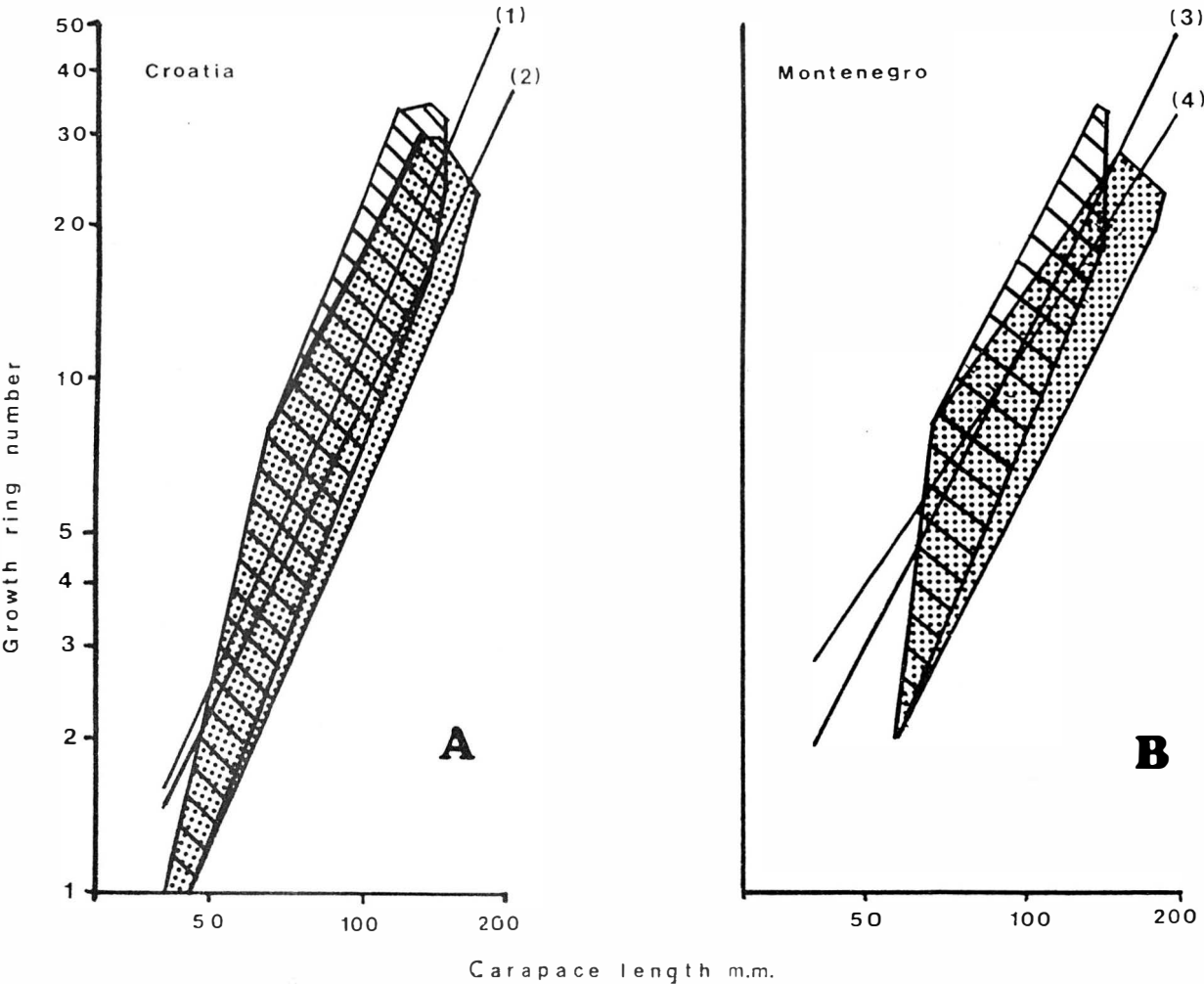


Fig. 4 Graphs on logarithmic coordinates of growth ring number plotted against carapace length in *T. hermanni* from Croatia (A) and Montenegro (B). The data have been converted into the smallest convex polygons which will enclose all the data points with male and female data treated separately. Hatched polygons represent females, stippled polygons males. The lines running through the polygons are derived from equations given in Table 2: these are explained in the text.

females $r = 0.95$) although good correlations (males $r = 0.89$; females $r = 0.90$) and better confidence intervals were found in Croatian animals. These equations indicate that in general, females grow faster than males, and that Montenegrin females grow faster than females from Croatia ($t = 2.25$, $P < 0.05$). Montenegrin males appeared to grow faster than Croatian males but the equations describing the data are not significantly different ($P > 0.05$). Fig. 4 is a graph of the data plotted as convex polygons on logarithmic coordinates and are shown with lines calculated from the four equations. These suggest that (for example) a female from Montenegro would require 33 years to achieve a carapace length of 200mm whereas this would take 56 years for a Croatian male.

SURVIVORSHIP

The age structures of the populations have been used to infer survivorship on the assumption that there were no conspicuous gaps in the age distributions of either population which would suggest periods of low recruitment or possible sampling error, i.e. annual recruitment rates and age structures have been assumed constant. Survivorship curves have been calculated by the method described by Deevey (1947). The survivorship curves in Fig. 5 have thus been calculated by taking the number of tortoises present at the beginning of each age class as a percent of the total population sample. Survivorship is higher in the Montenegrin population which until 19 years is 67.4 per cent (Fig. 5b); in Croatia the corresponding value is 42.5 per cent (Fig. 5a). Both populations have a higher survivorship until 19 years than a population from central Montenegro (Fig. 5a) described by Meek (1985). Male survivorship is higher than females in both areas with major departures in the male-female curves beginning around 16 years (Fig. 5b).

Mean annual recruitment has been calculated from the mean annual population increment until 19 years and expressed as a percentage of the total using the equation:

$$R_p = \frac{(T_n - t_0)18}{T_n} (100)$$

where R_p is the percent recruitment, T_n the total number of tortoises in each study area sample and t_0 the total number of tortoise over 19 years. This method gives a recruitment value that may only be empirical but it is useful in estimating mortality for the first 18 years. The calculations indicate that mean annual recruitment is lower in Montenegro (males 1.3%; females 2.7%; $\bar{x} = 1.8\%$) than Croatia (males 3.1%; females 4.0%; $\bar{x} = 3.2\%$).

