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FRONT COVER: Galapagos giant tortoise, *Geochelone elephantopus* (I. Swingland).

FEEDING STRATEGIES OF THE VIPER *VIPERA URSINII URSINII* (REPTILIA: VIPERIDAE) IN THE APENNINES

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ABSTRACT

During a three-year period of research on the viper *Vipera ursinii ursinii*, observations on diet composition and feeding strategies were obtained. The major food items in terms of percentage were orthopterans, followed by rodents, lizards, birds, spiders and beetles. A considerable seasonal change in the diet composition was noted: invertebrates predominated in the diet only between July and September, as compared to the spring diet which was made up of vertebrates.

INTRODUCTION

Numerous works have reported data regarding various aspects of the ecology of *Vipera ursinii*, including Baron (1980, 1989), Naulleau (1973, 1984), Kotenko (1989), Saint Girons (1975, 1978, 1979, 1980) and Saint Girons and Naulleau (1981). The most recent studies on the feeding behaviour of these vipers have been carried out by Baron (1989) on Mont Ventoux (France) and by Kotenko (1989) in various areas of the Ukraine, such as the Orlova island. However, the feeding patterns of the Italian viper populations, restricted as they are to a few of the Apennine massifs, are not very well-known, and have been discussed only in general, layman's works whose observations seem to lack a systematic approach (cf. for example Bruno and Maugeri, 1977, 1984; Bruno 1983).

The aim of this paper is therefore to present a systematic study carried out over a number of years on the feeding activities of *V. ursinii* in the central Apennines, in the hope that these data may prove of interest in providing a better knowledge of certain aspects of the biology of this mountain viper.

MATERIALS AND METHODS

The vipers were observed during the whole of their active cycle, i.e. from mid April until the end of September each year from 1987 to 1989. All the data reported in this paper were obtained by analysing the gastrointestinal contents of *V. ursinii* specimens captured in two locations in the Abruzzi Apennines (Valle di Campo Imperatore, Gran Sasso d'Italia; monte Velino), at an altitude ranging from 1600 to 1850m.

The vipers were divided into two categories according to size: (1) vipers longer than 28 cm in total length and (2) vipers shorter than 28 cm in total length. 76 vipers were examined in the first category (of which 43 had identifiable food residuals in their gastrointestinal apparatus; $\bar{x}$ = 56.6%) and 12 in the second category (of which 7 had food remains in the intestine $\bar{x}$ = 58.3%). On the whole, the ingested matter was easily recognizable, mainly because only a few species of

potential prey are to be found in the habitats of these mountain vipers, including one species of Lacertidae (*Podarcis muralis*), two bird species (bearing in mind that *Anthus s. spinoletta* and *Phoenicurus ochruros* are the only species that nest at ground level in the valleys inhabited by *V. ursinii* and therefore may be prey to these snakes), and some invertebrates (particularly Orthoptera).

The small mammals of the studied areas are less known, and therefore we have not a complete list of the species inhabiting these environments; however, we have found in the viper stomachs only seven specimens of a Microtidae species. Since these remains had been particularly damaged by the digestive process, we have not identified the species in question, but, referring to Toschi's (1965) keys and to Graf's (1982) data, we believe that the rodent in question might be *Microtus nivalis*.

The vipers over 28 cm long were palpated in order to make them regurgitate their ingested prey, and were then immediately released. Since this operation may be dangerous for smaller specimens, these were analysed using Kjaergaard's method (1981).

Unfortunately, these methods do not always allow for the examination of all the gut contents. In order to overcome this problem it was necessary to analyse the faeces of 34 other vipers (all excluded from the total number of specimens quoted earlier, and all belonging to category 1).

Often it was possible to obtain more than one prey item from a single specimen, so the overall number of prey is considerably higher than the total number of animals caught (95 prey obtained from 43 specimens belonging to category 1 and 14 prey taken from seven specimens in category 2).

The ingested biomass was calculated by applying the same methods utilized by Brana *et al.* (1988), that is to say considering the "fresh" weight of the ingested prey if it was in very good condition. Obviously, when using the "fresh" weight there is the possibility that the weight may be underestimated. This risk was avoided by using this method only in a limited number of cases where the ingested prey had not been at all damaged by the digestive process (21.1% of the cases).

The food niche breadth (B) was calculated using Simpson's (1949) diversity index:

$$B = 1/\sum p_i{}^2$$

where p_i = the frequency with which each ith prey category was used. With this formula, all the Orthoptera remains were included in one category, while the other categories were made up of Microtidae, Motacillidae, Lacertidae, Coleoptera and Opilionidae.

In order to be able to study the feeding periods and the frequency of meals, 21 specimens (8 males and 13 females and all belonging to category 1) were marked and then released into a confined area (of approximately 1.5 hectare) with a superimposed grid system, situated in the Valle di Campo Imperatore (Gran Sasso) at approximately 1750m. The 21 vipers were marked by scale-clipping, and were excluded from the number ($N = 76$) of vipers over 28cm in length mentioned earlier.

RESULTS

COMPOSITION OF THE DIET

Vipers over 28cm long. The total of 95 ingested remains obtained and identified shows a considerably high degree of invertebrates present in the diet of these ophidians (83.2% of the identified prey), particulary Orthoptera (78.9%). Vertebrate remains were common, amounting to 16.8% of the total number of prey; these consisted of 6.3% Lacertidae (Reptilia, Sauria), 7.3% juvenile Microtidae (Mammalia, Rodentia), and 3.1% nestling Motacillidae (Aves, Passeriformes) (Table 1, Fig. 1).

FIG. 1. Percent frequency of the preyed taxa (black columns) and their relative biomass percentages (striped columns) in *V.ursinii* in the studied environment: 1 = Lacertidae, Reptilia; 2 = Microtidae, Mammalia; 3 = Motacillidae, Aves; 4 = Orthoptera, Insecta; 5 = Other Prey (Coleoptera, Insecta; Opilionidae, Arachnida). These data are referred to specimens of more than 28 cm. in overall length.

Longer than 28 cm.	$N = 43$	
	n	$\%n$
Podarcis muralis	6	6.3
Microtidae	7	7.3
Anthus s. spinoletta	3	3.1
Orthoptera Tettigonidae	6	6.3
Orthoptera Acrididae	46	48.4
Orthoptera undet.	23	24.2
Coleoptera undet.	1	1.2
Opilionidae undet.	3	3.2
	95	100

Shorter than 28 cm.	$N = 7$	
	n	$\%n$
Podarcis muralis	1	7.2
Orthoptera undet.	10	71.4
Silphiidae (*larva*)	1	7.2
Opilionidae undet.	2	14.2
	14	100

TABLE 1. List of prey obtained from the gastrointestinal tract of *Vipera ursinii* captured in the Italian Apennines.

	n	n'	n/n'
Podarcis muralis	6	6	1
Microtidae	7	4	1.7
Anthus s. spinoletta	3	1	3
Orthoptera	75	29	2.6
Coleoptera	1	1	1
Opilionidae	3	2	1.5

TABLE 2. Distribution of the total number of prey ($n = 95$) in relation to the total number of stomachs ($n' = 43$). (Vipers >28 cm. in total length.)

	n
Podarcis muralis	2
Rodents undet.	3
Orthoptera undet.	29
Chilopoda undet.	1
Coleoptera undet.	2
Undetermined Animal Residues	7

TABLE 3. List of prey residues obtained from 34 excreta of vipers >28 cm. in length. n is the total number of the excreta in which a single kind of prey has been discovered.

These 95 ingested remains were obtained from only 43 vipers ($\bar{x}$ = 2.2 prey/stomach), and their distribution (in relation to the total number of stomachs) is carried to Table 2. Other prey residues were also obtained from some viper excreta (n = 34); this analysis revealed a fragment of a Chilopoda species, which was not observed in any other case during our research (see Table 3).

However, with regards to the biomass ingested, the overall percentage of vertebrates increases to a grand total of 54.2% of which 21.9% is made up of Lacertidae, 26.5% of Microtidae, and 5.6% of Motacillidae. In terms of biomass, the various species of Orthoptera constitute 45.4% of the total biomass ingested, while other invertebrate species (Coleoptera and Oplionidae) only make up 0.3% of the total (Fig. 1).

Vipers under 28cm long. Of the 14 ingested samples obtained (from only 7 specimens), no less than 13 consisted of Arthropoda (92.9% of the total), and only one of a very young Lacertidae (7.2%), less than a month old (Table 1).

ANNUAL FEEDING CYCLE AND SEASONAL DIETARY CHANGES

According to Baron (1989), the feeding period of the *V. ursinii* populations of Mont Ventoux is extremely limited, lasting from the end of June to the end of September, with an overall active period of approximately 6 months in adult males and approximately 5 months in adult females.

Our findings coincide widely with those of Baron, but the feeding period appears to start earlier among the Italian populations (at the beginning of June), while the end coincides completely with the observations made on the French populations.

The feeding patterns of individual specimens vary considerably from period to period (Fig. 2). On the whole, it is possible to conclude that a low percentage of specimens feeds in June (12.5% of males and 23% of females respectively), while from July to September these percentages reach very high values: in males the maximum percentages were obtained in July and August (100% of the specimens), and in females in July and September (after their births) (again 100%). Pregnant females also usually feed during their gestation period, and for example, we observed a female eating a young hamster (weighing 8g) only 7 days before giving birth (in captivity).

	J	F	M	A	M	J	J	A	S	O	N	D
AM												
AF												
Y												

AM = Males (longer than 28 cm.)
AF = Females (longer than 28 cm.)
Y = Young specimens (shorter than 28 cm.)

- - - - - - - annual activity cycle
⊢─────⊣ annual feeding cycle
◢◤ phase with predominant (more than 70%) vertebrate species in the diet
phase with predominant invertebrate species in the diet (more than 70% of the diet composition

FIG. 3. Pattern of the annual activity cycle in the studied populations of *Vipera ursinii.*

A considerable seasonal change was observed in the composition of the vipers diet (P <0.001), presumably in accordance with the availability of prey (Fig. 3). Thus, in June, when Orthoptera are not easily found in the areas under study, the few vipers that feed (approximately 19% of the specimens) prey exclusively on small vertebrates (81.8% of all the ingested vertebrate remains obtained during this research study). Females appear to feed more frequently at this time than males (differences significant at P <0.01), who never feed before the end of the mating season (75% of the marked vipers left in the confined area (as described in "Materials and Methods") who fed in June were females, and 66.6% of the prey obtained in June came from female specimens). 100% of the rodents obtained in this study, 100% of the bird remains and 16.6% of the lizard remains were obtained from the gastrointestinal apparatus of females in June, while only 50% of the total remains of Lacertidae were obtained from males during this month.

From July to September, as a result of the "population explosion" of the various species of Orthoptera found in the high pastures in the Abruzzo mountains, vertebrates practically disappear from the vipers' diet altogether (only two specimens of *Podarcis muralis* were removed from the vipers' stomachs during this period) and are replaced by Orthoptera, which then became the main nutritional resource for the vipers in the area (92.6% of
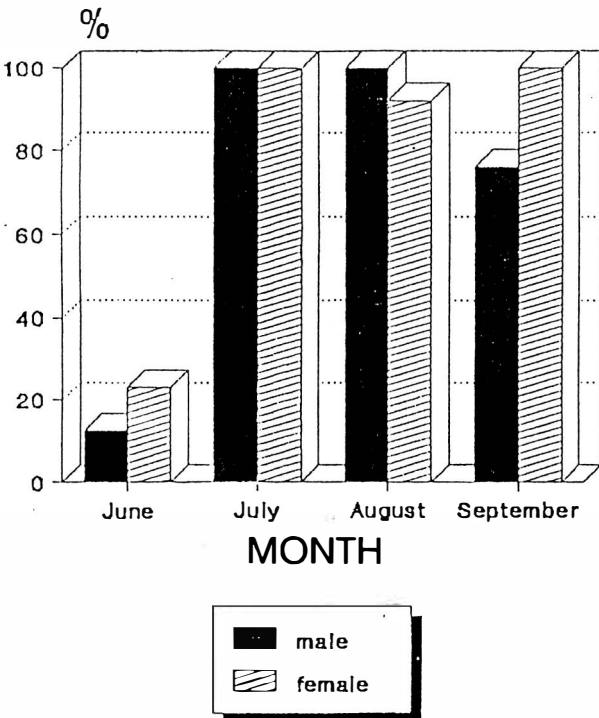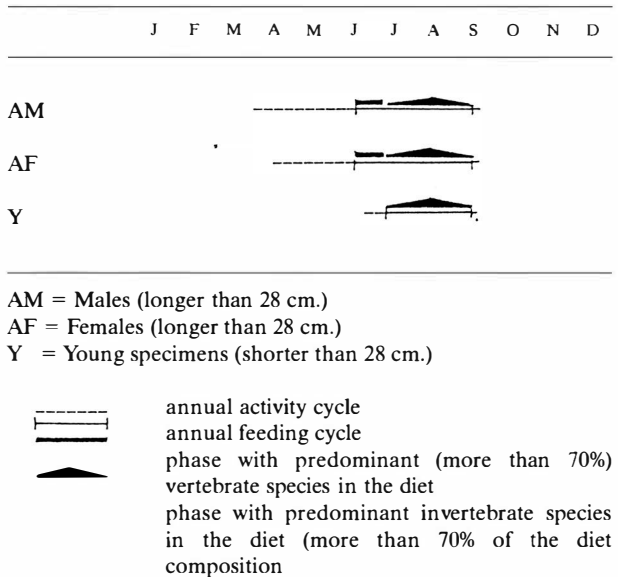

FIG 2. Percentages of males and adult females which feed in the different months of the annual feeding cycle, in the *Vipera ursinii* populations of the studied areas.

the total prey obtained). Both sexes prey on the various species of Orthoptera indiscriminately. These are chosen without any particular criteria except size. Only grasshoppers over 15mm long are preyed upon by vipers in category 1, while those in category 2 (and in particular those under 22cm long) prey upon Orthoptera smaller than those mentioned earlier. It should be borne in mind that only 5.3% of the Orthoptera found in the stomachs of the vipers in category 1 were smaller than those mentioned above and, furthermore, these were not very much smaller (with length ranging between 11 and 13.5mm). Here too, the data recorded in this study are largely in accordance with Baron's (1989) findings.