MORTALITY

A total of six dead tortoises were found on the study area none of which appeared to be recent deaths since there were no soft tissue remains. Of these four (two males, one female and one unsexed) were from Croatia. Based on the number of growth annuli on the scutes these were all old animals with at least 24 annuli on the males (c. lengths 148 and 150mm) and 20 annuli on the female (c. length 144mm) with the unsexed

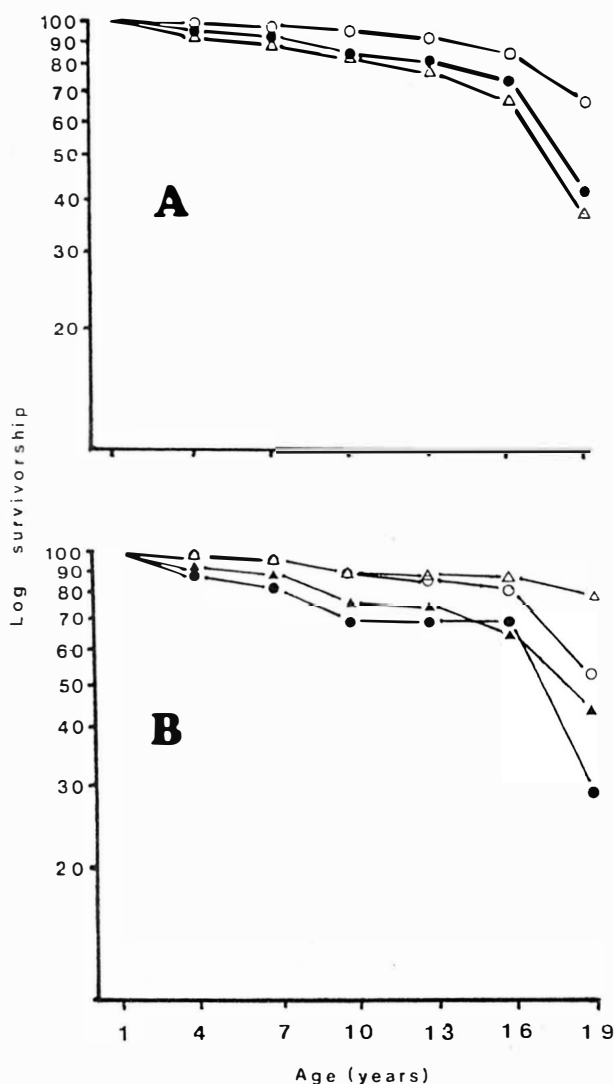


Fig. 5 General survivorship curves for *T. hermanni* in Montenegro and Croatia until 19 years (Fig. 5a). Open circles represent Montenegro, solid circles Croatia and triangles data for Montenegro from Meek (1985) for comparison. Fig. 5b shows distinct male-female survivorship curves for Montenegro (this study) where males are open triangles, females open circles and Croatia where males are solid triangles and females solid circles.

animal showing adult size. The dead animals from Montenegro appeared to be males with at least 21 and 25 annuli (128 and 148mm carapace lengths). The skeletal remains of the shells and many other bones of these and the three sexed Croatian tortoises were intact suggesting perhaps mortality during the winter dormancy. The percentage of dead tortoises to the total field samples (total = dead plus living tortoises) was 3.05 per cent in Croatia and 2.3 per cent in Montenegro.

INJURIES

Eighteen tortoises (14.2 per cent) in Croatia and eight tortoises (9.3 per cent) in Montenegro were found to have sustained injuries. These included, in Croatia, carapace scutes absent (probably from fire damage), cracked shells, dents in the carapace and one animal

with the right rear limb absent. In Montenegro they consisted principally of dented or cracked shells. One female (c. length 178mm) in addition to having lost part of the anterior section of the carapace, had also lost the left rear limb. Fig. 6 shows the frequency distributions of damaged tortoises in relation to their age. Figs. 6a and 6b show the simple numerical frequencies; Fig. 6c and 6d the frequencies when corrected for the bias in age class frequency. Fig. 6 demonstrates two main points 1) In both areas females sustained more injuries than males and 2) Croatian tortoises sustained injuries at earlier ages (although no animal in Croatia had serious injuries below 14 years).

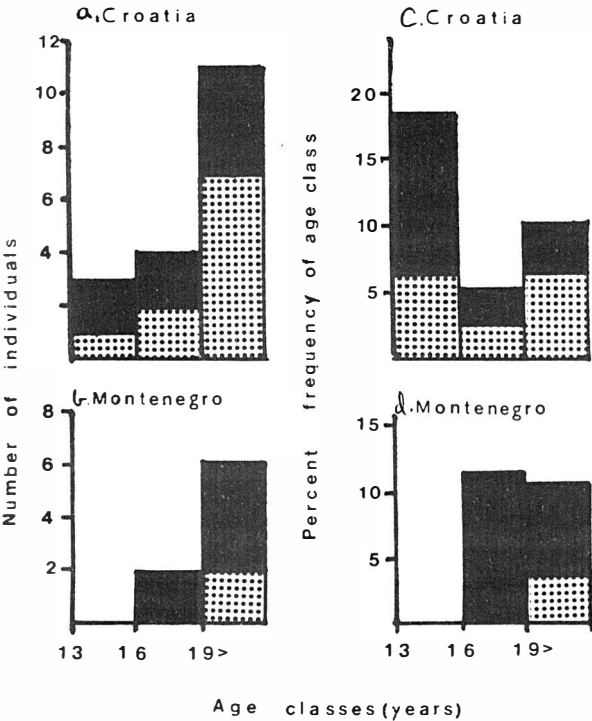


Fig. 6 Histograms showing shell damage and injury distribution in relation to age in *T. hermanni*. Upper histograms show data for Croatia, lower histograms data for Montenegro. See text for discussions and Fig. 2 for bar keys.

DENSITIES

Population densities have been estimated using the 'triple catch' method (Ricker, 1958) where sampling was divided into three periods each of two days duration with one day non-sampling intervals between. On the first occasion tortoises were marked and released and after the one day interval a second sample was taken with recaptures noted and unmarked animals given new distinguishing marks. On the third sampling period recaptures from the first and second samples were recorded with unmarked tortoises. Density has been calculated using:

$$D_2 = \frac{(N_2 - M_{1,2})(N_2 + 1)M_{1,3}}{(M_{1,2} + 1)(M_{2,3} + 1)}$$

where N_1 are the total captures on day one, N_2 the total captures on day two, N_3 the total captures on day

three, $M_{1,2}$ the recaptures on day two of tortoises marked on day one, $M_{1,3}$ the recaptures on day three of animals marked on day one and $M_{2,3}$ the recaptures of animals on day three of the animals marked on day two. Table 3 shows the numbers for the sampling periods for both areas. In Croatia this indicated 226.6 tortoises in 2.8ha and in Montenegro 58.3 tortoises in a 1.3ha area. Thus population density estimates were 80.92ha⁻¹ in Croatia and 44.83ha⁻¹ in Montenegro (although in Montenegro the area sampled included the agricultural zones, so the densities in natural zones would be somewhat higher).

	Period 1	Period 2	Period 3
Montenegro	N1 = 25	N2 = 23	N3 = 19
	—	M1, 2 = 6	M1, 3 = 6
	—	—	M2, 3 = 5
Croatia	N1 = 40	N2 = 39	N3 = 37
	—	M1, 2 = 5	M1, 3 = 4
	—	—	M2, 3 = 3

TABLE 3: Triple catch analysis to estimate population density of *T. hermanni* in Croatia and Montenegro. Further details are given in the text.

BIOMASS DENSITY

Using the results from population density estimates, biomass density has been calculated. In this paper density has been estimated by taking the mean biomass of the population in g times the population density. Thus in Croatia where the mean biomass was 681.93g, a biomass density of 55.2kg ha⁻¹ is indicated. In Montenegro mean biomass was 892.0g which gives a biomass density estimate of 39.9kg ha⁻¹. These values exceed the density calculated by Meek (1985) for a population of *T. hermanni* at Budva but the mathematics used in that study underestimated biomass density since it is based on the allometric relationship of body mass with carapace length. A more accurate (and simpler) method if mass is known is the one used in this paper. This would give an estimate of 26.8kg ha⁻¹ in Budva which is in slightly better agreement with the results of this study.

ANNUAL BIOMASS PRODUCTION

Biomass production has been calculated by the method described by Iverson (1982). It is based principally on the assumption that the population is stable, and therefore that biomass lost to mortality is an approximation of biomass production. Annual biomass production is thus found by estimating the number of tortoises in each age class per hectare and the number of tortoises lost each year from the age classes. The resulting estimate is found by:

$$ABp = \sum (ACm \times ACb)$$

where annual biomass production (ABp) is derived from the age class mortality (ACm) and the mean biomass of each age class (ACb).

The calculations indicate that in Croatia biomass production is 4.367kg/ha annually and in Montenegro 2.413kg/ha annually. The ratios of biomass production to biomass density (i.e. relative annual turnover in biomass) are therefore 0.07 in Croatia and 0.06 in Montenegro. These values exceed the ratios of 0.034 and 0.042 for *Geochelone gigantea* Coe *et al.*, 1979) but are lower than the 0.21 calculated for *Chrysemys picta* (Iverson, 1982).

MATE SELECTION

The mean carapace lengths of males observed courting, attempting to mount or copulating with females were significantly shorter than their corresponding female partners in both areas: Croatia, males \bar{x} = 126mm females \bar{x} = 150mm, $F_{1,10}$ = 10.76, $P < 0.01$; Montenegro males \bar{x} = 128.5mm females \bar{x} = 147mm, $F_{1,18}$ = 15.71, $P < 0.001$. There were no significant inter-population differences ($P > 0.05$) between the sizes of males or between the sizes of females involved in sexual activity. Neither population showed evidence ($P > 0.05$) for the 'Big Male' effect (O'Donald, 1983), that is that males from either population involved in sexual activity had greater mean carapace lengths than their population means, which is in agreement with the data for *T. hermanni* in Greece and France (Swingland and Stubbs, 1985).

NESTS AND HATCHLINGS

Two nesting females were observed in Croatia on the morning of 2 June. Both females had selected sites about 1 metre from deep shade and each deposited 3 eggs. The mean egg length of both clutches was 30.3mm (range 26-33mm) and mean width 23.3mm (range 23-24mm). Three other nests where the young had apparently recently emerged were found on the Croatian site in late September. Four hatchlings were

found near one of these nests and these had carapace lengths ranging from 31-45mm (\bar{x} = 38.5mm) and body masses from 10-19g (\bar{x} = 15g).

FOOD PLANTS

The largest food plant sample was collected in Croatia (n = 22). The majority of these were from the Leguminosae (n = 11; 5%) although other families were also collected (Table 4). However, the samples were collected over two seasons and as can be seen in Table 4 the Leguminosae were not present in the Autumn sample and were thus an exclusive summer food plant (78.6 per cent) with, interestingly, mushrooms forming part of the Autumn diet. The Montenegrin sample was smaller (n = 11) and consisted only of any early Summer collection. Here the Leguminosae although present, are less prominent (n = 2; 18.8 per cent).

It is recognised that these are small samples but the data do appear to suggest two points worth considering. The first is the possibility of a seasonal shift in diet in Croatian *T. hermanni* with a more restricted diet based on Leguminosae in Summer shifting to a broader range of plant food in Autumn. The second is that the Leguminosae are less important in the Summer diet of Montenegrin *T. hermanni* although whether the close proximity of human activities has some influence here is unclear. An earlier food plant sample from *T. hermanni* in Montenegro also living in close association with humans (although in rather less close proximity) showed 33.3 per cent to be Leguminosae (Meek, 1985).

MORPHOMETRICS

The morphometric analysis has been based on body mass (the x variable) since this is the only variable

	Family	Genus	Species	n	Comments
Croatia (summer)	Leguminosae	Medicago	—	6	
	Leguminosae	Medicago	echinata	1	
	Leguminosae	Trifolium	campestre	3	
	Leguminosae	Vicia	—	1	
	Compositae	Compositae	pieris	1	
	Plantaginaceae	Plantago	—	1	
	Rosaceae	Prunus	cerasus	1	fruits (plum)
Croatia (autumn)	Umbelliferae	—	—	2	
	Compositae	—	—	1	
	Labiatae	Thymus	—	2	
	Rosaceae	Malus	domesticus	1	fruits (apple)
	Basidiomycetes	Agaricus	arvensis	2	mushrooms
Montenegro	Araliaceae	Hedera	helix	2	
	Chenopodiaceae	Chenopodium	—	2	
	Aristolochiaceae	Aristolochia	—	1	
	Plantaginaceae	Plantago	—	1	
	Leguminosae	Medicago	echinata	2	
	Scrophulariaceae	Pedicago	—	1	
	Cruciferae	Brassica	oleracea	1	cabbage

TABLE 4: Food plants of *T. hermanni* in Croatia in summer and autumn and in Montenegro in summer. The number of observations of feeding on a particular plant (n) are also shown.

Eqn. No.	Sex	Pop	y	y_o	95% C.lim.	x_o	b1	b2	95% C.lim.	P	r	n
(5)	P	M	C.L.	133.78	1.01	790.24	0.33	0.33	0.01	n.s.	0.98	84
(6)	P	C	C.L.	116.14	1.02	511.43	0.33	0.34	0.01	n.s.	0.97	124
(7)	M	M	S.W.	45.64	1.04	631.31	0.46	0.47	0.03	0.05	0.98	45
(8)	F	M	S.W.	42.97	1.02	779.05	0.39	0.40	0.03		0.97	45
(9)	M	C	S.W.	35.97	1.04	359.39	0.47	0.49	0.03	0.01	0.96	80
(10)	F	C	S.W.	33.99	1.05	442.03	0.41	0.42	0.02		0.97	61
(11)	P	M	4V.S.	33.46	1.02	790.24	0.29	0.32	0.03	n.s.	0.90	84
(12)	P	C	4V.S.	28.89	1.02	511.43	0.29	0.31	0.02	n.s.	0.91	124
(13)	M	M	P.L.	102.59	1.01	631.31	0.28	0.28	0.01	0.001	0.99	45
(14)	F	M	P.L.	119.48	1.01	779.05	0.34	0.34	0.03		0.99	45
(15)	M	C	P.L.	86.99	1.01	359.39	0.32	0.32	0.01	0.05	0.98	80
(16)	F	C	P.L.	97.30	1.02	425.33	0.34	0.34	0.01		0.99	66
(17)	M	M	T.L.	37.54	1.06	631.31	0.72	0.77	0.09	0.001	0.93	45
(18)	F	M	T.L.	23.71	1.07	779.05	0.42	0.51	0.09		0.82	45
(19)	M	C	T.L.	22.10	1.14	414.14	0.74	0.84	0.14	0.001	0.89	43
(20)	F	C	T.L.	15.17	1.05	614.32	0.42	0.46	0.06		0.92	45