FREQUENCY OF FEEDS

The frequency with which vipers feed seems to differ in the various phases of the annual feeding cycles. In June and in the first ten days of July the vipers eat irregularly (on average only once during the whole period), while they feed much more often in the second half of July to September (in fact, during this period, vipers caught 1-7 large Orthoptera (over 3.5cm long) every 2-3 days ($\bar{x}$ = 4.2; n = 79), which they keep in their mouths until the victim has become completely immobilised and can be swallowed. Furthermore, taking into account that adult V. ursinii usually catch prey that weigh less than 8g (or swallow a total quantity of prey lower than this in terms of weight), stomach contents are small. Baron (1989) also noted this in the Mont Ventoux vipers, unlike Bruno and Maugeri, who wrote in 1977 (p. 172) "Un esemplare adulto sembra che possa ingollare fino a 100 cavallette al giorno".

DISCUSSION

The diet of the V. ursinii populations studied includes species belonging to eight families (of which three are vertebrates) and eight genera. Relative to the size of the food niche breadth, the value (B = 1.57) is considerably lower than any which have been obtained in various populations of V. aspis (Saint Girons, 1980; Luiselli and Agrimi, 1990), V. berus (Brana et al., 1988). The food niche breadth was remarkably wider in June than in the following months (Fig. 4). The essential differences between V. ursinii and the other European species of Vipera are not only in the value of the food niche breadth, but also in the taxonomic composition of their diet, since in the abovementioned species (V. aspis V. berus, V. seoanei) the adult diet is predominantly composed of small mammals (Soricidae, Muridae and Microtidae). They constitute over 60% of the prey in V. aspis in western France (Saint Girons, 1980) and in central Italy (Luiselli and Agrimi, 1990), of V. berus in England (Prestt, 1971), Poland (Pomianowska, 1974) and Italy (Luiselli, 1990), of V. seoanei in the Cantabricos mounts (Braña et al., 1988), of V. latastei in Spain (Bea and Braña, 1988), while they are largely substituted by orthopterans in the case of V. ursinii.

Extremely important differences also emerge from a comparison of the diet of the young vipers (in the first three years of life). Lizards make up a large part of the diet of the other palaearctic species (from 31.5% in the case of V. berus specimens in England (Prestt, 1971) to 80% of those studied by Pielowsky (1962) in Poland; from 80.77% of V. aspis specimens in central Italy
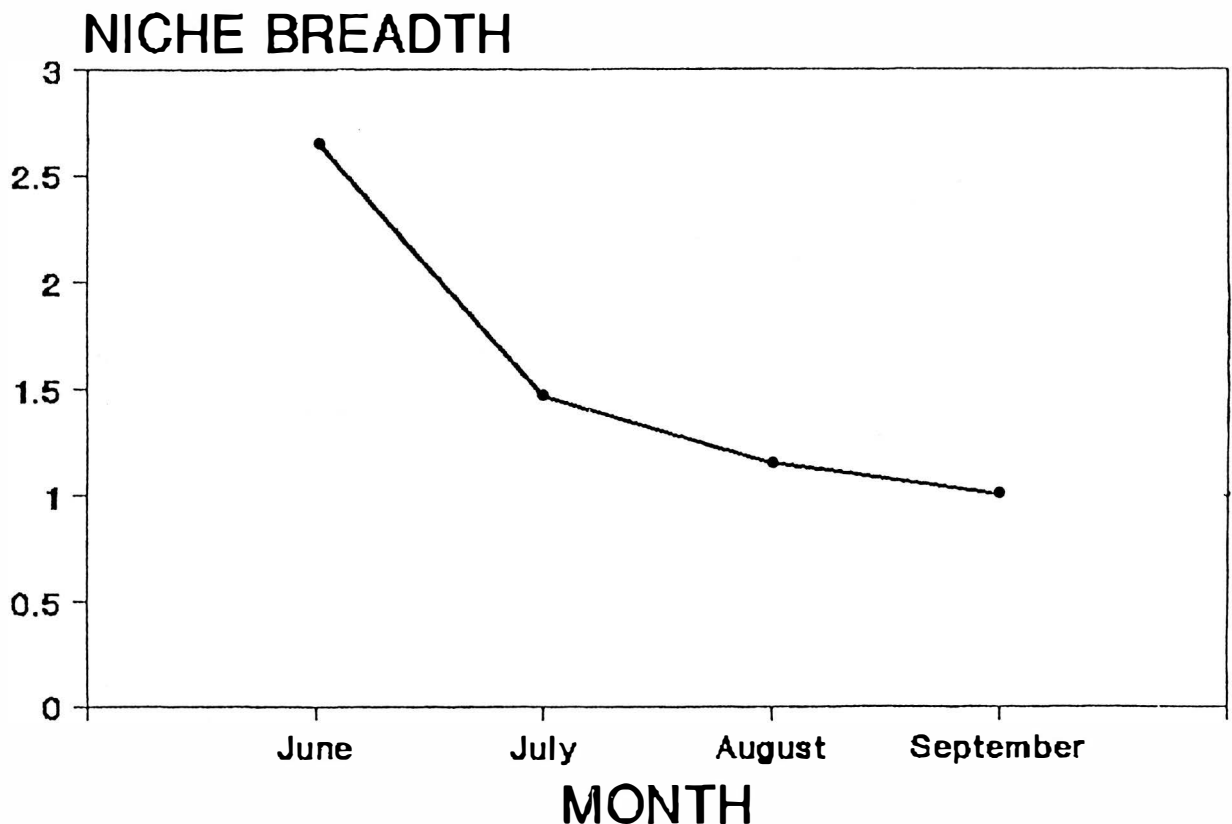

FIG 4. Monthly variation of the food niche breadth (calculated using a Simpson's diversity index, 1949) applied to the taxonomical composition of the diet.

(Luiselli and Agrimi, 1990), to 100% of those in western France (Saint Girons, 1980); in the case of young Orsini's vipers, however, their diets consists, almost exclusively, of arthropods. Moreover, with the exception of *V. ursinii*, the other species of *Vipera* catch invertebrates only in exceptional cases, as recorded by Smith (1951) and Pomianowska (1974) in the case of *V. berus*, Bea and Braña (1988) in the case of *V. latastei* and by Beschov (1977) in the case of *V. ammodytes*.

In the *V. ursinii* populations studied in this paper lizards, generally weighing under 8g, form the main prey in the first part of the annual feeding cycle (66.6%), particularly for male vipers (75% of the cases recorded in June, and 50% in August). Microtidae were caught only by females, and only in late June (in this period they represented 63.6% of the prey caught by females, and 66.6% of the feeds, taking into account that all three *Anthus* fledglings were found in one stomach, and that a *Podarcis* was extracted from another stomach). The three *Anthus s. spinoletta* fledglings were found in a 415mm long female caught in late June in Valle di Campo Imperatore. With regard to this, it is possible to state that preying on fledglings is a fairly rare occurrence that takes place only with species that nest in *Juniperus communis nana* bushes, where vipers often shelter.

Invertebrates, abundant in the diet of *V. ursinii* in Ukraine (Kotenko, 1989) and France (Baron, 1980, 1989), strongly predominate in th diet (97.5%) only between July and September, as compared to the spring diet, which is made up only of vertebrates. It is thus possible to conclude that there is a considerable seasonal influence on the diet. A seasonal change was noted by Kotenko (1989) in the populations of *renardi* subspecies on the island of Orlova (Ukraine), where the vipers prey on ducks and sand-pipers in May-June, and on *Microtus arvalis* and *Lacerta agilis* during the other months.

Furthermore, with regards to the duration of the trophic period, there are important differences between the two-size categories of vipers, given that those in the second group usually begin their annual activity in the first ten days of July (feeding begins shortly after the middle of the month), at the beginning of "Orthoptera phase" of the annual trophic cycle. In this case also our data largely agree with those of Baron (1989), since this period of activity lasts about three months (or a little longer) in both Italy and France.

In addition, the annual feeding cycle seems to be less tied to the reproductive state than it is in other species of temperate zone vipers such as *V. seoanei* (Braña *et al.*, 1988), for example. In fact, the males and the females begin feeding after the mating period, which is usually around the middle of May, and feeding continues until the end of September. This constitutes an exception to the general model, which envisages an interuption of the trophic period in pregnant females during the second phase of the gestation period (Prestt, 1971; Saint Girons, 1979).

Finally, in comparison with other temperate zone vipers, *V. ursinii* employs some remarkably different predatory techniques. Unlike the other vipers, they hold the prey in their mouth until it is swallowed and, under our observation in captivity, tend to use this technique both with Orthoptera and with rodents and lizards.

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PHOSPHATE AND CALCIUM LEVEL VARIATIONS IN THE PLASMA OF THE SNAKE *VIPERA ASPIS* DURING THE ANNUAL CYCLE AND THE REPRODUCTIVE PERIOD

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ABSTRACT

The measurement of phosphate and calcium levels in the plasma of *Vipera aspis* during two consecutive year cycles shows significant seasonal variations. For males and non-breeding females, phosphate levels are higher during the active period of the year than during hibernation. Conversely, calcium levels appear generally more elevated for the hibernating period than for the active period. Breeding females present an important increase of phosphate and calcium levels with a peak near ovulation. Clearly, this phenomenon is related to vitellogenesis. The relationship between plasma phosphate and calcium levels and bone tissue mineralization is discussed, the latter being the only reservoir of these mineral salts available to the snake.

INTRODUCTION

Literature on annual variations of plasma calcium and phosphate levels in non-mammalian vertebrates is scarce (see Dacke, 1979; Clark, 1983). Variations of calcium level have been studied more than those of phosphate. It appears that fish (Booke, 1964; Meunier, 1978) and amphibians (Robertson, 1978; 1985) present significant annual variations of calcium level. For reptiles, we are not aware of any publications dealing with calcium and phosphate variations during the entire annual cycle. During the breeding period, however, female fish (Lopez and Martelly-Bagot, 1971; Martelly, Milet, Legrand, Girard and Fontaine, 1979), amphibians (Dacke, 1979), reptiles (Dessauer and Fox, 1959; Dacke, 1979) and birds (Dacke, 1979) are all known to exhibit an increase of plasma calcium and phosphate levels. These data suggest that the regulation of plasma calcium and phosphate levels in these groups is quite different from that of mammals, because they show such high and significant natural annual variations. Nevertheless, for reptiles and especially for snakes, the available data are so scarce that they prevent any general conclusions concerning phosphocalcic regulations.

This work, part of a more general study dealing with the phosphocalcic metabolism of *Vipera aspis* (Alcobendas and Castanet, 1985; Alcobendas and Baud, 1988; Alcobendas, 1988; Alcobendas, Baud and Castanet, 1991), presents data concerning plasma calcium and phosphate level variations in this species during the annual cycle and breeding period.

MATERIALS AND METHODS

MATERIAL

Some of the vipers used in this study originated from a wild population living in the center of France (Loir et Cher), (capture permission delivered by the french Ministry of Environment). Before the beginning of the experiment these vipers remained at least six months in captivity. A second sample was born at the laboratory, from parents which also originated from the same locality. Finally some females caught in nature in June were immediately punctured.

The breeding conditions used at the laboratory correspond to an artificial seasonal cycle defined by an active period of 8 months with high temperature and a light cycle similar to that encountered in nature (from March to October) during which vipers feed and reproduce, and a hibernating period of 4 months (November to February) with low temperature, darkness and no food. These breeding conditions provide vipers in good physiological condition, all year round. All the vipers used in this study had reached sexual maturity.

Intracardiac punctures were conducted monthly, using a standstill system fitted to the snakes (Naulleau, Fleury and Boissin, 1987). 400 to 500 µl of blood are taken monthly from each viper. This technique was used for two years in some vipers and did not cause any trouble to the animals which went on eating and reproducing normally.

METHOD OF MEASUREMENT

The blood samples were centrifuged (Beckman centrifuge) for three minutes at 15,000 rpm. The plasma obtained was divided into two fractions. The first, stored at 4°C, was used, within 24 to 48 hours of the intracardiac puncture, for the measurement of phosphorus by direct colorimetry, without deproteinization (Phosphore Seratest Eurobio). The second fraction of plasma was stored at -18°C (no more than two months) before the measurement of calcium level by spectrophotometry of atomic absorption (Perkin Elmer Model 401 spectrophotometer).

STATISTICAL ANALYSIS

The individual values of plasma calcium and phosphate levels were recorded. Monthly average values were then calculated, according to the sex of the animals. The number of individuals punctured each month is indicated on the curves (Figs. 1-4).

The importance of calcium and phosphate level variations during the annual cycle, was estimated using analysis of variance. When the calcium and phosphate levels were compared between two periods of the year (e.g. active period compared with hibernation), the individual values were pooled for each period and the two periods compared as two groups of values using Student's t-test.

The two consecutive annual cycles of calcium and phosphate levels were compared using the Student t-test for paired series derived, in this case, from an analysis of variance (ANOVA).

When the calcium level was compared between sexes (very small samples), in January and February 1985, we used the non-parametric Mann-Whitney U-test.

RESULTS

MALES AND NON-BREEDING FEMALES

Phosphate level. During the two annual cycles, 1984 and 1985, plasma phosphate levels did not show significant differences between males and non- breeding females, regardless of the month (Fig. 1).
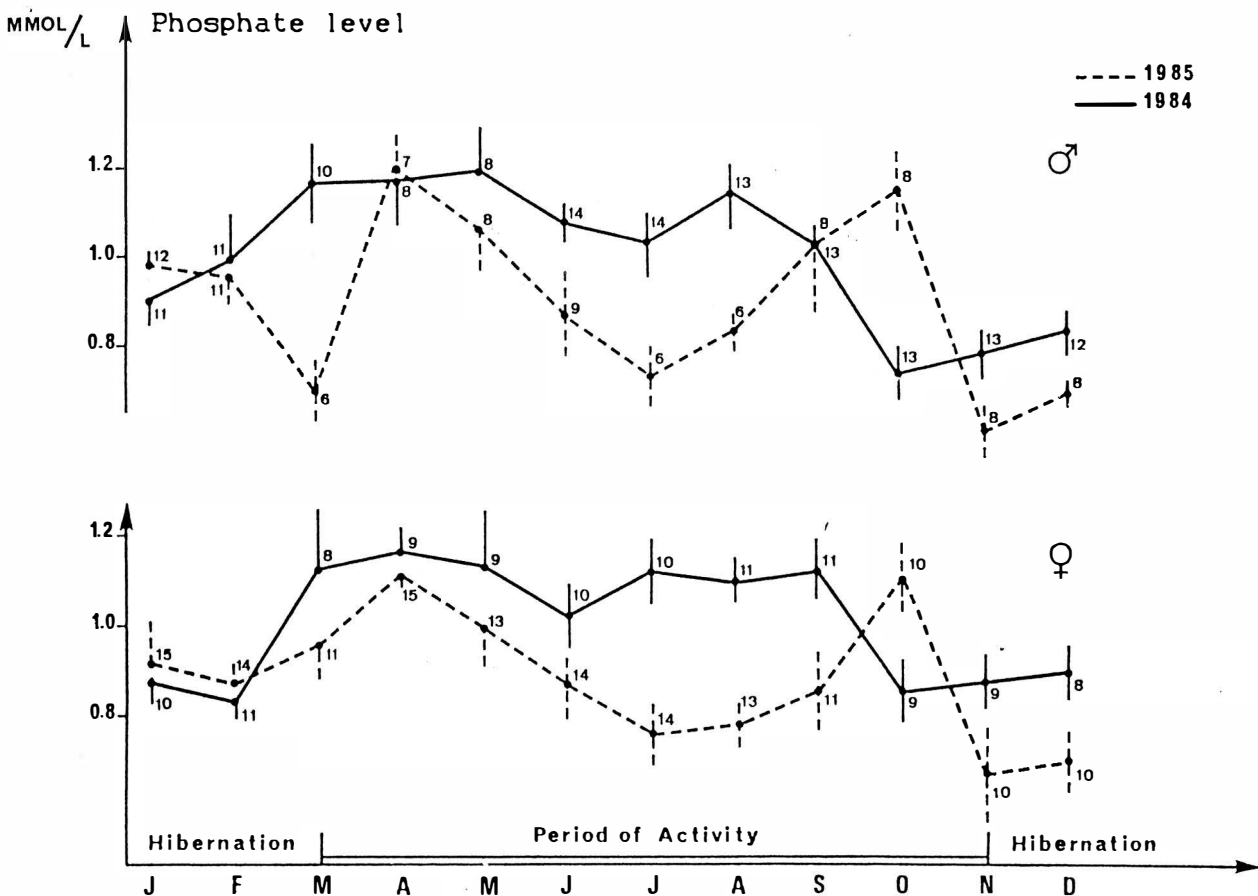

Fig. 1. Comparison of the annual variations of plasma phosphate level for the *Vipera aspis* males and non breeding females during two consecutive annual cycles, 1984 and 1985 (numbers = n; bars = ± SD).

For each annual cycle, we observed in both sexes significant monthly variations of phosphate level (*1984,* males: $F_{10,118}$ = 2.47, females: $F_{10,95}$ = 2.54, $P < 0.01$; *1985,* males: $F_{11,86}$ = 2.50, females: $F_{11,122}$ = 2.25, $P < 0.01$). The values appeared to be more elevated for the active period than for the hibernating one. A shift of one month could be observed between the two annual cycles: the phosphate level increased in March for 1984 but in April, for 1985, and decreased in September for 1984 but in October for 1985.

A comparison of the two consecutive annual cycles in females, with the test for paired series, showed differences (t = 2.20, df = 11, $P > 0.05$). For males, the differences between the two annual cycles were not significant (t-test, df = 11, $P > 0.05$).

Calcium level. In 1984, the monthly values of calcium level were not equivalent between sexes. For the non-breeding females, the calcium level showed significant variations during the annual cycle ($F_{11,116}$ = 2.40, $P < 0.01$): i.e. lower from April to August than from September to March (t = 2.57, df = 91, $P < 0.05$). For the males, the calcium level also showed significant variations during the annual cycle ($F_{11,116}$ = 1.87, $P < 0.05$). But these variations were not as well marked as for females. The calcium level increased slowly from June to November. It decreased significantly in December and remained low until February. The calcium level increased again in March (at the end of the hibernation) but decreased in April-May (Fig. 2).

In 1985, the differences of the monthly calcium levels between sexes were not so marked. They were significant only in January (n_1 = 9, n_2-n_1 = 8, U<39, $P < 0.05$) and February (n_1 = 10, n_1-n_2 = 4, U<36, $P < 0.05$) where the calcium level was higher in females. For both sexes, the calcium level values showed significant variations during the annual cycle (males: $F_{11,75}$ = 2.58, females: $F_{11,125}$ = 2.40, $P < 0.01$). Two periods could be identified. The first one — January to July — was characterized by higher values while the second period — August to December — was characterized by lower values (males: df = 85, females: df = 135; both t = 2.57, $P < 0.01$).

BREEDING FEMALES

The breeding female group had a heterogeneous origin. Differences between the laboratory born females and those that had been recently caught in nature were noticeable.

Annual variations of phosphate level. The values of phosphate level of the breeding females born in the laboratory present significant variations during the annual cycle ($F_{10,22}$ = 2.30, $P < 0.05$). The phosphate level appeared significantly higher in March or April (according to each individual), than during the rest of the year. The maximal values obtained were 2 or 3 times higher than the average measured during the rest of the year (Fig. 3).
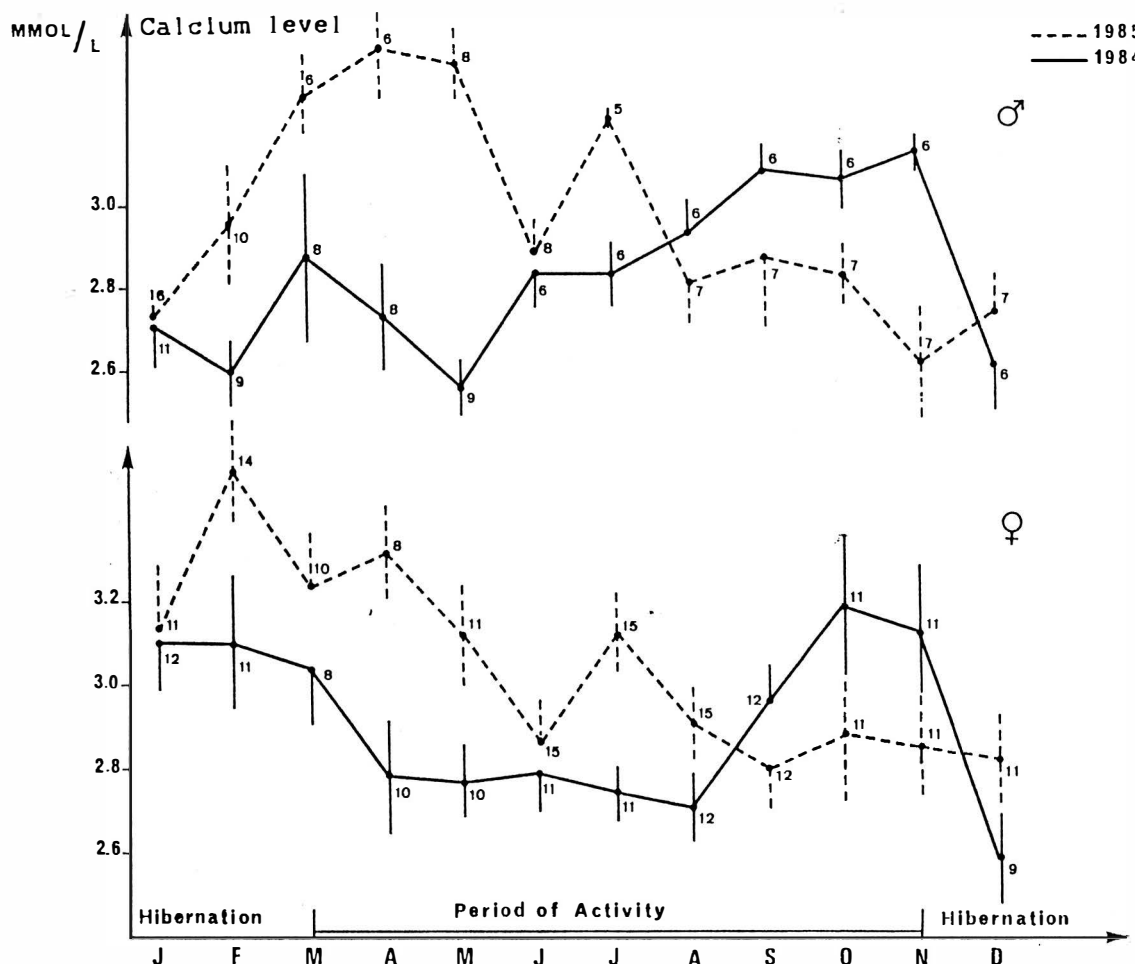

Fig. 2. Comparison of the annual variations of plasma calcium level for the *Vipera aspis* males and non breeding females during two consecutive annual cycles, 1984 and 1985 (numbers = n; bars = $\pm$ SD).
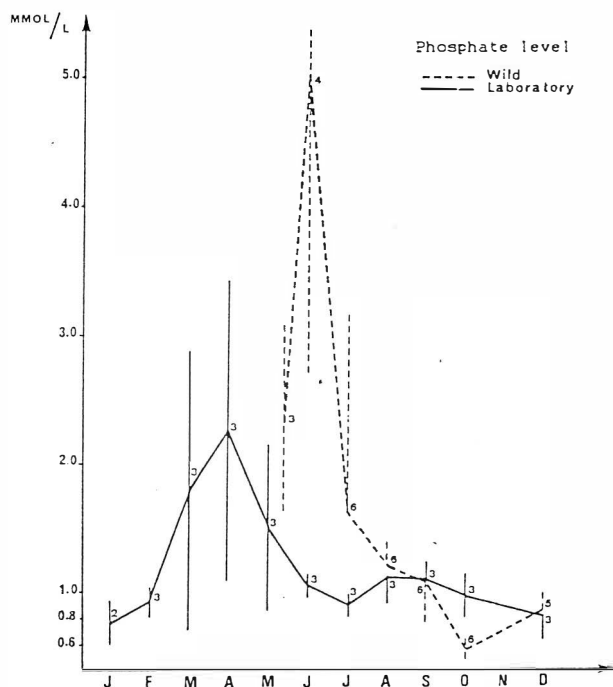
Fig. 3. Annual variation of plasma phosphate level for *Vipera aspis* breeding females. For the wild vipers, we do not possess values of phosphate level from January to April.

For the breeding females caught in nature, the phosphate level showed significant variations during the annual cycle ($F_{7.33} = 3.23$, $P < 0.01$). High values appeared in June or July, according to each individual. The maximal values obtained appeared five times higher than the average, measured for the rest of the year. For these females, we did not have the phosphate level values at the beginning of the breeding cycle (March to April).
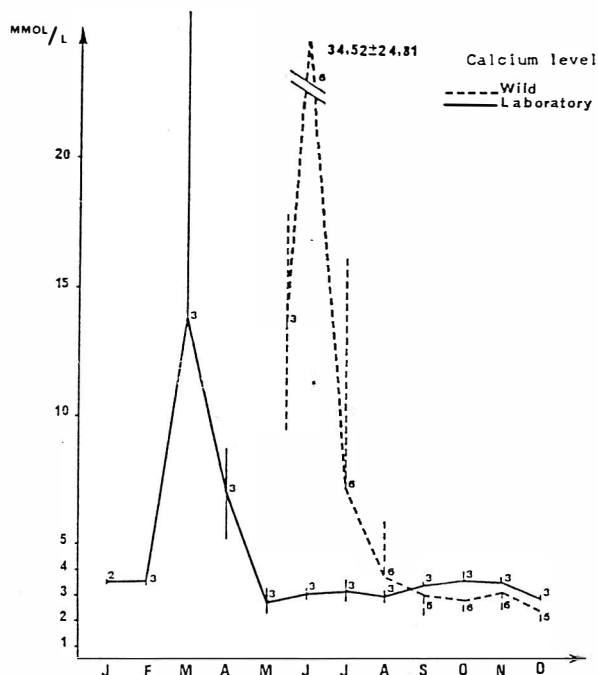

Fig. 4. Annual variation of plasma calcium level for *Vipera aspis* breeding females. For the wild vipers, we do not possess values of calcium level from January to April.

The annual variations of calcium level. The calcium level of the females born in the laboratory showed, in March or April depending on the individual, values significantly higher than the rest of the year ($F_{11.23} = 2.23$, $P < 0.05$). The maximal values were 5 or 10 times higher than the values measured for the rest of the year (Fig. 4). For the females caught in nature, the calcium level values were significantly higher in June or July than for the rest of the year ($F_{7.36} = 3.21$, $P < 0.01$). The maximal values measured were 10 or 15 times higher than the average ones obtained for the rest of the year. For these wild vipers, we did not have data for the beginning of the breeding cycle (March-April).

Thus, for plasma calcium and phosphate levels, the maximal values obtained for the females caught in nature were more elevated than those obtained for the females born in the laboratory. For each category the increase of the two parameters was synchronous each year, but we note that these peaks appeared earlier in the vipers born in the laboratory.

DISCUSSION

The results presented here, reveal important variations of plasma phosphate and calcium levels during the annual cycle, for non-breeding vipers between two consecutive years and for breeding females during the reproductive period.

CALCIUM AND PHOSPHATE LEVELS IN MALES AND NON-BREEDING FEMALES

Although the variations of plasma phosphate and calcium levels of *Vipera aspis* between the two consecutive annual cycles do not appear similar, these differences are not significant. An equivalent result has been observed in the eel (Fontaine *et al.*, 1969). Such variations appear characteristic of heterothermic vertebrates, taking into account the peculiarities of their physiology, more dependent on environmental conditions than homeothermic animals. These variations suggest that the regulation of phosphate and calcium levels in heterotherms is different than that is observed in mammals.

Although the phosphate level of plasma appears to be directly related to diet, since it increases when the vipers begin to eat during early spring, we have seen that the increase in phosphate level can be postponed, e.g. by one month in 1985. Furthermore, the yearly 7 months duration of high phosphate level values is invariable. Thus, this duration seems to be independent of variations in external conditions. Clark (1972) suggests the possibility of endocrine regulation of phosphate level in reptiles. The data concerning *Vipera aspis* tends to support this hypothesis. Pending the availability of more data, we consider that the variations of phosphate levels for the non-breeding vipers seem to be correlated with the yearly activity of the animals, the lower values always being observed during hibernation, the higher during the active season.

The variations of plasma calcium level reported here in the males of *Vipera aspis* appear to be similar to those in the frog *Rana pipiens* as reported by Robertson (1977). In *Vipera aspis*, the calcium level presents complex annual variations which are apparently difficult to link to environmental conditions or to a particular

physiological condition. The regulation of the calcium level also appears to be partially independent of the feeding season, but is probably related to endogenous factors. Such a hypothesis is supported by the fact that the calcium level for females is already high in February 1985, when the vipers are still in hibernation, and not feeding. Later, in autumn 1985, when the vipers are still actively feeding, the calcium level drops.

During the two annual cycles, calcium levels appear higher for females than for males in February and March. This could be related to a preparatory phase of vitellogenesis in the adult females. Because females do not eat during that time, the calcium needed has to be released from a mineral salt reservoir (see below).