TABLE 5: Model 2 allometric equations of the form $y/y_o = (x/x_o)^b$ relating selected dimensions of the shell or tail length y in mm with body mass x in grams by the geometric mean of y (y_o), geometric mean of x (x_o) and exponent b . Confidence intervals for y_o are the x/\pm type, for b the \pm type. Correlation coefficients r , number of observations n and significant differences P (when applicable) between equations for males and females are also given. For comparative purposes corresponding exponents that would be found by Model 1 regression (b1) are shown. Montenegrin data are indicated as M, Croatian data as C, other abbreviations are: C.L. (carapace length) S.W. (supracaudal scute width) 4V.S. (4th vertebral scute width) P.L. (plastron length) T.L. (tail length).

which can be regarded as representing the whole body. However, body mass be subject to error and thus Model 2 regression has been used in the analysis. Model 2 equations have the form:

$$y/y_o = x/x_o)^b$$

where shell dimensions or tail length y in mm are related to body mass x in g by the geometric means of $y(y_o)$ and $x(x_o)$ and exponent b . The differences between the two methods are only minor when the correlation coefficient (r) for the data are high; when r is low Model 2 equations produce steeper slopes.

The results are shown in Table 5 where the separate male and female equations have been calculated by including the data from immatures although when the exponents are not significantly different the data sets have been combined and comprehensive equations produced. High correlation coefficients have been found for most of the data sets and thus there would be little difference between the exponents had they been calculated by Model (1) regression, the exponents for which are also shown in Table 5. The lowest correlations concerned 4th vertebral scute width and tail length giving some disagreement between regression exponents (see Table 5). The widest confidence intervals were for tail length (0.06-0.14) suggesting rather greater variation in size than in the other characters measured.

The sexual dimorphic trends found earlier in a central Montenegrin population of *T. hermanni* (Meek, 1985) are confirmed here; principally the relatively wider supracaudal scute in males Montenegro, $t = 2.05$, $P < 0.05$, Croatia, $t = 3.04$, $P < 0.01$ and relatively longer plastrons in females, Montenegro

$t = 3.3$, $P < 0.01$; Croatia $t = 2.06$ $P < 0.05$. Tail length which was not measured in the earlier study (Meek, 1985) also differed between males and females with that of males being relatively longer (Montenegro $t = 3.02$ $P < 0.01$; Croatia $t = 4.12$, $P < 0.001$). Inter-population differences in morphometric characters were found only in male plastron length which was relatively longer in Croatian males ($t = 3.09$, $P < 0.01$).

DISCUSSION

The differences observed in survivorship, age spans and growth rates in Yugoslavian *T. hermanni* are important life history characteristics but were they primarily related to the close proximity of the Montenegrin population with humans? Stubbs and Swingland (1985) have already suggested that the ecology of *T. hermanni* in woodland areas in southern France was linked to the traditional horticultural practices of the local people. Apparently the key factors were the establishment and maintenance of clearings in the forest for crop growing which provided nesting areas for the females and also the control of mammalian predators thus reducing nest predation. It is unlikely that in Montenegro crop growing areas were important in increasing tortoise nesting success since extensive natural clearings were a regular feature of scrubland areas in the region (Fig. 1) and were used by the females for nest sites. Control of mammalian predators did occur and this could increase tortoise survivorship but additionally and perhaps more importantly the areas was extensively irrigated which may improve both the quality and availability of food

plants during the hot dry Summer. However, agricultural activities could be involved in reducing the densities of tortoises by confining the animals to natural zones within such areas, since although tortoises were observed on the perimeters of crop growing areas, there was no movement onto these areas apart from one instance of a tortoise feeding on cabbage.

Previous studies on the population ecology of *T. hermanni* have indicated low numbers of both immatures and hatchling tortoises (e.g. Meek and Inskoop, 1981; Meek, 1985) and several theories have attempted to explain this, i.e. low detectability or differences in habitat selection between adults and immatures. Recently however Stubbs and Swingland (1985) have suggested, from recapture data on juveniles, that immature *T. hermanni* do indeed constitute only a small proportion of the population. This would be in agreement with the general population dynamics of *T. hermanni* which operates at the 'K-endpoint' of the r-K continuum where densities are high and inter- and intra-specific competition intense leading to a highly efficient utilisation of environmental resources. Such a strategy invariably leads to the channelling of all available energy into the production of a few extremely fit offspring (Pianka, 1970). Female *T. hermanni* produce only small numbers of offspring which suffer high mortality at the egg stage (Stubbs and Swingland, 1985) and probably also within the months following hatching. The results in this paper of the adult-juvenile ratios in Croatia appear indirectly to support a high mortality of hatchlings, which were relatively more common in Autumn than in Spring. Predators probably contribute to hatchling mortality (e.g. rat snakes *Elaphe* and mammals in some areas) but perhaps more important is mortality from environmental factors such as late Summer droughts or winter-kill.

Intra and inter-population differences in growth and maximum sizes have been observed in other species of chelonians from within a single geographical area (e.g. Cagle, 1946; Gibbons, 1967; Hulse, 1976). In certain chelonians food quality has been cited as an explanation for differences in growth rates and this could explain the faster growth rates of Montenegrin females compared with females from Croatia. The constant irrigation of the Montenegrin study site, if it does indeed improve the quality of the wild plants may be important in this respect since it could provide this population with an overall superior diet through the active year. The larger size of Montenegrin males in comparison to males from Croatia is also interesting and appeared to be related to the Montenegrin males living longer and also their slightly faster rates of growth but it is not immediately obvious as to why only males and not females from Montenegro have significantly longer life spans than Croatian tortoises. Cagle (1946) attributed differences in size and growth between populations of *Pseudemys scripta* to age differences between populations but Gibbons (1967) believed that inter-population differences in size in *Chrysemys picta* could not be explained in this way and suggested that food quality was the primary controlling factor.

Shell damage and injuries are common in Mediterranean tortoise populations (e.g. Lambert, 1982; Meek, 1985) but it is not clear how important these are in contributing to mortality rates. For example, can they be used in the way lizard tail loss has been used as a mortality index? The data in Fig. 6 appears to show that there was an increasing likelihood of injury with age and increases in size in *T. hermanni* but whether these were the result of accidents or predator attacks is not known. Potential predators on large tortoises are probably few particularly in the Montenegrin population although the fact that Croatian tortoises suffered injuries at earlier ages is interesting and may indicate at least some degree of predation from carnivorous birds or mammals. Nevertheless although based on only a small sample size it is somewhat surprising that most of the remains of the dead *T. hermanni* on the study areas showed little or no signs of physical injury suggesting that other factors also contribute to mortality rates, perhaps heat death as found for *Geochelone gigantea* (Bourne and Coe, 1978).