CALCIUM AND PHOSPHATE LEVELS IN BREEDING FEMALES

We will define a breeding female as a female which, after mating, realizes a complete vitellogenesis followed by oviductal embryonic development. A non-breeding female is a female which, after hibernation, does not mate and does not carry out a complete vitellogenesis.

In our laboratory, we noted that only the females which have mated realize vitellogenesis. Considering the small size of our sample, we cannot maintain that mating is a causal factor of vitellogenesis but our experiment gives some credibility to this hypothesis. The only differences in the monthly values of calcium and phosphate levels between breeding and non-breeding females are peaks of calcium and phosphate for the breeding females. This observation is consistent with the rough data obtained by Izard, Detrait and Bocquet (1961) showing an increase of calcium and phosphate in spring, but for a sample of pooled male and female blood.

The temporal localization and the intensity of the peaks show important individual variations, independent of the origin of the vipers (laboratory or nature). This variability is demonstrated by the importance of the standard deviation observed only for the peaks. As it is not always easy to capture wild females in the beginning of the active season, we cannot establish if the increase of calcium and phosphate levels begins in May or earlier. Dessauer and Fox (1959) in a study of another snake, *Thamnophis sauritus*, showed that the increase of calcium and phosphate in the vitellus occurs "near ovulation" and not all along the period of vitellogenesis. We have shown that for females born in the laboratory, for which the timing of ovulation has not yet been determined but probably appears earlier than in wild vipers, as observed by Naulleau and Bidaud (1981), calcium and phosphate levels peak for one month, and do not last as long as the duration of vitellogenesis. Females of *Vipera aspis* in the wild ovulate in June (Saint Girons, 1957; Naulleau and Bidaud, 1981), when the peaks of plasma calcium and phosphate appear. These data suggest that the increase of calcium and phosphate levels does not last more than one month for the wild asp vipers, as for *Thamnophis sauritus*. Our results support the idea that the peaks of plasma calcium and phosphate level which only appeared in the breeding females are almost certainly linked to vitellogenesis. This phenomenon exists in all non mammalian vertebrates (see Dacke, 1979) and

corresponds to storage in the ovules of the elements needed for embryonic development (Packard, Tracy and Roth, 1977; Packard and Packard, 1984; Packard, Packard and Gutzke, 1984). The delay of two months which exists between the wild and laboratory born females is probably caused by the different living conditions of the two groups. Standardized laboratory breeding conditions in laboratory are known to influence the timing of biological events (e.g. mating, birth) (Naulleau, 1975; Naulleau and Bidaud, 1981; Castanet and Naulleau, 1985). Our laboratory conditions, conducive to an active metabolism from the beginning of March to the end of October, may explain why these biological events come sooner in the yearly cycle of laboratory specimens.

ORIGIN OF MINERAL SALTS

The mobilization of mineral ions, essentially calcium and phosphate, results from different processes, depending on the group of vertebrates considered: uptake of mineral salts from their aquatic environment for cyclostomes, chondrichthyans and amphibians (Dacke, 1979), and from scales and bone tissue in bony fishes (Fontaine, Bertrand, Lopez and Callamand, 1964; Lopez and Martelly-Bagot, 1971). Martelly et al. (1979) noticed in *Anguilla anguilla*, a direct relationship between higher serum values of calcium and phosphate and the decreasing mineralization of bone, during experimental maturity. Birds obtain mineral ions by dissolution of medullary bone (Benoit and Clavert, 1947; Meister, 1951; Simkiss, 1975; Dacke, 1979). Reptiles extract mineral salts from bone tissue and/or from endolymphatic sacs, depending on the species (Edgren, 1960; Suzuki, 1963; Dacke, 1979; Wink and Elsey, 1986).

What is the origin of the important quantity of mineral salts needed during the vitellogenesis in *Vipera aspis*? The increase of calcium and phosphate in plasma appears just at the end of the hibernating period for the females caught in nature. As most of these vipers had not eaten since the beginning of the hibernating period, four or five months before, the mineral salts in their blood must have an origin other than dietary. It is known that vipers, like most other snakes, do not possess salt reservoirs other than bone tissue (Alcobendas, 1989). Moreover, during vitellogenesis, a significant increase of bone porosity is observed in the vertebral bone of the breeding females, and in this part of the skeleton only (Alcobendas, 1989). Consequently, a close relationship can be hypothesized between vertebral bone tissue resorption and the providing of mineral salts to the vitellus in *Vipera aspis* via increased plasma calcium and phosphate levels. This process of bone resorption, in addition to a strong decrease in the degree of the vertebral bone mineralization observed during the hibernating period for all the vipers (Alcobendas and Castanet, 1985), offers a strong case that bone tissue, and especially the vertebrae, acts as the only calcium and phosphate releasing reservoir when those ions are needed by the organism of the Asp viper.

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CONTRIBUTION TO THE THERMAL ECOLOGY OF *TESTUDO MARGINATA* AND *T. HERMANNI* (CHELONIA: TESTUDINIDAE) IN SEMI-CAPTIVITY

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ABSTRACT

Data on the thermal ecology of *Testudo marginata* and *T. hermanni* are presented. The two species are eurythermic and thermoconformers. There are no differences in the thermal relations between the species.

INTRODUCTION

The majority of studies on the thermal ecology of the Reptilia concern mainly lizards, and relatively few deal with chelonians (Meek and Avery, 1988). In chelonians, thermoregulatory behaviour has been observed in all the three major life forms: terrestrial, semi-aquatic and marine (Avery, 1982). The study of chelonians' thermal relations are interesting for several reasons, such as their hemispherical shape, the very large size that some species reach and the fact that the terrestrial forms move only very slowly (Meek and Avery, 1988).

In Greece there are three terrestrial species: *Testudo graeca*, which is widespread and is found in N. Africa, the Mediterranean region, Asia Minor, Middle East and Anatolia; *T. hermanni*, which is distributed in the Balkan peninsula, southern Italy, eastern Spain and southern France; and *T. marginata*, the largest of the European species. This has a restricted distribution to the south of Mount Olympus in Greece, and Sardinia as an effect of human introduction during the past 100 years (Keymar and Weissinger, 1987). There are ecological data on the population structure, activity and thermal ecology of *T. graeca* and *T. hermanni*. However, these data are restricted to spring and summer in northern Greece.

In this work we present initial data on the thermal ecology of *T. marginata* and *T. hermanni*, which are sympatric in southern Greece, under semi-captive conditions.

METHODS

The measurements and the observations were carried out in a 150m² yard in Hymmitus mountain (Attika,Greece) from February to November 1989. The proportion of basking and shaded areas during the day was similar to the proportion in the natural habitat. Moreover the animals had the opportunity to move into suitable night-time retreats. A total of 245 body temperature measurements were taken from four (two males and two females) individuals of *T. marginata* and four (two males and two females) of *T. hermanni*. The specimens were collected from the neighbouring area and were of similar size.

Body temperatures were measured inserting an electronic thermometer into the cloaca. Then, the air temperature was measured 15 cm above the animal and the substrate temperature at the place where they were found. Also, their behaviour (basking, active, hidden) was observed and their sex was confirmed.

RESULTS

THERMOREGULATION

Average cloacal (Tb) temperatures of active male and female animals for both species are given in Table 1. There is no significant difference between their body temperatures (*T. marginata* $t = 0.77$, $P>0.05$; *T. hermanni* $t = 0.78$, $P>0.05$).

Species	Male			Female		
	Tb°C	S.D.	*N*	Tb°C	S.D.	*N*
T. marginata	25.5	6.1	74	24.7	6.6	72
T. hermanni	27.2	4.9	55	26.3	5.8	44

TABLE 1. Descriptive statistics for body (Tb) temperatures of the two sexes of *T. marginata* and *T. hermanni*. *N*: number of measurements.

Species	Tb°C			Ta°C			Ts°C			
	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	*N*
T. marginata	25.0	6.5	8.0-34.7	21.9	5.9	8.4-35.2	22.4	6.2	7.9-40.2	146
T. hermanni	26.5	5.7	14.7-33.3	23.4	5.3	14.4-35.0	24.3	5.5	17.1-38.3	99

TABLE 2. Descriptive statistics for body (Tb), air (Ta) and substrate (Ts) temperatures of *T. marginata* and *T. hermanni*. $\bar{x}$: mean values. *N*: number of measurements.

Average cloacal (Tb), air (Ta) and substrate (Ts) temperatures of active animals for both species are given in Table 2. There is no significant difference between the body temperatures of the two species ($t = 2.19$, $P>0.01$). The mean annual body temperature when the animals are active is higher than the mean annual air temperature for both species. (*T. marginata* $t = 3.57$, $P<0.05$; *T. hermanni* $t = 4.70$; $P<0.05$).

In Fig. 1 the mean monthly temperatures (body, air, substrate) are given for the two species when active. There is a significant difference in body temperature among the months (*T. marginata* ANOVA $F = 37.14$, $P<0.05$; *T. hermanni* $F = 12.03$, $P<0.05$). Using ANOVA and *t*-tests, we found that there are no significant differences in the body temperatures of *T. marginata* during the months March, April, May ($F = 3.36$, $P>0.05$), June, July, August ($F = 3.18$, $P>0.05$), November and February ($t = 0.49$, $P>0.05$). There is a significant difference between October and November ($t = 3.55$, $P<0.05$). The corresponding data for *T. hermanni* are similar; March, April, May ($F = 1.79$, $P>0.05$); June, July, August ($F = 2.8$, $P>0.05$). There is no significant difference between October and February,the beginning and the end of the hibernation period ($t = 0.41$, $P>0.05$). Therefore the data for every group of months are pooled and given in Table 3.

T. marginata was active between body temperatures of 8°C to 34.7°C. At lower temperatures the animals were inactive, whereas at temperatures higher than 35°C they retreated into the shade and continued their activity. There was no significant difference between their body temperatures when the animals basked or moved (*T. marginata* $t = 0.30$, $P>0.05$; *T. hermanni* $t = 0.19$, $P>0.05$).

The body temperatures of the *T. hermanni* individuals when active ranged between 14.7°C and 33.3°C. Regarding the upper limit, the behaviour of *T. hermanni* was the same as *T. marginata*. Below the lower limit *T. hermanni* hibernated buried in the soil.

There is a positive correlation between Tb versus Ta and Tb versus Ts when *T. marginata* is active (Tb v. Ta: $y = 5.27 + 0.9x$, $r = 0.81$, $P<0.05$; Tb v. Ts: $y = 5.75 + 0.85x$, $r = 0.82$, $P<0.05$ Fig.2). These slopes are not different from a value of one. (Tb v. Ta: $t = 1.89$, $P>0.05$; Tb v. Ts: $t = 2.86$, $P>0.05$).

Moreover, there is a positive correlation between Tb and Ta and Tb and Ts when *T. hermanni* is active (Tb v. Ta: $y = 5.46+0.9x$, $r = 0.83$, $P<0.05$; Tb v. Ts: $y = 6.86 + 0.81x$, $r = 0.58$, $P<0.05$ (Fig.3). These slopes are not
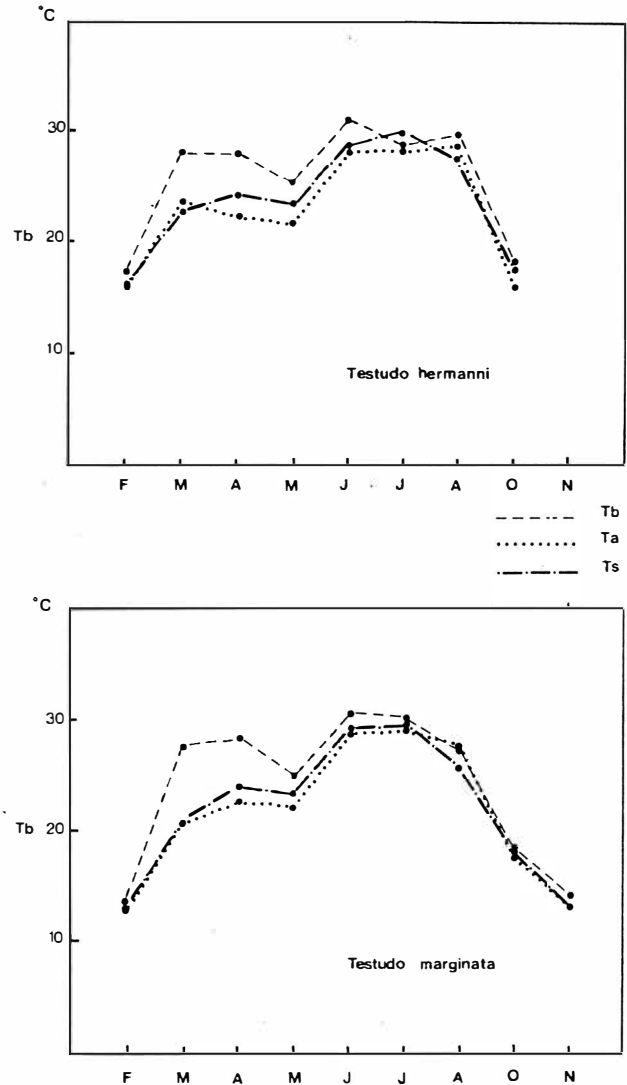
Fig. 1. Mean monthly body (Tb), air (Ta) and substrate temperatures (Ts) of *T. hermanni* and *T. marginata*.

different from a value of one (Tb v. Ta: $t = 1.41$, $P>0.05$; Tb v. Ts: $t = 2.87$, $P>0.05$).

ACTIVITY PERIOD

In spring, most of the *T. marginata* individuals are active throughout the day but there is also a high percentage of observations of inactive animals in the sun. In summer, the animals are active during the

Season	Tb°C		Ta°C		Ts°C		
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	N
T. marginata							
Spring	26.9	4.7	21.8	4.2	22.7	4.7	76
Summer	30.0	2.3	28.8	3.2	28.7	4.2	34
Autumn	18.8	1.8	17.5	1.5	18.1	1.5	20
Winter	13.6	3.0	13.6	2.9	13.1	3.2	16
T. hermanni							
Spring	27.0	5.3	22.6	4.1	23.9	4.5	56
Summer	30.0	2.3	28.5	3.0	28.7	3.8	28
before/after hibernation	18.2	2.9	19.4	2.2	17.4	3.5	15

TABLE 3. Mean body, air and substrate temperatures of *T. marginata* (top), and *T. hermanni* (bottom) among the seasons.

Fig. 2. Relationship between body temperature (Tb), and air temperature (Ta) in *T. marginata*.

Fig. 3. Relationship between body temperature (Tb), and air temperature (Ta) in *T. hermanni*.

morning and late afternoon. Inbetween, the animals were inactive. In fall, they are active from 10.00hr to 16.00hr. The same applies to *T. hermanni*. In winter the *T. hermanni* individuals hibernate buried in the soil. On the contrary, the individuals of *T. marginata* are active, depending on the weather conditions, and are never buried.
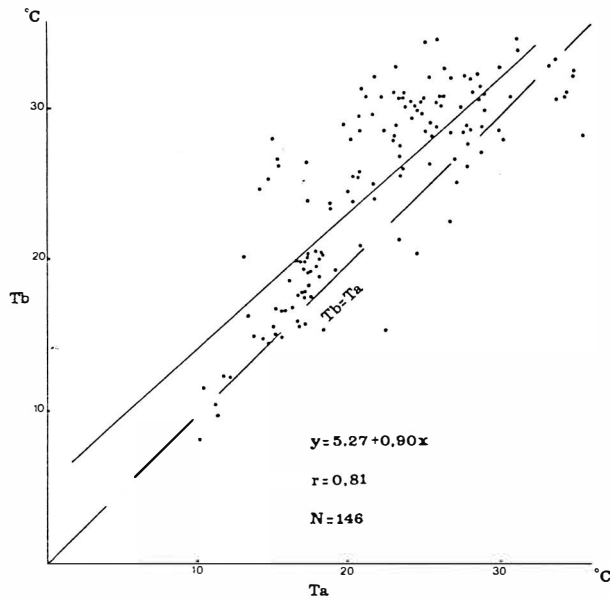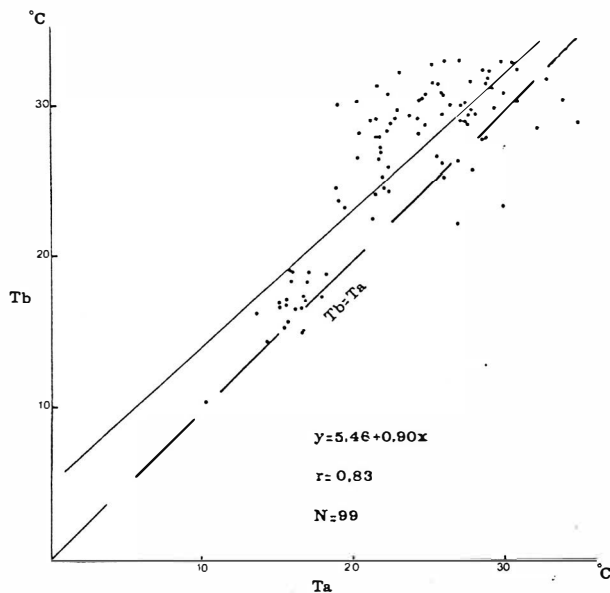
DISCUSSION

Spellerberg (1982) states that active body temperatures of Testudinidae range from 14°C to 38°C, with an average around 30°C. From our results it seems that body temperatures of *T. hermanni* vary between these limits but *T. marginata* can be active in lower body temperatures as well. Hailey *et al.* (1984) state that in French populations of *T. hermanni*, summer activity

occurred in body temperatures between 20° C and 35°C, mostly around 30°C. Meek (1988) gives for *T. hermanni* in Yugoslavia, summer body temperatures from 21°C to 34°C and in autumn from 16°C to 33°C. It is interesting that maximum body temperatures of 34°C-35°C have been measured in all the populations studied so far, except during cooler autumn weather (Meek and Avery, 1988).

Our results indicate that the two species behave mainly as thermoconformers. This is because (1) the slopes of the curves Tb v. Ta do not differ from one (Huey and Slatkin, 1976), and (2) even though the mean annual air temperature is lower than the mean annual body temperature, the mean monthly body temperatures of the specimens are similar to the corresponding air temperatures (Fig. 1) apart from those taken in the spring months.

Eurythermy and thermoconformity are good strategies for reptile species which are distributed in a climate where the environmental temperatures fluctuate widely (Huey, 1982), such as in Mediterranean ecosystems. Also, lower body-active temperatures enable the species to be active during the cool period of the year (Huey and Slatkin, 1976). These hypotheses are in agreement with our results.

The daily activity of reptiles depends on their thermal ecology (Huey, 1982). Consequently the two species regulate their activity period when the conditions are favourable for the maintenance of preferred levels of body temperatures. Therefore they avoid the midday high summer temperatures and are active in the morning and late in the afternoon. During the cooler seasons they are active in the warmer part of the day.

In conclusion, the two species seem to have the same thermal requirements apart from the fact that *T. marginata* can be active at lower body temperatures and appears to adopt a more opportunistic behaviour through the winter. The wider distribution of *T. hermanni* in northern regions seems to be related to its ability to hibernate in the soil and to thus avoid extremely low winter temperatures.

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SLEEP-LIKE BEHAVIOUR IN THE GALAPAGOS TORTOISE (*GEOCHELONE ELEPHANTOPUS*)

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ABSTRACT

Sleep-like behaviour of Galápagos tortoises (*Geochelone elephantopus*) was studied at Volcán Alcedo, Isabela Island, Galápagos Islands, Ecuador. At midday, most tortoises found asleep were in the open with head and limbs extended; during cooler evening hours, sleeping tortoises usually occupied forms with head and limbs withdrawn. Variability in sleep-like postures during different periods of inactivity probably reflects alternative thermoregulatory strategies. Forms occupied by inactive tortoises (*n* = 53) comprised vegetation (51%), soil (30%) and other tortoises (19%). The absence of native predators on Galápagos implies a thermoregulatory rather than antipredator function for form use.

INTRODUCTION

The electrophysiological and behavioural presence of sleep has been documented in several species of terrestrial chelonians (e.g., Vasilescu, 1970; Flanigan, 1974; Flanigan *et al.*, 1974; Ayala-Guerrero, 1988). However, Susic (1972) and Walker and Berger (1973) failed to detect evidence of sleep in *Caretta caretta* and *Geochelone denticulata*, respectively. Consistent with most studies of sleep in reptiles, the electrophysiological characteristics of sleep in chelonians have received more attention than behavioural or ecological aspects. Such an emphasis has emerged because of the interest of researchers in the evolution of sleep phenomena, in particular the electroencephalographic correlates of specific sleep states (see reviews by Karmanova, 1982; Meddis, 1983; Vasilescu, 1983). Consequently, all investigation of sleep in chelonians has taken place in the laboratory without corroborative field studies.

The studies above confirm that sleep in chelonians may be recognized in the field by simple behavioural criteria. Behavioural sleep is defined as behavioural quiescence associated with a stereotypic posture, an elevated arousal threshold, and rapid-state reversibility with relatively intense stimulation (Flanigan, 1974; Flanigan *et al.*, 1974). Several investigators reported that the limbs of sleeping tortoises are extended, usually posteriorly and parallel to the body axis; the head likewise is extended, and rests upon the plastron edge or substrate with the eyes closed (Flanigan, 1974; Flanigan et al., 1974; Douglass and Layne, 1978).

Under natural conditions, chelonians might exhibit much greater variability in sleep behaviour than that observed under laboratory conditions. In this paper we report and analyse our observations of sleep postures and sleep sites selected by Galápagos tortoises (*Geochelone elephantopus*) in their natural ecological setting. We further discuss how the patterns that we observed may reflect alternative thermoregulatory strategies.

METHODS

During 22-24 June 1984, we studied free-ranging tortoises (*G. e. vandenburghi*) from a large resident population (3,000-5,000 individuals; MacFarland *et al.*, 1974) on Volcán Alcedo, Isabela Island, Galápagos Islands, Ecuador. Tortoises were considered to be asleep when completely immobile with the head resting on the plastron or substrate and the eyes closed. However, without electrophysiological data we prefer to call this behaviour "sleep-like". For tortoises found in sleep-like repose, we recorded (1) whether the subject occupied a "form" (facing into a soil bank, vegetation or another tortoise; c.f. Auffenberg and Weaver, 1969; Judd and Rose, 1977; Strass *et al.*, 1982); (2) whether the head and neck were extended, partially extended or withdrawn; (3) the number of legs extended; (4) the composition of forms (soil, vegetation or another tortoise) when used; and (5) the substrate (soil or grass) upon which non-form users rested.

Observations were made at midday (1200-1400 hr) and near dusk (1650-1730 hr). Maximum and minimum daily temperatures during the study were 18.5°C and 15.6°C, respectively. Humidity ranged from 93.0% to 97.0%; all three days were mostly overcast. In several cases (<10%) we could not record all data for an individual without the risk of disturbing other nearby tortoises. Conventional two-sample chi-square tests (X^2 statistic; Siegel, 1956) were used to test for associations between variables associated with sleep-like behaviour.

RESULTS

Depending on the time of day, inactive tortoises assumed two distinctive postures: (1) at midday, most tortoises found asleep were in the open with head and limbs extended, whereas (2) during cooler evening hours, sleeping tortoises usually occupied forms with head and limbs retracted (Table 1). The substrate (soil or grass) selected by inactive tortoises in the open did not vary during these periods, nor did the composition of forms (Table 1).

Variable	Number of Tortoises		df	X^2	P
	Midday	Dusk			
Exposure					
Open	59	20	1	47.52	<0.001
Form	6	46			
Substrate					
Soil	22	14	1	3.20	0.07
Grass	26	5			
Form Composition					
Soil	3	13			
Vegetation	3	24	2	2.16	0.34
Other tortoise	0	10			
Head					
Extended	48	3			
Partially Extended	11	17	2	71.76	<0.001
Withdrawn	6	46			
Number of Legs Extended					
Zero	14	58			
One	12	7			
Two	23	2	4	64.84	<0.001
Three	15	0			
Four	4	0			

TABLE 1. Conditional cell totals for variables associated with tortoises in sleep-like repose at midday and dusk. Substrate comparisons are for tortoises in the open (non-form users).

Regardless of the time of day, the head and limbs of sleeping tortoises were more likely to be extended when in the open than when in forms, and there was a positive association between leg and head extension (Table 2). Forms occupied by tortoises during both periods combined ($n = 53$) comprised vegetation (51%), dirt (30%) and other tortoises (19%).

Variables	Number of Tortoises		df	X^2	P
Exposure X Head	Exposure				
	Open	Form			
Head Extended	50	1			
Head Partially Extended	22	6	2	81.90	<0.001
Head Withdrawn	7	45			
Exposure X Legs					
Legs Extended	54	5	1	41.37	<0.001
Legs Withdrawn	25	47			
Head X Legs	Legs				
	Extended	Withdrawn			
Head Extended	49	2			
Head Partially Extended	9	19	2	94.60	<0.001
Head Withdrawn	1	51			

TABLE 2. Conditional cell totals for variables associated with tortoises in sleep-like repose, independent of time of day.

DISCUSSION

Voigt (1975) described thermoregulatory postures in the desert tortoise (*Gopherus agassizii*) that were similar to our observations of *G. elephantopus*. At midday, when shade was often sought, heat was offloaded by extension of limbs and head; this posture was also maintained during periods of basking, when body temperatures rapidly increased. At night, heat was retained by a decrease in surface to volume ratio when the head and limbs were withdrawn. Our observations (see also Douglass and Layne, 1978; Auffenberg and Iverson, 1979) suggest that tortoises sleep much of the time when in these various postures. Hence, variation in sleep-like postures during inactivity likely reflects alternative thermoregulatory strategies.

In the absence of body temperature measurements, it cannot be determined whether the midday postures of *G. elephantopus* represented basking or shading behaviour. Considering the cool, overcast conditions at the time of our study, the tortoises were more likely trying to absorb rather than offload heat. In apparent contrast, the Aldabran tortoise (*Geochelone gigantea*), which must seek shade at midday during warm weather, remains active throughout cool, cloudy days (Swingland and Frazier, 1980).

The use of forms may reduce overnight heat loss from convection, conduction and radiation, and may reduce water loss as well (Auffenburg and Weaver, 1969; Judd and Rose, 1977). Forms may also provide concealment from predators during periods of inactivity (Strass *et al.*, 1982). Because native predators are absent from Galápagos (MacFarland et al. 1974), a thermoregulatory function for form use seems most plausible for Galápagos tortoises; however, antipredator strategies are still retained by *G. elephantopus* (Hayes *et al.*, 1988). Our observation that tortoises frequently aggregate at night suggests a possible thermoregulatory function similar to form use. Boersma (1982) found that aggregates of marine iguanas (*Amblyrhynchus cristatus*), also endemic to Galápagos, maintained higher overnight temperatures than solitary iguanas, as observed likewise in other reptile groups.

Maximization of heat retention during nocturnal inactivity may facilitate increased morning foraging time. Marlow (in Huey, 1982) found that burrow use by *G. agassizii* at night appeared to decrease morning basking time and increase foraging time relative to more exposed form users (see also McGinnis and Voigt, 1971). Heat conservation at night may also facilitate digestion and reduce vulnerability to predation (Boersma, 1982).

With the exception of studies by Susic (1972) and Walker and Berger (1973), there is ample evidence for behavioural sleep in chelonians. Walker and Berger (1973, 1980) argue that sleep in reptiles is merely an ectothermic manifestation of thermoregulatory behaviour, and not actual sleep. However, sleep and thermoregulation certainly are not exclusive activities in birds (Amlaner and Ball, 1983) or mammals (Walker and Berger, 1980), and recent electrophysiological evidence also refutes the position of Walker and Berger (Hartse and Rechtshaffen, 1982). Accordingly, we suspect that thermoregulation is a dynamic and integral aspect of reptilian sleep, both processes serving unique but complementary functions. The relationship between reptilian sleep and thermoregulation merits further investigation.

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BREEDING PATTERNS IN A FRINGE POPULATION OF FIRE SALAMANDERS, *SALAMANDRA SALAMANDRA*

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ABSTRACT

The fire salamander, *Salamandra salamandra,* population on Mt. Carmel was studied for 15 years. This is a particularly interesting population as it inhabits the southern-most habitat in which this species is found in Israel, and thus the south-eastern fringe area of its entire palaearctic distribution.

The ovoviviparous female breeds during both November and December. The November cohort is likely to die of desiccation as the ponds dry out due to interrupted rains. Only every third year (on average) is November wet enough to enable the ponds to contain enough water, to give the larvae a chance to survive to metamorphosis. Some of these larvae will have an advantage, due to their cannibalistic traits enabling them to prey on the later larval cohorts of December. These cannibalistic larvae develop rapidly and metamorphose at a greater size than the average larvae.

The survival of this salamander population depends on a balance between two conflicting strategies: early breeding and late breeding. The first is advantageous during years with early winter rains when the larvae can survive long enough to be able to prey upon the later larval cohorts. On the other hand, late breeding is advantageous in dry years when larvae in the early cohorts die of desiccation.