The biomass densities of Yugoslavian *T. hermanni* found in this and a previous study (Meek, 1985) are in good agreement with those found for other terrestrial chelonians (see Iverson, 1982 for a review) although they are greatly exceeded by the biomass densities of certain Island species (e.g. *Geochelone gigantea*, Coe *et al.*, {1979}). Scrub habitat, whether in Argentina (Auffenberg, 1969), United States (Auffenberg and Weaver, 1969) or Europe appears to support high densities of herbivorous tortoises, much higher, for example, than are found in desert areas (Iverson, 1982) and thus appears generally to be important habitat for terrestrial chelonians. Herbivorous tortoise biomass densities also greatly exceed the biomass densities of herbivorous lizards, (which have the highest biomass densities of any group of lizards), and also exceed the biomass densities of snakes (Iverson, 1982). Such data appear to suggest that tortoises are particularly successful in utilising environmental resources and indeed *T. hermanni* is often the most abundant or at least the most conspicuous vertebrate species in the ecosystems where it occurs apparently exceeding the density of the most common lizard species (Meek, 1986). However, Iverson (1982) has drawn attention to the possibility that in long lived species with high standing crop biomasses, the annual biomass production may be low (e.g. *T. hermanni* in Yugoslavia) rendering such species susceptible to population disturbances, and recovery from (for example) the effects of large scale collection will be slow or may not occur if at all.

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SHORT NOTE:

THE PARASITIC BURDEN OF THE FROG *RANA RIDIBUNDA* PALLAS, FROM SAUDIA ARABIA. A PRELIMINARY LIST OF PARASITIC HELMINTHS

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Few investigators have studied the helminth parasitic fauna of *Rana ridibunda* in Saudia Arabia (Nasher, 1979, Ramadan Banaja and Saoud, 1980 and Ali, Kalanthan and Rahman, 1981).

The author's intention is to give a preliminary list (Table 1) of Platyhelminths, Nematodes and Acanthocephala collected from frogs in Saudi Arabia, over a period of four years from 1980-1984. Collections were made in the periods January-February and October-November of these years.

Frogs were collected from two localities in the Eastern Province of Saudi Arabia. Collecting stations were in Al-Katif Oasis 26°33'30"N, 49°59'00"E and in primary and secondary irrigation drainage canals in the vicinity of Ain Barbara, about 2km east of the city of Al-Hofuf, Al-Ahsa (Hasa) Oasis, Eastern Province, Saudi Arabia.

To the best of my knowledge all species listed here, unless indicated otherwise, are recordings made for the first time in the Saudi Arabian frog *Rana ridibunda*.

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Host	Location	Taxonomic Grade of Parasite	Parasite	Location of Parasite	Comment
<i>Rana ridibunda</i> Pallas	Al-Katif	Phylum Platyhelminthes Class Cestoda	<i>Diphyllbothrium erinacei</i> Rudolphi 1819; Pleuroceroid larvae.	Encysted in Stomach wall of host.	Found in specimens of host collected in October-November. Large translucent sacs attached to stomach serosa. Short larvae. Average in a single host 1-2. Active in frog ringer.
				Wedged in between bundles of thigh, shank and arm muscles.	Found in specimens collected in January-February. Long pleuroceroids seen moving when muscle blocks were separated.
	Al-Katif	Phylum Nematoda	<i>Aplectana</i> Sps male and female immature stage described incident in <i>Bufo orientalis</i> and <i>Hyla arborea</i> in Asir, S. W. Saudi Arabia. Nasher A. K. (1979)	Rectum	Small nematode. Usual incidence one or two worms to a host. Heavy infestations of 8-10 to a host occurred rarely, and a frog with 30 parasites was also encountered.
	Al-Katif and Al-Hasa Oasis	Phylum Nematoda	<i>Abbreviata</i> sps larvae	Larvae in brown cysts located sub-cutaneously on body wall. Packets of cysts on either side of the urostyle and in the axilla of limbs. Heavy infestations also occurred in the superficial stomach wall and embedded deeply in its muscle. Cysts were found attached to gut musculature and mesenteries along the length of the entire G.I. Tract.	The larvae were microscopic and were released with difficulty by microdissection. When present they were numerous and therefore counting was difficult. In the urostylar region the host reaction to presence of parasite produced heavy melanin pigmentation around the larval cysts.
	Al-Katif and Al-Hasa Oasis	Phylum Nematoda	<i>Foleyella duboisi</i> Geddoelst 1916	In the body cavity on either side of the vertebral column.	Large Nematodes with translucent body wall. occurrence 2 to 4 worms usually. Occasionally heavy infestations of 13 worms were encountered in a single host. Worms were fragile. Due to host reaction to the presence of worms, mesenteries covered and wrapped up the worms.

Host	Location	Taxonomic Grade of Parasite	Parasite	Location of Parasite	Comment
<i>Rana ridibunda</i> Pallas	Al-Hasa Oasis	Phylum Nematoda	<i>Oswaldocruzia</i> sps (Female) Described incident in <i>Bufo orientalis</i> and <i>Hyla arborea</i> in Asir, S. W. Saudi Arabia Nasher, A. K., 1979.	Found free in the rectal contents and also deeply embedded in the mucosa of the large intestine. Rarely found in the stomach.	Incidence rare. Maximum one or two worms per host. Only one specimen was found in the stomach mucosa of a frog.
	Al-Hasa Oasis	Phylum Nematoda	<i>Polystoma</i> sps	Found free in the rectal contents of the host.	Not of common incidence.
	Al-Katif Oasis	Phylum Platyhelminthes Class Trematoda	<i>Diplostomum</i> (Tylodelphys) (Metacercariae)	In the body cavity near the axilla of the arms.	A few metacerciae were found attached to and covered by mesenteries (host reaction?).
			<i>Pleurogenoides compactus</i> (Stromi 1940)	Mucosa of duodenum, intestine and rectum. Rarely in urinary bladder.	All Trematodes usually covered over by a great deal of mucous.
			<i>Pleurogenoides Stromi</i> (Travassos 1930) Described incident in the small intestine of a 'Frog', Ali M. M., Kalanthan, A., Rahman, M. M., Riyadh, Saudi Arabia, 1981.	Mucosa of duodenum and rectum.	
			<i>Opisthoglyphe ranae</i> (Frölich, 1791)	Musoca of small intestine.	
			<i>Codonocephalus uringer</i> (Rudolphi, 1891) metacercariae.	Attached to gut mesenteries and body wall.	Examination of cyst in frog ringer revealed very slight laboured movement of metacercariae inside the cyst.
	Al-Katif Oasis	Phylum Acanthocephala	<i>Centrorhynchus</i> sps (immature stage)	In the mesenteries near the stomach and the upper region of the small intestine.	Parasite found inside bright orange cysts. Groups of three to four cysts were held together by host mesenteries. On Microdissection of the cyst, the juvenile form of the parasite was found. The cysts lost the bright orange colour when stored in alcohol.

TABLE 1: Parasites of *Rana ridibunda*.

SHORT NOTE:

ECOLOGICAL SEGREGATION BETWEEN *PODARCIS SICULA* AND *P. MELISELLENSIS*, (SAURIA: LACERTIDAE) IN YUGOSLAVIA

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INTRODUCTION

The Dalmatian Coast with ca. 3500 Adriatic islands supports a rich lizard fauna, notably the Wall

Lizards (*Podarcis* spp.) and Rock Lizards (*Lacerta* spp.). The habitat is generally either degraded scrub with *maquis* type vegetation growing over terraced hillsides, or *karst* type terrain.

MAP OF DALMATIAN COAST SHOWING LOCATION OF SITES STUDIED.