INTRODUCTION

The fire salamander, *Salamandra salamandra*, is found in Israel in three disjunct populations. The main population is located in the mountains of the Western and Central Galil (Degani and Warburg, 1978). In addition there are two smaller areas, separated from the main area: one to the northeast, and the other to the southwest of the main area. The first area is located in the north-eastern part of Israel at Tel Dan at the foot of Mt. Hermon (Degani and Mendelssohn, 1982). The second area is located south of the main one, in the northern part of Mt. Carmel (Warburg, 1986 a,b).

The population of salamanders on Mt. Carmel comprises the southeastern limit of its palaearctic distribution. Therefore, it is a fringe population inhabiting an area where conditions are presumably suboptimal to the animals. Otherwise, this species could just as well have penetrated other mountain ranges in the Mediterranean region of central Israel: Samaria and Judea where they are not found. Other palaearctic species of animals (or plants) have succeeded in colonizing this area (Yom — Tov and Tchernov, 1988).

The fact that the salamanders are not found south of Mt. Carmel is of interest, and provided the main stimulus for studying this isolated population for such a long period. It seems that salamanders in this area may have to cope, at times, with unsuitable conditions otherwise not encountered by their conspecifics inhabiting more favourable environments in the Galil mountains or in the center of the species' distribution (i.e. in Central Europe: Joly, 1968; Klewen, 1985).

MATERIALS AND METHODS

The study area was south of Haifa on the top of Mt. Carmel located towards its western slopes. The area surrounds four rock pools which are one of the main breeding sites for the salamanders in this area. The study started in 1974 and continues to the present day (1990). Animals were captured throughout the breeding season on stormy nights, immediately at the beginning of the rainy season (October or November). This continued for 9-10 weeks throughout the entire breeding season: from mid-October to the beginning of January.

The animals were identified individually by their typical yellow patterns. Their sex was determined by cloacal examination (see Warburg *et al.*, 1978/79), they were weighed, measured, photographed and finally released back into their habitat either during the same night or on the following night. As the yellow patterns on a black background on the dorsal side of the salamander hardly change throughout its lifetime, the salamander could be easily recognized throughout the study period by their photographs.

RESULTS

One hundred and twenty salamanders were captured during the 15 years of study. The average sex ratio was 1.5 male to 1 female. The pattern of capture shows that slightly more female salamanders were captured in December as compared to October-November (Fig. 1). Eighteen females were recaptured over the years. The females very rarely appeared more than once during the same breeding season. During the course of the study, only four females appeared twice during the same breeding season.

The females entered the ponds as soon as they arrived at the breeding site. They would then release their ova and the larvae hatched immediately upon contact with the water. The males rest on higher observation posts (stones, logs etc.), surrounding the ponds and will mate with the females upon their emergence from the ponds. The breeding pattern of the females (n = 42), shows an almost even distribution between the two main months of the breeding season: November and December (Table 1).
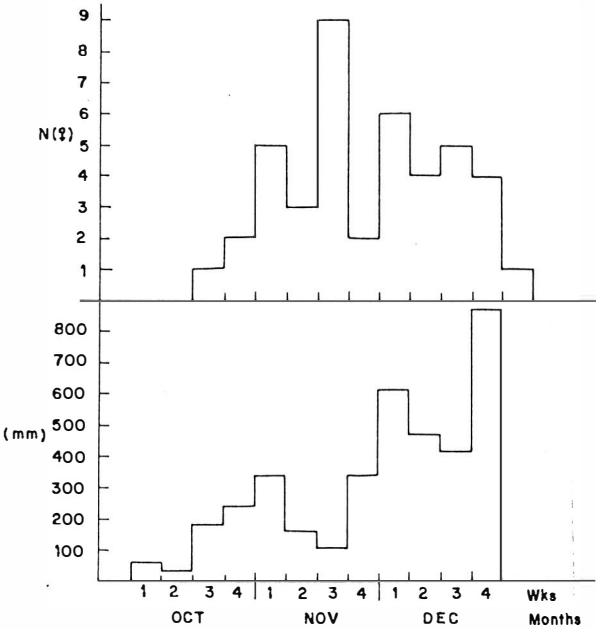
Fig. 1. Breeding patterns (top) of *Salamandra* females. on Mt. Carmel over a period of 15 years. Precipitation is given for the same period (bottom).

During October-November when the rainy period starts, the dry ground is not yet soaked with water. The soil dries out whenever there is a pause in the rains which happens quite often during this period (Table 2). Thus, there is a rather good chance that the early larvae deposited in October-November will die of desiccation (Fig. 2). If the break in the rains is not longer than 7-10 days, the larvae could survive on the mud under the stones. Throughout the study period, ten Novembers out of fifteen (2/3) were drier than December months (Table 2). December received on average about twice as much rainfall as compared to November (Table 2, Fig. 1). During December the soil is saturated with water, and less likely to dry out especially as December temperatures are lower than those of November. Thus the larvae deposited during December do not die because of desiccation as the ponds remain filled with water.

The survival of *Salamandra* on Mt. Carmel is a result of adaptation to two main factors: food and weather (Table 3). If food is scarce more larvae may become cannibalistic. If rains come early and in sufficient quantity, the early (November) larvae will survive. However, if rains are late, the November larvae will die, and only the late (December) larvae will survive (Table 3).

DISCUSSION

The breeding migration and the appearance of salamanders near the ponds depends on the first heavy rains towards the end of autumn. In *Ambystoma talpoideum*, it seems that the breeding migration is related to the cumulative rainfall during the breeding period (Semlitsch, 1985). Migration during the breeding season in *Ambystoma macrodactylum*, takes place on rainy nights after heavy rains (Anderson, 1967; Beneski, Zalisko and Larsen, 1986) much like here.

Larvae hatch out of the egg envelope immediately upon contact with water, (Warburg, Degani and

Months	OCT.	NOV.	DEC.	JAN.	Total
Weeks					
1		5	6	1	
2		3	4		
3	1	9	5		
4	2	2	4		
Total	3	19	19	1	42
(in %)	7.2	45.2	45.2	2.4	100

TABLE 1: The number of females bearing young and the date they gave birth.

	IX	X	XI	XII	I	II	III	IV	V	Total
					(1973/4-1988/9) (in mm)					
1973/4	0	20.0	151.0	36.0	309.0	65.0	40.0	38.0	0	659.0
1974/5	0	0	67.0	403.0	116.0	176.0	46.0	0	0	808.0
1975/6	0	3.0	69.0	231.0	80.0	157.0	62.0	41.0	6.0	649.0
1976/7	0	54.0	184.0	162.0	150.0	55.0	142.0	125.0	0	872.0
1977/8	0	54.0	28.0	354.0	164.0	41.0	73.0	10.0	0	724.0
1978/9	0	38.0	36.0	223.0	101.0	54.0	65.0	16.0	3.0	536.0
1979/80	0	70.0	94.0	270.0	208.0	174.0	59.0	48.0	0	923.0
1980/1	0	32.0	2.0	181.0	224.0	99.0	70.0	15.0	0	623.0
1981/2	0	13.0	116.0	25.0	57.0	156.0	65.0	6.0	3.5	441.0
1982/3	0	1.0	173.0	220.0	206.0	154.0	110.0	3.0	5.0	872.0
1983/4	0	3.0	177.0	30.0	107.0	53.0	84.0	59.0	0	513.0
1984/5	0	45.0	97.0	123.0	77.0	156.0	9.0	102.0	0	609.0
1985/6	0	47.0	51.0	171.0	100.0	141.0	24.0	24.0	28.0	586.0
1986/7	1.0	31.0	287.0	198.0	105.0	46.0	97.0	16.0	2.0	783.0
1987/8	0	104.0	18.0	365.0	167.0	197.0	91.0	9.0	0	951.0
1988/9	0	8.0	65.0	165.0	*	*	*	*	*	*
Average	0	32.7	100.9	197.3	144.7	114.9	69.1	34.1	3.2	703.3
(n)	(16)	(16)	(16)	(15)	(15)	(15)	(15)	(15)	(15)	(15)

TABLE 2: Average Monthly Rainfall in Beit Oren (near Damun) on Mt. Carmel. (Data Courtesy of the Israel Meteorological Service, Beit Dagan.)
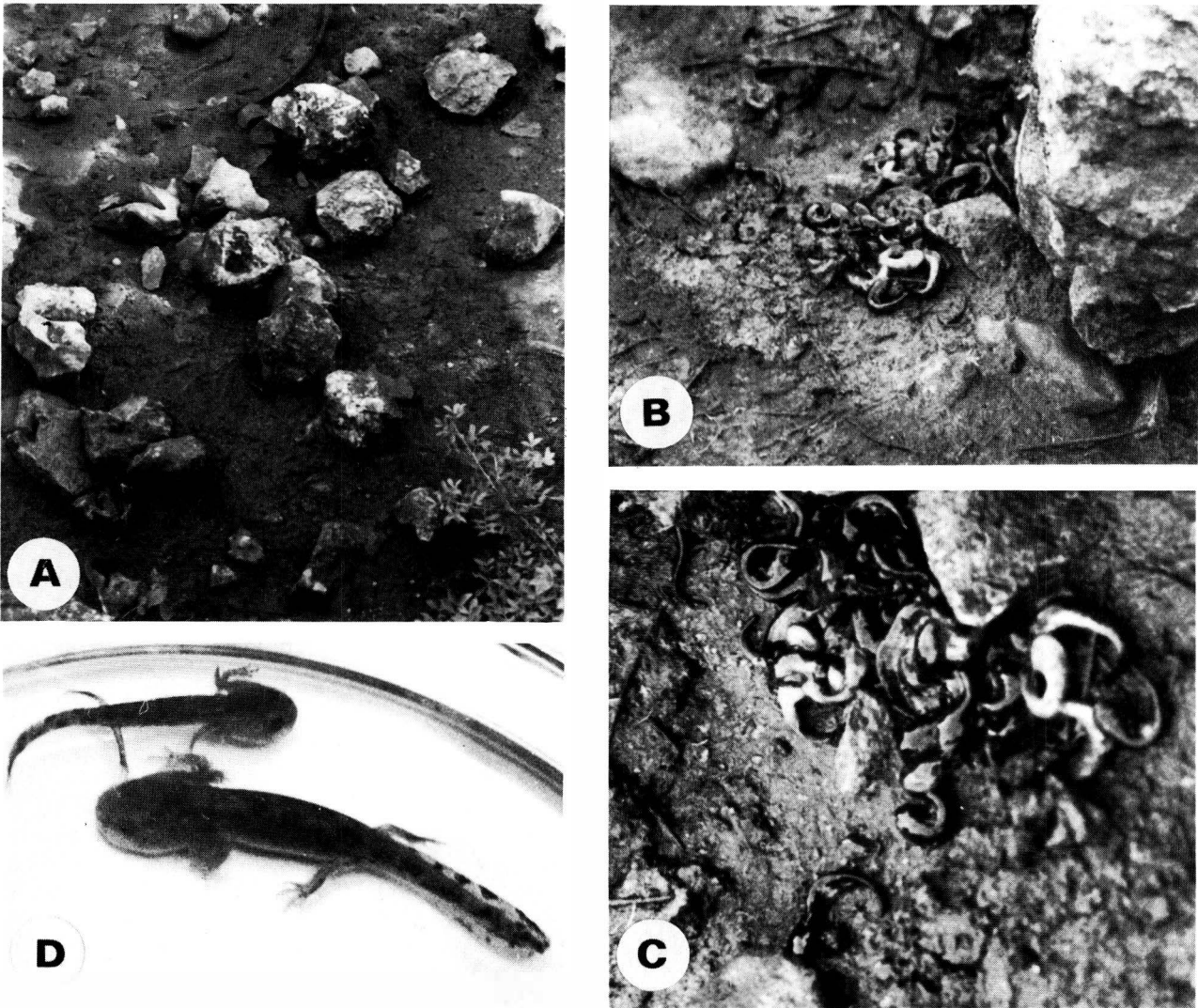
Fig. 2. Photograph of the dry breeding ponds on Mt. Carmel (A). Salamander larvae were found on the mud under a stone in a dry pond. The larvae were still alive and survived later in the lab (B,C). Five-week old larvae belonging to the same batch raised without extra food, one of them cannibalistic (D).

FOOD		WEATHER			
		NOVEMBER BREEDING		DECEMBER BREEDING	
Egg		Egg		Egg	
Larvae		Larvae		Larvae	
Food Scarce	Food Abundant	Dry November	Rainy November	Dry November	Rainy November
|	|	|	|	|	|
Development Retarded	Development Rapid (no cannibalism)	Larvae Survive 1 wk, on mud	Increased Cannibalism	Food Abundant (Due to enriched organic matter from dead November larvae)	Larvae Provide Prey for November Larvae
|	|	| |	|		|
Late Metamorphosis	Early Metamorphosis	Rains No Rains	Development Rapid		No Survivors
|		| |	|	|	
Small Juveniles (except for cannibals)	Normal Juveniles	Larvae Larvae Survive Perish	Early Metamorphosis	Rapid Development (No cannibalism)	
		|	|	|	
		Increased Cannibalism	Large Juveniles	Normal Juveniles	
		|			
		Late Metamorphosis			
		|			
		Few Large Juveniles			

TABLE 3: Factors affecting survival of *Salamandra salamandra* larvae in rock-pools on Mt. Carmel.

Warburg, 1978/79). Duration of larval deposition lasts mostly up to one hour, sometimes longer up to a few hours, and on rare occasions (in the lab), even up to four days (Warburg et al., 1978/79). If the same pattern occurs in nature it could explain why some females visit the pond more than once during the same season possibly releasing larvae on each occasion.

In a permanent water body at Tel Dan in the Upper Galil, the salamanders seem to be active throughout the year (Degani and Mendelssohn, 1982), and thus their breeding season may extend into spring. Similarly, in Europe the breeding season may extend over a period of five months (Zakrzewski, 1970). In the centre of its distribution *Salamandra* larvae metamorphose after 12-16 weeks (Zakrzewsky, 1970), whereas larvae on Mt. Carmel metamorphosed normally after 6-8 weeks.

We have recently attempted to estimate the longevity of the salamanders on Mt. Carmel (Warburg in prep). The estimate is based on the growth rate of a juvenile salamander (a male) born and raised in the lab. After three years it was released into the breeding site from where its mother had originated. This salamander was recaptured several times since, and its growth rate can give an indication of the general growth rate of these salamanders in their natural habitat on Mt. Carmel. Furthermore, a skeletochronological investigation of the same population (currently in progress) indicates a similar pattern (Warburg, in prep).

Based on these techniques of estimating longevity, we can assume that the average age of the salamanders on Mt. Carmel is about 10.5 years (about 6 years old when first captured, and then recaptured for another 4.5 years on average, Warburg, in prep.). We can also assume that the females reach their reproductive stage when they first appear at the ponds (at the age of 6). If so, they probably continue to breed for at least four years (We found females that were captured year after year and bred in the lab each time.) As the average brood is about 100 larvae (Warburg, et al., 1978/79, the latest figure obtained since then, is 98 larvae averaged from 22 batches), a female can produce (at least) a total of about 400 larvae throughout her reproductive life.

From previous studies we have found that in almost every cohort there are a few cannibalistic larvae growing much faster than the other larvae in the same cohort (Degani, Goldenberg and Warburg, 1980 and Figs. 2, 3). Preliminary studies have shown that the cannibalistic larva is found more often in larval cohorts of October-November. On the other hand cannibalism can also be artificially induced by selectively feeding a larva more frequently. This causes the larva to grow faster than other larvae in the same batch and it will become cannibalistic.

As was shown in *Hynobius* larvae (Kusano, Kusano and Myawaki, 1985), cannibalism depends on the difference in size of the larvae. The cannibalistic morphs of *Ambystoma tigrinum* larvae developed faster than the normal larvae (Lannoo and Bachmann, 1984). Survival of *Ambystoma maculatum* larvae depended greatly on their developmental rates (Shoop, 1974). The larger larvae of *Ambystoma tigrinum* metamorphosed at a larger size, and were therefore less vulnerable (Rose and Armentrout, 1976). Moreover, these larvae eventually became larger adults (Semlitsch, Scott and Pechmann, 1988). On the other hand, *Ambystoma talpoideum*
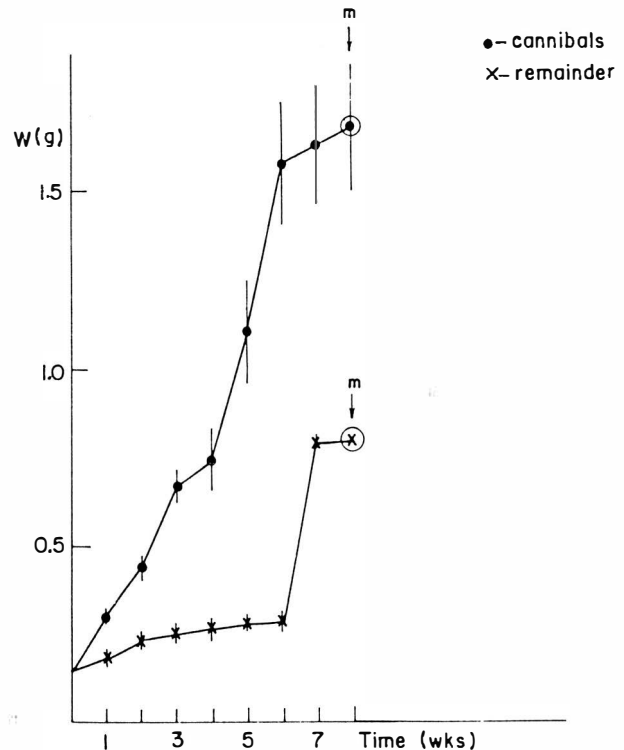

Fig. 3. Growth of *Salamandra* larvae belonging to the same cohort. Cannibalistic larvae grow much faster than the remainder, and metamorphose at a larger size. Cannibalism appears also in the remaining larvae after 6 wks. (± SE). m — date of metamorphosis.

metamorphosed later in the season (thus larval life is prolonged), but metamorphs were not significantly larger (Semlitsch, 1987; Semlitsch et al., 1988). In anurans (*Scaphiopus couchi*), there is a positive correlation between size at metamorphosis and length of larval period (Travis, 1984; Newman, 1989).

In only about a third of the 15 year period of study was November rainy enough to enable the ponds to contain water during the dry intervals between the rains (Tables 1,2). Therefore, only about 33% of the progeny of females breeding in November would survive. Most of the time (2 out of 3 years), the ponds are likely to dry out before the larvae had a chance to metamorphose. Larvae deposited during these "wet Novembers" will have the best chance to survive as they will become cannibalistic, and will feed largely on the later December cohorts. In such years (of wet Novembers), only few of the December larval cohorts will have a chance to survive (Table 3).

If the female is always an early (November) breeder, and as only every 3rd or 4th year will have a wet November, then one out of four breeding efforts is likely to be successful.

On the other hand if the female is a late December breeder two-thirds of her progeny may have a chance of survival. This is because the "dry" November larval batches will not survive, and thus the ponds are free of a major predator. In that case they may have a shorter period to develop possibly resulting in smaller metamorphs.

In other amphibians leading a precarious life in deserts, longevity is the key factor enabling the survival of the population (e.g. *Bufo punctatus*, Tevis, 1966). In

Scaphiopus couchi, less than 10% of the ponds produced metamorphs, largely because of early desiccation (Newman, 1987). It seems therefore that early breeding is of sufficient selective advantage every third year on average, to maintain this trait in this fringe population of *Salamandra* population on Mt. Carmel.

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SHORT NOTES

NEW RECORDS OF MOROCCAN HERPETOFAUNA

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Information concerning the distribution of Moroccan amphibians and reptiles was summarized by Bons (1967). Since this date numerous new data have been published describing increases in distribution ranges of many species. This new information has been compiled recently by Mellado and Dakki (1988), although new data is constantly being published (see Schouten and Thevenot, 1988; Destre *et al.*, 1989; Valverde, 1989a, b; Mellado and Olmedo, 1990).

This note presents more new data concerning herpetofaunal distribution in former Morocco (Western Sahara excluded) and describes (1) considerable increases in the distribution of some species, (2) new localities for some species, and (3) the confirmation of the existence of some species in previously poorly surveyed areas. These records have been selected from a considerable amount of new observations made by the authors since 1982, in addition to existing material deposited since 1952 in the collection at the Estacion Biologica de Doñana, Seville. The latter has been recently described by Ignacio de la Riva and the second author of this note (in preparation). In Table I appears a list of 45 new localities for 29 species of Moroccan herps, whose geographic situation is mapped (Fig. 1).

Species	Date	Location	Code	Observers
Pleurodeles waltl (Salamandridae)	240486	Puente fomento (Chechaouen)	1	JAM*
,, ,,	050686	Talamagait	5	JAM
Salamandra salamandra (Salamandridae)	170587	Djebel Bouhalla (Chechaouen)	2	CI&LLJ*
Alytes obstetricans (Discoglossidae)	210582	Djebel Tazekka (Taza)	15	JM&GO
Discoglossus pictus (Discoglossidae)	001186	Ouled berrehil (Taroudant)	29	JM&LJ
,, ,,	110587	Cascade de Ouzoud (Azilal)	18	JAM&IR*
,, ,,	080587	Agoudal	19	JAM&IR*
Bufo bufo (Bufonidae)	090587	El Ksiba	17	JAM&IR*
,, ,,	010687	Taforaet	9	JM
Blanus cinereus (Amphisbaenidae)	280382	Bab Bou Idir (Taza)	14	GO&JM
Trogonophis wiegmanni (Trogonophidae)	000062	Sidi Ifni	31	RT*
Gekonia chazaliae (Gekkonidae)	090566	Inezzgane	30	EK*
Hemidactylus turcicus (Gekkonidae)	150778	Peñon de Alhucemas	4	AJ
Ptyodactylus oudrii (Gekkonidae)	080587	Tizi tirherhouzine (Agoudal)	20	JAM&IR*
Quedenfeldtia trachyblepharus (Gekkonidae)	080587	Tizi Tirherhouzine (Agoudal)	20	JAM&IR*
Saurodactylus mauritanicus (Gekkonidae)	010789	Souk el Had (Mrirt)	16	JAM&JM
,, ,,	040686	Talamagait	5	FFP&JAM*
,, ,,	000489	Torres de Alcalá	3	JAM
Stenodactylus petriei (Gekkonidae)	250389	Erg Chebbi (Merzouga)	24	MG
Tarentola annularis (Gekkonidae)	051165	Mulekta (Zag)	33	JAV*
Tropiocolotes tripolitanus (Gekkonidae)	000066	Inezzgane	30	EK*
Uromastix acanthinurus (Agamidae)	310161	Zaîo	7	AP*
,, ,,	070586	Mechra Hommadi	8	LLJ&JAM*
Chalcides mauritanicus (Scincidae)	000061	Beni Enzar	6	AP*
Sphenops boulengeri (Scincidae)	000461	Figuig	25	AP*
,, ,,	030587	Erg Chebbi (Merzouga)	24	JAM&IR*
,, ,,	160388	Tamgrout	26	LJ&JM
Mesalina rubropunctata (Lacertidae)	220786	Ouarzazate	27	AM*
,, ,,	160487	Erg Chebbi (Merzouga)	24	JM
,, ,,	230388	Erfoud	22	LJ&JM
Podarcis perspicillata (Lacertidae)	070587	Oued Todra (Tinerhir)	21	JAM&IR*
Ophisops occidentalis (Lacertidae)	060687	Oued Betoun (El Ateuf)	12	IR*
,, ,,	190487	Ain Beni Mathar	11	JM
Psammodromus algirus (Lacertidae)	030587	Rissani	23	JAM&IR
,, ,,	190263	Sidi Ifni	31	RT
Psammodromus blanci (Lacertidae)	060489	Col de Jerada (Jerada)	10	LJ&JM
Ophisaurus koellikeri (Anguidae)	120582	Debdou	13	GO&JM
Varanus griseus (Varanidae)	040587	Erg Chebbi (Merzouga)	24	IR&JAM
,, ,,	140486	Tamgrout	26	JM
,, ,,	000084	Tan Tan	32	LLJ&JAM
Eryx jaculus (Boidae)	000852	Zaîo	7	AP*
Boaedon fuliginosum (Colubridae)	000070	Aoulouz	28	JU&MU
Psammophis sibilans (Colubridae)	260490	Ouarzazate	27	LLJ&JAM
Bitis arietans (Viperidae)	000070	Aoulouz	28	JU&MU
,, ,,	000085	Ouled Berehil (Taroudant)	29	JU&MU

TABLE 1 (previous page). List of new localities of Moroccan amphibian and reptile species. Indicated are the dates of observation or capture, the name of the location, the coding assigned to these locations in Fig. 1., and the observers' initials. The initials JM and JAM refer to the authors, and the remaining to those named in the acknowledgements. Species are named according to Mellado and Dakki (1988). Observations marked * denote specimens preserved in the collection of the Estación Biológica de Doñana, Seville.
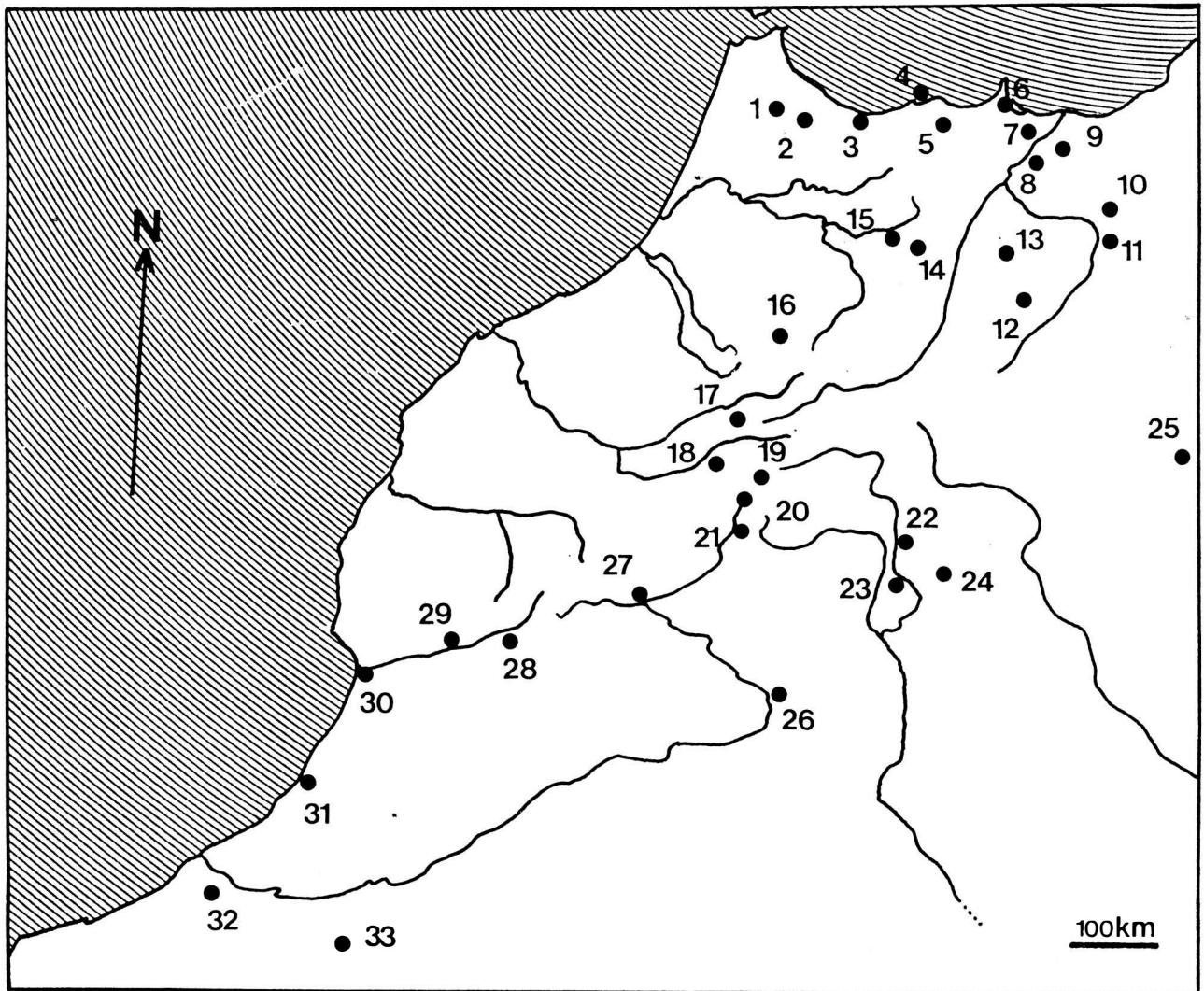

Fig. 1. Shows the geographical location of the sites appearing in Table 1.