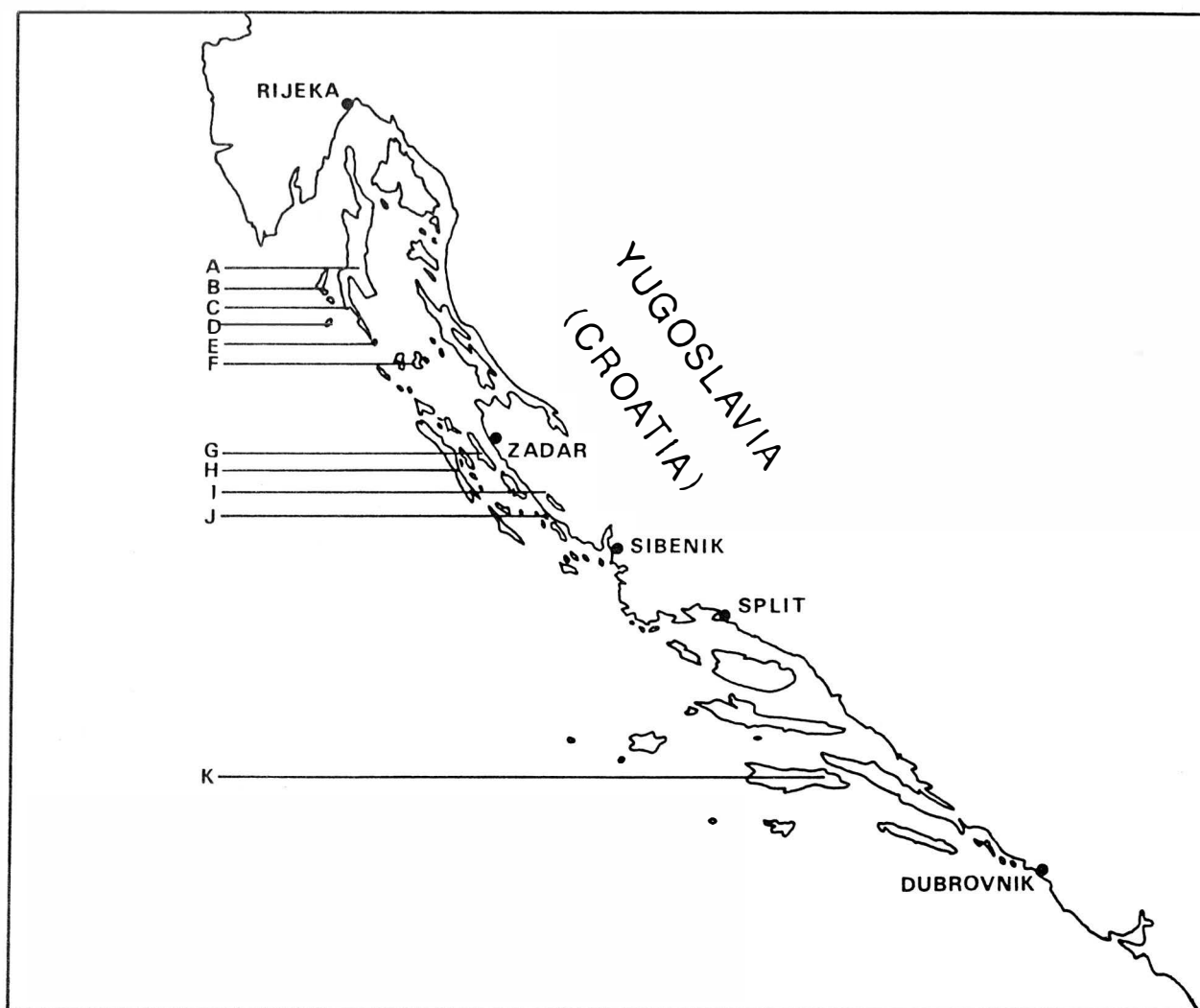


Fig. 1 Map of the Dalmatian Coast showing named sites and the species found at each site.

KEY A Cres (*P. melisellensis*), B Unije (*P. sicula*), C Losini (*P. melisellensis*), D Susak (*P. sicula*), E Ilovik (*P. sicula*), F Olib (*P. sicula*), G Ugljan (*P. melisellensis* and *P. sicula*), H Dugi Otok (*P. melisellensis*), I Vrana (*P. sicula*), J Vrgada (*P. sicula*), K Korcula (*P. melisellensis*).

Two widely distributed lacertids in the region are the Italian Wall Lizard (*Podarcis sicula*) and the Dalmatian Wall Lizard (*P. melisellensis*). Several workers have studied the distribution and interactions of these species, notably Radovanović (1959). In 1985 we carried out a study of the habitat differences between the two species so that the potential for interspecific competition could be investigated.

METHODS

Observations were made at one mainland and 10 island sites each with considerable variation in the types of habitat present. These are indicated in Fig. 1. The majority of the observations were made during the lizards' peak period of activity, viz. early to mid-morning on hot and sunny days. The following methods were used during the study:

(i) Using a set of pre-defined micro-habitats, the location of each lizard was recorded whilst the recorder walked in a random fashion over suitable terrain. Such counts were made for fixed time periods of either 20 or 30 minutes. The micro-habitats were defined as follows:

- A Intact walls
- B Collapsed walls
- C Base of wall
- D Isolated boulders
- E Herbaceous vegetation
- F Woody vegetation

- G Path, track or road
- H Open stony ground (*karst*)
- I Edge of vegetated bank
- J Sandy bank
- K Dead twigs, branches or reeds
- L Edge of a path or road
- M Edge of cultivated land
- N Other micro-habitats

(ii) For paths, tracks or roadsides, lizards were recorded in the same way as (i) for similar time periods, but without the random element of direction.

RESULTS

The abundance of lizards in each micro-habitat is shown in Fig. 2. The data show that *P. melisellensis* has a marked preference for dry-stone walls, especially overgrown and collapsed ones. In contrast, *P. sicula* was much more more diverse in its choice of micro-habitat, being present in *all* the predefined micro-habitat categories and showing no marked preference, but with an affinity for vegetated open ground and paths. In addition to these data, the following qualitative observations on the various species were made:

(i) At most sites, only either *P. melisellensis* or *P. sicula* were present, not both. On Ugljan, however, both species were present although they appeared not to be in sympatry. Coastal to the island's main road, in