These data reveal important increases in previously know distributions for nine species. Thus, amongst amphibians, *Pleurodeles waltl* expands its range to the east, now occupying the whole of the Rif mountains. *Discoglossus pictus* appears in the Souss Valley. *Bufo bufo* is detected in an isolated eastern locality (Djebel Beni Snassen) situated between the principal core areas of this species in Atlantic Morocco and Algeria (Doumergue, 1901; Pasteur and Bons, 1959). Amongst reptile species, *Saurodactylus mauritanicus* has a disjointed distribution with two core areas, one in the SW and the other in the NE of the country. These new data enlarge these existing areas to the north and the west respectively. *Mesalina rubropunctata* is expanding the northern limit of its known area. *Psammodromus algirus* is extending its distribution towards the south, both on the Atlantic coast (Sidi Ifni) and in the interior, penetrating the Sahara by means of the oases (Rissani). Particularly outstanding is the case of *Sphenops boulengeri*, whose range is expanding some 400 km to the west, reaching the upper Draa valley. *Ophisaurus koellikeri* appears in an isolated locality (Gada de Debdou), which now constitutes the eastern boundary of

its range. Finally, *Eryx jaculus* now appears as far north as Morocco (where previously it was only known in Hauts Plateaux, Bons, 1967) as in the Oran region of Algeria (Doumergue, 1901).

Expansions of lesser importance appear in a further six species. *Blanus cinereus* extends its area to the east. *Trogonophis wiegmanni* advances to the south along the Atlantic coast. *Geckonia chazaliae* now reaches the mouth of the river Souss. *Uromastix acanthinurus*, a typical desert species, now appears in semi-arid ecosystems in the NE, very close to the Mediterranean coast. *Chalcides mauritanicus*, a species previously only known in a single site in Morocco (Mellado, Caputo and Nascetti, 1987), reaches on the west the foothills of the Rif mountains. *Podarcis perspicillata* confirms its presence in the pre-desert zones on the southern slopes of the High Atlas.

Amongst the species with few recorded localities in the study area, new data for a further eleven species are presented (note however that some of the species considered in the above paragraphs, e.g., *Chalcides mauritanicus*, are also found in few localities). Amphibians include *Salamandra salamandra* (five

localities previously recorded; Pasteur and Bons, 1959) and *Alytes obstetricans* (previously only observed in the Rif mountains and since found by Libis, 1984, in Middle Atlas). Reptiles include *Hemidactylus turcicus*, before only cited in three places: Casablanca, Ouezanne (Pasteur and Bons, 1960) and *Lixus* (Stemmler and Hotz, 1972). *Stenodactylus petriei*, was only known from three localities: Meski, Bou Denib and to the north of Erfoud (Bons, 1967; Stemmler and Hotz, 1972). *Tarentola annularis* was present in a single place (close to Tarfaya; Joger, 1984). *Ophisops occidentalis* and *Psammodromus blanci*, each previously recorded in only two localities respectively (Bons, 1967). *Varanus griseus* was previously present in only six places (Bons, 1959). Amongst snakes, *Boaedon fuliginosum* only had three previous recordings (Bons, 1967). *Psammophis sibilans* has recently been discovered in a single Moroccan locality (Valverde, 1989a) whereas *Bitis arietans* had only two previously known locations (Bons, 1967).

Included finally are a group of localities confirming the presence of some species in previously poorly surveyed zones within their distribution ranges. Such is the case with *D. pictus*, *B. bufo*, *Quendenfeldtia trachyblepharus* and *Ptyodactylus oudrii* in the central High Atlas, with *Tropiocolotes tripolitanus* in the Souss valley and with *V. griseus* in the upper Draa valley.

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MYCOPHAGY IN A FOSSORIAL MICROHYLID *COPIULA FISTULANS* IN NEW GUINEA

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This work resulted from the observation of a captive *Copiula fistulans* (Menzies and Tyler) eating carrion. The diet of microhylids is generally unknown but frequently hypothesised to include small arthropods such as ants and termites (Emerson, 1985; Menzies, 1976; Zweifel and Tyler, 1982; Zweifel, 1972). Frogs usually only eat live moving prey, using the prey's movement as the stimulus to the feeding response (Ingle, 1971; Tyler, 1976). It therefore appeared that *C. fistulans* was using a stimulus other than movement and that its diet could be unusual. Examination of the stomach contents of other specimens revealed large quantities of non-animal matter.

Frogs were collected at various locations within 30 kilometres of Lae (Morobe Province, Papua New Guinea) and killed by freezing as soon as possible after capture (usually within 30 minutes, but occasionally up to two hours after capture) to halt digestion of stomach contents. Stomach contents were examined under a binocular microscope with an ocular micrometer. Relative masses of stomach contents were estimated visually, and arthropods were measured, counted and identified as far as possible.

Observations on captive frogs were made over a period of approximately one year, during which time the frogs were housed in a glass aquarium 70cm x 30cm x 40cm high furnished with soil and rocks and a bowl of water. Observations were made at night in a darkened

room using a flashlight. The frogs became accustomed to the flashlight and disturbance.

In captivity the frogs were observed to eat live grasshoppers, dead grasshoppers, a dead decomposing earthworm, small unidentified arthropods (1mm long), fungi and butcher's saw-mince. Butcher's saw-mince comprises the particles of meat and bone which are a by-product from sawing up frozen meat.

The stomach contents of 10 frogs were examined (Table 1). "Stomach full" is a subjective judgement. However it is considered to be an accurate evaluation of the frog's feeding state as the spherical shape of a full stomach is easily distinguished from the elongated shape of an empty stomach. In view of the small sample size the relative volume of animal to vegetable matter was not measured or estimated with any degree of accuracy. However, the quantity of non-animal matter was such that it is most unlikely to have been ingested accidentally. Furthermore, most of the vegetable matter could be identified as gill-fungi (Order Agaricales, Class Hymenomycetes, Subdivision Basidiomycotia), with a cap diameter of from 3 to 22mm. Four out of ten frogs had large quantities of fungal tissue in the gut, while another two had much mucous material in the gut, which was probably partly-digested fungus.

These observations raise two points worthy of discussion, firstly the use of olfaction as a feeding cue, and secondly the adoption of herbivory or omnivory by an adult anuran.

The existence of the ability to detect odours in adult anurans has been demonstrated for different species by different workers, (Martof, 1962; Shinn and Dole, 1978; Shinn and Dole, 1979), and the use of odours in prey selection and the feeding response has also been demonstrated (Shinn and Dole, 1978; Shinn and Dole, 1979). Feeding on non-moving prey has also been

documented (Ingle, 1971; Freed, 1988) although in Freed (1988) it is not clear whether the frog had previously perceived the prey's movement and then subsequently consumed a stationary food item. Similarly Poulson and Hutchison (1987) mention feeding Xenopus on "frog brittle". The consumption of carrion and saw-mince observed in captive *C. fistulans* demonstrate that it does not invariably use prey movement as the feeding cue. Fungi in particular do possess distinctive odours and small mammal mycophagists probably locate fungi by odour (Fogel and Trappe, 1978). Therefore it seems likely that *C. fistulans* is using odour as the feeding cue.

It is well known that anuran larvae consume plants, carrion, etc., however the consumption of non-animal food by adult anurans has only rarely been reported (Winston, 1955; Tyler, 1958; Alexander, 1964; Zug, Lindgren, and Pippet, 1975; Simon, 1983; da Silva, de Brittopereira, and Caramaschi, 1989). The evolution of herbivory in an adult anuran should not be surprising as it simply represents a shift in one character from one stage in the life cycle to another. Ruibal and Thomas (1988) report such a shift, describing how larval *Lepidobatrachus laevis* are carnivorous, possessing a gut which has a gross morphology resembling the adult gut. Therefore both morphologically and behaviourally these tadpoles resemble adults in some aspects of their feeding. *C. fistulans* adults may be evolving in the opposite direction towards herbivory, although there was no gross morphological evidence to support this. Indeed until the diet of other microhylids has been investigated comparison of gut morphology between species would be inconclusive. Alexander (1964) notes that *Bufo marinus* ate both cooked and raw vegetables and canned dog foods. He also refers to other reports of *Bufo* eating vegetable matter. Simon (1983) noted that brooding male *Cophixalus parkeri* (Microhylidae) had significantly more vegetable matter (mainly moss) in the

Record number	1	2	3	4	5	6	7	8	9	10
Date	12/12/85	16/01/86	23/01/86	29/01/86	05/06/86	29/07/86	08/08/86	18/06/87	24/06/87	29/03/88
Snout to vent length	?	?	35mm	16mm	29mm	24mm	?	29mm	22mm	29mm
Calling Yes/No	Yes	Note 1	Yes	No	Yes	No	No	No	No	Note 2
Stomach Full-Note 3	Full	Full	Full	Full	Full	Full	Full	Full	Half	Full
Stomach contents										
Arthropods										
Ants	1		1	2			5	1	21	3
Beetles				2			1			
Wasps									1	
Unidentified Insects	Parts	1 or 2		Parts		6	2		Parts	Parts
Unidentified Other		3						1		
Snails		1								
Nematodes		Several			2					
Plants										
Fungi (Agaricales)		2 or 3	3 or 4		Much					1 or 2
Other		Some		Little		Much				
Stones/Soil	Some	Some	Little				Little	Some	Some	
Mucous	Much							Much		
Unidentified							2	Much	Some	Some

TABLE 1. *Copiula fistulans* — stomach contents

NOTES

1. Found on surface, probably disturbed by writer.
2. Gravid Female.
3. Stomach full is a subjective judgement.

stomach than non-brooding frogs. He refrained from drawing any conclusions from this observation in the absence of further behavioural and physiological studies. *Hyla truncata*, a neotropical treefrog, has been reported to eat fruits, (da Silva, de Brittopereira and Caramaschi, 1989) and their observations parallel these in many ways (the frogs had to be killed soon after capture to halt digestion, some specimens had only eaten fruits, others only arthropods).

The consumption of fungi by anurans has not to the writer's knowledge been reported previously. A large volume of literature exists on mycophagy, summarised by Fogel and Trappe (1978) and more recently by Bennet and Baxter (personal communication). Insect mycophagy was discussed by Martin (1979), who also summarised the nutritive characteristics of fungal tissue. In terms of energy content fungal tissue compares favourably with many fruits and vegetables, but contains less energy than seeds, nuts or animal tissue. It also possesses some problems of digestibility due to the fungal wall polysaccharides, mainly chitin (Martin,

1979). Arthropod exoskeletons also include chitin, but these are not normally broken down by vertebrate digestive systems. Judging from the formless stomach contents observed in *C. fistulans* when digestion has proceeded somewhat the fungal cell walls do not present a serious obstacle. Fogel and Trappe (1978) note that fungal cell cytoplasm is readily digested by small mammals, while cell walls are sometimes digested. Fungal tissue is a good source of protein, choline, the B-vitamins, contains many enzymes and provides an ample supply of water (review in Martin 1979). Therefore it is generally agreed that fungi form a readily available and nutritious food. The high water content of fungi may be especially important to *C. fistulans* which is a terrestrial microhylid (Menzies and Tyler 1977) normally found in well drained localities where free water may be scarce (personal observation). It has been postulated that the absence of free water has contributed to the evolution of terrestrial eggs (Goin and Goin 1962) and it may well also be a factor in the evolution of mycophagy in this terrestrial microhylid.

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BOOK REVIEWS:

Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Albert Schwartz and Robert W. Henderson. (1991). 720 pp. University of Florida Press, Gainesville. £66.95, cloth.

If you are interested in herps (you clearly are!), have visions of West Indian islands (rum, sandy beaches, coconut palms, iguanas) and appreciate a fine painting as a dust jacket (the beautiful orange and green anole *Anolis mamoratus* from Guadeloupe) you will probably pick this book up. It is heavy, and a glance at the price sends a tingle down your spine — £66.95! Can you even afford to look at it?!

Arnold Schwartz and Robert Henderson, pioneers and veterans simultaneously, of West Indian herpetology have produced a third synthesis. The first, Schwartz and Henderson 1985 is an identification guide; the second (1988) is a check-list and as such a revision of Schwartz and Thomas (1975). The latter, curiously, is omitted from references in the present volume. Anyone studying West Indian amphibian and reptiles must encounter at least one of these authors' joint publications. The justification for the content of the present book are summarised best by the authors themselves: "The work stems from our conviction that as much information as possible concerning West Indian amphibian and reptiles should be brought between two covers. Our concerns have been two-fold, systematic and ecological but we have gone beyond systematics and ecology in this work to deal with whatever information we have been able to derive from the published literature and our respective researches and field data."

The book is arranged systematically. Information on each species is provided under the following headings: Type-locality, Holotype, Description, Illustration (references to where these may be found), Distribution (global through to presence/absence on individual islands (including introductions) and altitudinal range — in imperial units!), subspecies and, finally, natural history. A map or maps show the distribution of species in the region or, if appropriate, the location of records on individual islands. The information so presented is succinct, accurate and reasonably up-to-date. References (of which there are 41 pages) are mostly pre 1990 and must represent the most complete list available for West Indian herpetology. There are, however, some gaps. For example, Williams's (1983) review of speciation in West Indian *Anolis* is not mentioned, Bennett and Gormans' (1979) paper on *Anolis bonairensis* and other species is relevant if slightly outside the region, and Schoener's (1967) seminal paper on *A. conspersus* from the Cayman Islands should have been included. A proper index would have been most useful but is curiously absent.

That this book is the single most useful source of information on West Indian terrestrial and freshwater amphibians and reptiles is beyond doubt. However, I wish that *more* had been included. Inclusion of sea turtles would have made the book truly comprehensive. My main concern, however, is that there is an almost complete lack of information on conservation biology. Even if there *is* no information, we need to know. A

section dealing with the presence or absence of "official" protection and exploitation of amphibian and reptiles in each country would have been useful, as would the designation of species (where appropriate) with respect to Red Data Book and CITES categories. In addition I feel it should have been possible to have presented information on current status. For example, the authors record that the skink *Mabouya mabouya* is native on Dominica where it is widespread (Bullock and Evans, 1990) and on St Lucia where, however, it is rare or extinct (Corke, 1987). It might be argued that accurate information on the conservation and status of West Indian herptiles is too fragmentary as to warrant inclusion in a book of this kind. However, *there are* relevant publications. For example, Corke's (1987) analysis of the conservation status of the reptiles of Maria Islands off St Lucia, Johnson's (1988) compilation of conservation profiles of selected Caribbean islands and, most recently, Sajdak and Henderson's (1991) article on the decline of Lesser Antillean racer snakes (*Alsophis*) are all relevant.

There is little more to add; I have found this book to be enormously useful. It is an essential reference work for anyone working on West Indian amphibians and reptiles and is likely to remain so for a long time.

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THE HERPETOLOGICAL JOURNAL

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   > Dunson, W.A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83-101. Botelho, S.Y., Brooks, F.P. & Shelley, W.B. (eds). Philadelphia: University of Pennsylvania Press.
   > Dunson, W.A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American Journal of Physiology* **216**, 995-1002.

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