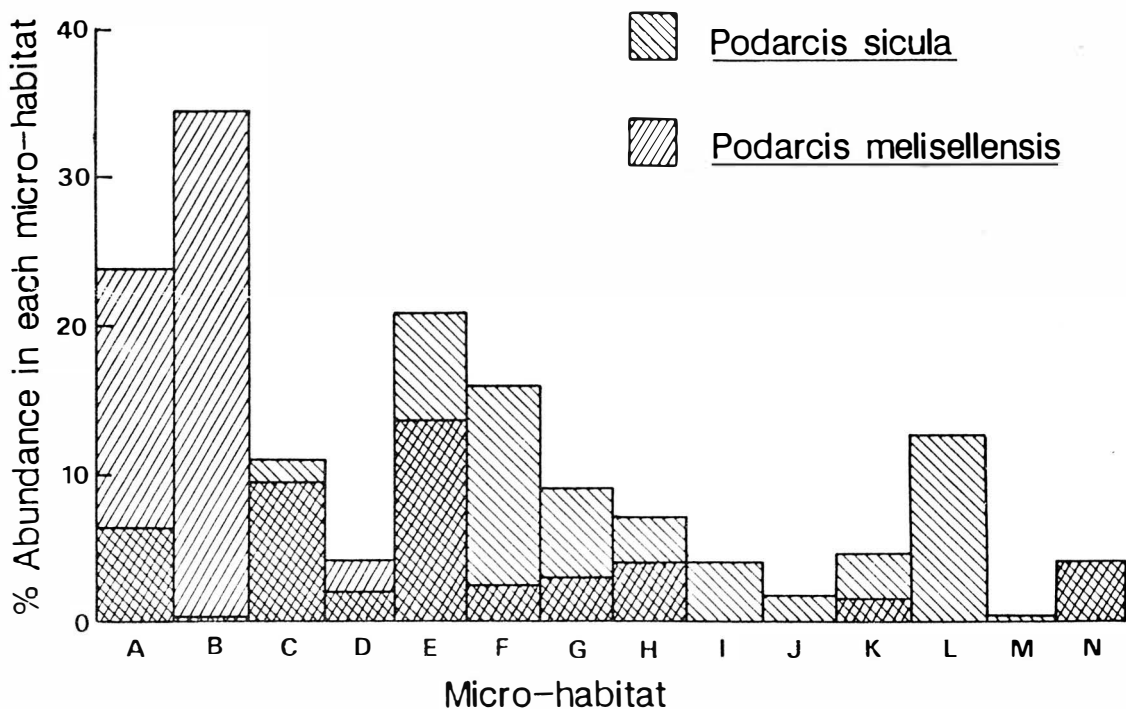


Fig. 2 The abundance of *P. melisellensis* and *P. sicula* in each micro-habitat.

KEY A Intact walls, B Collapsed walls, C Base of wall, D Isolated boulders, E Herbaceous vegetation, F Woody vegetation, G Path, track or road, H Open stony ground (*karst*), I Edge of vegetated bank, J Sandy bank, K Dead twigs, branches or reeds, L Edge of a path or road, M Edge of cultivated land, N Other micro-habitats.

the town of Preko, *P. sicula* was abundant. Inland from the road, however, only *P. melisellensis* was present (in the *maquis*).

(ii) Both *P. melisellensis* and *P. sicula* were observed in a variety of colour and pattern combinations. Among populations of the former species, the boldly-marked green-backed variants tended to prefer lush green vegetation, whereas the unmarked brown variants were usually more abundant on or near walls and in *karst* terrain. A melanistic specimen was found in such terrain on Cres.

DISCUSSION

In most of the locations studied, there were at least five of the micro-habitats present. Therefore, it was assumed that those micro-habitats with the highest proportion of a species are the 'preference' of that species. On the basis of this, the likelihood of competitive exclusion between *P. sicula* and *P. melisellensis* could be assessed. In earlier work, Radovanović (1959) postulated that *P. sicula* was invading the range of *P. melisellensis* via a competitive advantage, namely superior size. He tested this hypothesis by introduction experiments on several small islands, and concluded that competitive exclusion was indeed occurring. Subsequently, Nevo, Gorman, Soulé, Suh Yung Yang, Clover and Jovanović (1972) revisited some of Radovanović's sites and found evidence to both support and refute his theory. They also found evidence from the island of Mali Obrovanj to suggest that the two species could coexist on one island, provided that at least two distinct habitat-types were present, indicating that they were probably not sympatric.

Our observations from Ugljan support their findings, although it should be stated that Ugljan is a very large island when compared with Mali Obrovanj, which only measures 80 x 50m. Clover, (1979) likewise, has observed that on some of the larger Adriatic islands, such as Ciovo, both species may occur together. This phenomenon of the two species occupying separate habitats on the rare occasions where they both occur on the same island, coupled with our observations of the lizards' preferred habitats among separate populations, suggest that the two species are not likely to be competing for the same resource and thus competitive exclusion is probably not occurring.

In addition to these findings, observations were made on the Sharp-Snouted Rock lizard (*Lacerta oxycephala*) and *P. melisellensis* on the island of Korcula, where the two species appeared to be sympatric. *L. oxycephala* was, however, much more adept at climbing than the latter species. In Korcula town, *L. oxycephala* coexisted with the Turkish Gecko (*Hemidactylus turcicus*) with which it had comparable climbing abilities but, unlike the gecko, was diurnal. Thus *L. oxycephala* appeared to avoid total niche overlap with *P. melisellensis* by the superior climbing abilities of the former species, and with *H. turcicus* by the nocturnal habits of the latter species.

In summary, competition between *P. sicula* and *P. melisellensis* is avoided by:

(i) geographical separation of the individual island populations of each species, or by

(ii) significant habitat and behavioural differences between the two species where they do occur together; namely that *P. sicula* is a particularly bold, opportunist and conspicuous species preferring vegetated and open land near human habitation. In contrast, *P. melisellensis* is a more conservative species preferring a more rocky, overgrown habitat, especially dry-stone walls, often away from human habitation.

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SHORT NOTE:

ASPIDURA IN THE MALDIVES

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Laidlaw (1902) in reporting on the amphibians and reptiles of the Maldives, noted a unique record of *Aspidura*, a genus of Sri Lankan snakes (cf. Phillips, 1958). Gans and Fetcho (1982) later cast the record in doubt in reviewing the genus, as the record was undocumented by a specimen and the occurrence otherwise unlikely.

Through the courtesy of Dr. K. A. Joysey I was recently able to examine the reptilian materials in the collections of the Cambridge University Museum of Zoology. To my surprise I discovered their R7.357/2 catalogued as from Male Atoll, Maldives Islands and accessioned as from J. S. Gardiner, M. A., on 20 June 1900. Clearly this is the specimen referred to. It has been identified as *Aspidura trachyrocta*, as it has a preocular, undivided subcaudals and 15 rows of dorsal scales. It measured only 78 + 12mm (snout-vent plus tail length), suggesting that it must be a recent hatchling (cf. Gans and Fetcho, 1982, Fig. 1).

Discovery of a single hatchling individual cannot be used as evidence for the occurrence of this species in as unlikely a location. *Aspidura trachyrocta* is not only a

montane form, but the most common and widely distributed species of the genus. Unlike *A. guentheri* it neither occurs in the southern lowlands, nor does it reach coastal localities. The specimen likely represents an individual transported in trade with horticultural materials, either as an egg or as a hatchling. Supported by grant G-BSR-850940 from the U.S. National Science Foundation.

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BOOK REVIEWS:

(1) *Hybrid Origin of a Unisexual Species of Whiptail Lizard, Cnemidophorus neomexicanus*. in *Western North America: New evidence and a Review*. Charles J. Cole, Herbert C. Dessauer, and George F. Barrowclough. American Museum Novitates, Number 2905, pp. 1-38, (1988).

From a number of previous studies, it was established that the unisexual diploid New Mexico lizard *Cnemidophorus neomexicanus*, as well as many other parthenogenetic lizard species, originally resulted from the natural hybridisation of bisexual diploid species *Cnemidophorus inornatus* and *Cnemidophorus marmoratus*. The conclusion about the hybridogenic origin of this species was drawn from analysis of karyotypes, electrophoretic studies of proteins and comparative study of geographical distributions and ecological peculiarities of *C. neomexicanus* and its supposed parent species (Lowe a. Wright, 1966, *J. Arizona Acad. Sci.*, 4(2): 81-87, and others).

In the present study, the authors investigated this hypothesis on some new material. Using various methods, they studied samples of *C. neomexicanus* from the vicinity of Lordsburg, New Mexico, a southwestern geographic extreme population, and from the northern part of its range, near Pena Blanca, New Mexico. Also studied were samples of this species from localities between the two mentioned above and several samples of the proposed ancestral bisexual species, *C. marmoratus* and *C. inornatus*, including some from the vicinity of Lordsburg where they are sympatric with *C. neomexicanus* today. For comparison, samples of *C. gularis*, *C. sexlineatus*, and *C. septemvittatus* — bisexual species related to *C. inornatus* which should not be ignored as possible ancestors alternative to *C. inornatus* were also studied. Comparisons were made of the habitat preferences, external morphologies (colour patterns, character of pholidosis and all analysed with univariate and multivariate methods), karyotypes, protein electrophoresis and viability of eggs and offspring through several generations produced by captive *C. neomexicanus* kept and reproduced in isolation from males.

With the help of the above methods, the authors set themselves the task to answer the following fundamental questions:

1. Are the various data, including the morphological data, consistent with the hybrid origin hypothesis for *C. neomexicanus*, the probable ancestors being *C. marmoratus* and *C. inornatus*?
2. Given the mixture of habitats and associated species of *Cnemidophorus* in the Lordsburg area, do the *C. neomexicanus* individuals there constitute a reproducing population, or are they newly generated, and possibly sterile hybrids of the first generation?
3. Are the specimens of *C. neomexicanus* from Lordsburg similar to those from the Rio Grande

Valley, particularly from a northern latitude, a different habitat, and a site where the two ancestors were not found together with the *neomexicanus* samples?

As a result of the studies made, it was confirmed that *C. neomexicanus* is indeed of hybrid origin. This is indicated by the following facts received anew and those already known to the reader.

In all proteins of the bisexual species of *Cnemidophorus* studied by the method of electrophoresis most gene loci bear alleles in the homozygous state (typically about 5 per cent of the loci scored per individual). Contrary to this, in the hybridogenic species *C. neomexicanus* the level of heterozygosity is 34 per cent, which is considerably higher than in any bisexual reptile species of non-hybrid origin. The karyotype of *C. neomexicanus* is characterised by a great number of heteromorphic pairs of chromosomes as compared to all non-hybrid bisexual species. It has 1 haploid set of the *C. marmoratus* species and 1 haploid set characteristic of the bisexual species from the *C. sexlineatus* group. The other haploid karyotype might have been contributed by *C. septemvittatus*, *C. gularis*, *C. sexlineatus* or *C. inornatus*. However, the number of banded set II chromosomes in *neomexicanus* suggested that *C. sexlineatus* was not involved. The complete combination of traits observed in *C. neomexicanus* can be attributed to hybridisation between certain known bisexual species of *Cnemidophorus* having geographically and ecologically relevant distributions.

The origin of this species by the *C. marmoratus* X *C. inornatus* scheme is supported first of all by the following data. The electrophoretic examination of 92 alleles (in homo- and heterozygous state) elicited all the alleles and all the loci simultaneously in *C. neomexicanus*, *C. marmoratus* and *C. inornatus*.

Genotypically, *C. inornatus* fits as the second ancestor for *C. neomexicanus* substantially better than any other investigated species. Observation on preferred habitats, geographic distribution, and external morphology, while not as clearly interpreted in terms of genetic determination of the characters, also are consistent with and strongly favour the *C. marmoratus* X *C. inornatus* hybrid origin hypothesis for *C. neomexicanus*.

The populations of *C. neomexicanus* isolated at present belong to the same electrophoretic clone, having, though, some genetic and morphological differences. The mechanism of their origination is not quite clear. It has been suggested that *C. neomexicanus* lizards of Lordsburg probably colonised the area following dispersal from the Rio Grande Valley.

The literature quoted includes 72 sources.

I. S. Darevsky

(2) *World Checklist of Threatened Amphibians and Reptiles*. Prepared by Brian Groombridge and published by the Nature Conservancy Council. 138 pages, softback, 1988: £16.

Checklists are necessarily functional publications, not the best of bed-time reading. The bulk of this one is taken up by catalogues of species appearing on Appendices I, II or III of the Convention on International Trade in Endangered Species (CITES) or which feature in the IUCN Red Data Book (RDB), or both. Each species is listed under its scientific name, alongside which are given common vernacular names, CITES/RDB category, indication of major exploitation (food, skins, etc.) where known, and relevant published references (549 of which are cited at the back of the volume). I have no doubt that these lists are comprehensive, accurate and up-to-date; the author has an unrivalled reputation in this area, and reviewers of comparable competence (among which I certainly do not include myself) impossible to find. The main work is preceded by a rather brief preface and introductory notes, in which the purpose of the publication is made clear: it is intended primarily for use by the Nature Conservancy Council as a guide for the assessment of applications for import and export permits for herpetofauna entering or leaving the United Kingdom. In this specific role I am sure it will fulfill its function admirably. However, my strongest feelings after perusing the work concerned what was left out rather than what was included. There must be many naturalists, scientists and herpetologists in general that know little or nothing about the meaning or implications of CITES, the basis on which species are listed on it, and so on. So here is a plea to the author, and the publishers, for an extended version of this checklist directed at a wider audience. Such a booklet might include such things as: definitions of the

CITES Appendices and RDB status categories (the present publication assumes these are known by the reader); summaries of numbers of species from each Order in each category; and, most importantly, some discussion of the reasons why species are so listed. I did a few sums of my own on the basis of the main checklist, and finished up rather puzzled on a number of points. No Caecilians or Amphisbaenids are listed by CITES or the RDB: are none as endangered as any of the species listed in the better-known families? In percentage terms, there is great inter-family variation from the above two groups (no protection) through the other amphibia (less than 2 per cent of anuran and urodele species are listed in all CITES Appendices), lizards and snakes (up to 6 per cent listed), testudines (about 50 per cent listed) up to crocodilians (virtually all listed). I also found it odd that there were substantial discrepancies between CITES and RDB assessments; more than twice as many anurans feature on CITES Appendices than in RDB categories, whereas with urodeles there are five times more RDB entrants than CITES ones!

It would be interesting to see these matters discussed by those responsible for allocating species to CITES and the RDB. One consequence of the most recent CITES updating exercise, at Ottawa in 1987, was criticism of the scientific basis for deriving these schedules. A particular example was the listing of all the *Dendrobates* ('arrow poison') frogs on Appendix II, when by all accounts most are abundant and not obviously endangered. Let's hope some future publication on threatened species will include this broader educational remit and let us all know the whys and wherefores of conservation legislation enacted on our behalf.

Trevor Beebee

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